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# Age Differences in Foraging Patterns and Spatial Associations of the White-Faced Capuchin Monkey (*Cebus capucinus*) in Costa Rica.

by

Katherine Claire MacKinnon ©

A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for
the degree of Master of Arts

Department of Anthropology

Edmonton, Alberta

Fall, 1995

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled AGE DIFFERENCES IN FORAGING PATTERNS AND SPATIAL ASSOCIATIONS OF THE WHITE FACED CAPUCHIN MONKEY, *CEBUS CAPUCINUS*, IN COSTA RICA submitted by KATHERINE CLAIRE MACKINNON in partial fulfillment of the requirements for the degree of MASTER OF ARTS.

Linda Marie Fedigan
Linda Marie Fedigan

Owen Beattie

Jan O. Murie

Date August 29, 1995

# DEDICATION

This thesis is dedicated
to my parents,
for their unwavering
support and love.

# ABSTRACT

Age differences in foraging behavior and spatial association patterns are examined in white-faced capuchin monkeys (*Cebus capucinus*) at Santa Rosa National Park, Cost Rica. Foraging behaviors are examined from an ontogenetic perspective, and differential habitat exploitation is examined at four stages of development: independent infant, small juvenile, large juvenile, and adult. Approximately 337 hours of frequency data were collected in the form of ten-minute instantaneous focal samples on two study groups. Foraging behaviors are divided into four categories: feeding behaviors, food types eaten, substrates acted upon, and locations used in the canopy. C. *capucinus* individuals living in the same social group exhibit great variation across age classes in activity profiles. Developmental factors appear to explain the original predictions outlined for age class differences in foraging behavior.

Spatial association patterns were also examined in the form of nearest neighbor proximity scans. There is a pattern of development in terms of spatial association preferences. Particularly, small juveniles and adults prefer to associate with members of their own age classes for a greater percentage of proximity scans than the other age classes. These strong preferences, particularly with small juveniles forming peer groups, seem to be socially motivated.

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# TABLE OF CONTENTS

# LIST OF TABLES

# LIST OF FIGURES

# CHAPTER 1

## Introduction

The present study is an examination of age class differences in foraging behavior and spatial association patterns of white-faced capuchin monkeys (*Cebus capucinus*) at Santa Rosa National Park, Costa Rica. The study was conducted during the wet season months between April and September, 1992, and during the dry season months between January and April, 1993. The general focus of this study is the feeding patterns and behaviors present in two social groups of *Cebus* monkeys. Specifically, the age class differences in foraging behavior are examined from an ontogenetic perspective, and differential habitat exploitation is examined at four stages of development: independent infant, small juvenile, large juvenile, and adult. These four age classes are considered distinct, not only because of chronological differences, but also because of various characteristics that place one apart from the other (i.e. body size and weight, social interactions, etc., Appendix 7).

In chapter two, age class differences in foraging behavior are presented, through an examination of feeding behaviors, food items eaten, substrates acted upon and locations utilized in the habitat. Chapter three presents the spatial association patterns in the study groups, and discussion of the development of these affiliative states across the age classes. To conclude, chapter four summarizes the main findings contained in chapters two and three, and the overall conclusions of the present study.

## The Study Site

Santa Rosa National Park is located in the Guanacaste province of Northwestern Costa Rica, about 35 km northwest of Liberia, adjacent to the PanAmerican Highway. It is 10,800 ha in size and most of the park is at an elevation of 280 m above sea level. As a result of the natural topography and past land-use practices, the vegetation is a mixture of grassland (*Hyparrhenia rufa*), dry deciduous forest (including: *Spondias mombin, Luehea candida, L. speciosa, Bursera simaruba*, etc.), and semi-evergreen forest (including: *Hymenaea courbaril, Mastichodendron capiri, Manilkara chicle*, etc.) (Chapman, 1987).

This Pacific coastal zone region is described as a tropical dry forest (Freese, 1977) and has two distinct seasons. The dry season is characterized by virtually no rainfall from mid-December to mid-May. During this time, the many deciduous plant species in this area lose all of their leaves and the land is parched and dry. A few non-deciduous species such as *Manilkara chicle, Hymenaea courbaril*, and *Ficus* spp. keep their leaves throughout the dry season or drop them for a very short period of time (i.e. *H. courbaril* for 1-2 weeks, Janzen, 1983; Chapman & Fedigan, 1990). Rainfall ranges between 900 and 2400 mm annually (Chapman, 1987), with an average of 1500 to 2000 mm (Janzen, 1983). Almost all of this rain falls between the months of May and December.

In addition to a vast representation of flora, Santa Rosa supports a substantial diversity of fauna: 115 species of mammals, 253 species of birds, 100 species of reptiles and amphibians, and over 10,000 species of insects (Boza, 1988). The potential predators of *C. capucinus* at Santa Rosa National Park are five species of cats: puma (*Felis concolor*), jaguar (*F. onca*), ocelot (*F. pardalis*), margay (*F. wiedi*), and jaguaroundi (*F. yaguaroundi*), boa constrictors (*Boa constrictor*), and several raptors.

In a recent census (1983-84) 28 *C. capucinus* groups were counted in Santa Rosa, with an average group size of 14 animals (Fedigan, 1986). Most of the capuchin ranges overlap with the ranges of the other two nonhuman primate species, howler monkeys (*Alouatta palliata*) and spider monkeys (*Ateles geoffroyi*).

## The Study Species

The genus *Cebus* consists of four species: *C. apella, C. albifrons, C. olivaceus* (formerly *C. nigrivittatus*), and *C. capucinus*. These monkeys are arboreal, diurnal, medium-sized primates with robust bodies and semi-prehensile tails. The species are commonly divided into two morphological groups, "tufted" (*C. apella*) and "non-tufted" (*C. albifrons, C. olivaceus* and *C. capucinus*), based on the amount of erect hairs on either side of the crown (Napier & Napier, 1985). The primary differences between the four species, though, are coat color, coat pattern and geographical range (Freese & Oppenheimer, 1981). They are all somewhat similar in diet and behavior.

*Cebus capucinus*, the subject of this study, ranges from Belize to northern Colombia and is the only *Cebus* species that occurs in Central America (Fleagle, 1988). The other three species are sympatric to some degree, and are found primarily in the Orinoco and Amazon River basins of South America. *C. apella* has the most extensive range of any New World monkey and occurs throughout most of Amazonia, the Brazilian coastal forests, and northern Argentina.

All four species are moderately sexually dimorphic and live in large multi-male, multi-female social groups of 4 to 30 individuals (Freese & Oppenheimer, 1981), with *C. capucinus* having an average group size of 15 animals (Fragaszy, *et al.*, 1990). There is usually an alpha male in the group, although *C. capucinus* display lower rates of intra-group agonism than the other *Cebus* species (Freese, 1978; Janson, 1986).

Like all capuchins, *C. capucinus* are omnivorous feeders. They specialize on fruit and insects, but their diet also consists of a wide variety of food sources (see Appendices 5-6 for food items recorded during this study). In addition to leaves, shoots, buds, flowers, petioles, seeds and nuts, they also eat vertebrate food items such as birds, eggs, bats, squirrels, lizards, frogs, coati pups, and other small mammals (Newcomer & De Farcy, 1985; Fedigan, 1990; Galetti, 1990 pers. obs.). They are extremely active animals and spend most of their day feeding, foraging and traveling.

Why are capuchins effective foragers? Capuchins are considered to be highly intelligent, primarily because of dexterous manipulative abilities. This manipulative ability is apparent in their foraging behavior: they break open small and large branches, unroll palm fronds and other leaves for hidden insects, and reach into the holes and crevices of virtually any substrate (Gibson, 1986). Primate extractive foragers derive their skills from two aspects of neocortical structure. First, the sensory and motor cortices that control the hand are particularly enlarged, as is the visual cortex (Clark, 1960).

Second, large-brained primates such as *Cebus* show differential enlargement of the neocortical association areas (Passingham, 1973). It is thought that the differential enlargement of neocortical association areas provides the skills needed for constructing complex object relationships and complex manipulative abilities (Gibson, 1990). The documented studies of tool use in *Cebus* describe how palm nuts are repeatedly pounded against another surface until opened (Izawa & Mizuno, 1977; Struhsaker & Leland, 1977; Anderson, 1990), how marine oysters are opened by the use of stones and other oysters (Parker & Gibson, 1977; Fernandez, 1991), and how sticks are used to groom wounds or to contact a potentially dangerous object (Cooper & Harlow, 1961; Westergaard & Fragaszy, 1987; Boinski, 1988; Richie & Fragaszy, 1989; Visalberghi, 1990). The combination of manipulative skills and an opportunistic feeding strategy allow the highly adaptive *Cebus* species to exploit different dietary habitats. Age class differences might reflect the acquisition of skills needed for constructing complex object relationships and complex manipulative abilities. The work represented in this thesis is a small part of Dr. Linda M. Fedigan's larger, long-term study of *Cebus capucinus* in Santa Rosa National Park, Costa Rica.

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# CHAPTER 2

## Age Differences In Foraging Behavior of *Cebus capucinus* at Santa Rosa National Park, Costa Rica

### INTRODUCTION

Age and sex differences in behavior have been observed in many primate species (e.g. Pereira, 1988; Boinski & Fragaszy, 1989; McGuire *et al.*, 1994; Byrne & Suomi, 1995); in particular, age and sex differences for the genus *Cebus* have been examined by Fragaszy (1990), Fragaszy & Visalberghi (1990), Fedigan (1993), Rose (1994a,1994b), and Fragaszy & Boinski (in press). The present study examines the ontogeny of foraging behavior in *Cebus capucinus*. Although a number of factors influence and constrain the development and expression of foraging skills, proposed explanations for age differences in foraging skills generally fall into three theoretical categories: developmental, social and ecological (Boinski & Fragaszy, 1989; Fairbanks & Pereira, 1993; Janson & van Schaik, 1993; Byrne & Suomi, 1995). By no means should these three be seen as mutually exclusive, especially in a primate genus such as *Cebus*, which displays a remarkably complex behavioral repertoire. For the purposes of the present study, however, age differences in foraging behavior will be examined solely from an ontogenetic, or developmental, perspective.

Capuchins are extremely active and inquisitive foragers, displaying highly-developed manipulative skills that enable them to exploit a wide variety of substrates and food types (Freese & Oppenheimer, 1981; Gibson, 1986; Visalberghi & Antinucci, 1986;

Brown & Zunino, 1990; Chapman & Fedigan, 1990; Fedigan, 1990; Fragaszy & Boinski, in press; pers. obs.). Developmental changes in foraging behavior are extensive in *Cebus* but have received little detailed study except in laboratory settings (e.g. Mathieu *et al.*, 1976; Parker & Gibson, 1977; Chevalier-Skolnikoff, 1989 & 1990; Fragaszy, 1990; Visalberghi, 1990). To understand the ontogeny of foraging behavior, it is helpful to document the increasing foraging skills exhibited by the members of the various age classes. For example, only when an individual has acquired the necessary motor and cognitive skills to exploit previously inaccessible food types, can it successfully make the transition from one dietary pattern to another. Generally, the influence of cognitive development on the successful exploitation of certain food types, has been examined only by psychologists in controlled laboratory studies (e.g. Visalberghi & Fragaszy, 1995).

Previous studies of age differences for the genus *Cebus* have focused on the wedge-capped capuchin (*C. olivaceus*) in Venezuela (e.g. Fragaszy, 1986 & 1990; Fragaszy & Boinski, in press) and on *C. apella* in captivity (e.g. Fragaszy, 1990; Byrne & Suomi, 1995). Overall, dietary profiles (which may reflect foraging skills) of immature males and females are quite similar (Fragaszy, 1986), suggesting that sex differences may not become significant until later subadult/adult stages. Given this, one might assume that immature animals develop foraging behaviors slowly. This gradual assumption of foraging skills by immatures may permit the development of specializations that reflect individual learning.

The objective of my study was to document foraging behavior differences across age classes in *C. capucinus*, to relate differences to developmental explanations, and to compare these findings with those of past *Cebus* studies. Many factors no doubt influence the development and expression of foraging skills (e.g. cognitive abilities, manipulative skills, different dietary profiles, etc.). For the purposes of the present study, however, data taken on four categories of foraging patterns are examined: feeding behavior, food type, substrates used, and location in canopy. Data were taken on these four categories to determine if there were any age class differences in overall foraging behavior in the *C. capucinus* study groups. Do independent infants and juveniles have different patterns of feeding behavior than their adult counterparts? Do they eat different food items? Do they utilize different substrates while foraging? And do they occupy different areas of the canopy?

The highly dexterous and manipulative abilities that characterize *C. capucinus* have only been systematically examined in controlled laboratory settings (Parker & Gibson, 1977; Visalberghi & Antinucci, 1986; Visalberghi, 1990; Adams-Curtis, 1990). By observing age-related differences in foraging behavior in wild *C. capucinus* groups, specifically, how it develops in the context of a tightly structured and complex social system, an increased understanding of development of foraging skills can be attained. As my study was conducted during both wet and dry seasons, and the habitat varies greatly between these seasons, comparisons are made between the two time periods.

## Foraging Behavior Hypothesis and Predictions:

The central hypothesis of this study is that individuals in different stages of development will behave differently while foraging. Specifically, individuals of different age classes will have different rates for specific types of feeding behaviors, food items eaten, substrates used, and locations in the canopy. Several predictions were made about age class differences in these four components of foraging behavior, based on obvious constraints of body size and development, and on previous findings about the ontogeny of skills in infant and juvenile capuchins.

### Feeding behaviors

1) Adults will exhibit a greater variety of "complex" feeding behaviors than independent infants and small juveniles. Behaviors defined as "complex" involve more than one step or action, and thus may require the acquisition of motor and/or cognitive skills. Three of the 13 behaviors (BREAK OPEN WITH HANDS AND/OR MOUTH, CARRY IN HANDS AND/OR MOUTH, and PROBE Appendix 1) analyzed were considered to be complex; that is, involving a series of steps or actions and often requiring a greater time investment by the foraging individual. 2) Independent infants will exhibit less efficient feeding. They will make "mistakes" more often (i.e. at a greater frequency rate), where the behavior GRAB AND MISS is defined as a "mistake" (Appendix 1). Also, a lower rate of eating for time observed is predicted to result, at least in part, from the less efficient and immature foraging techniques of independent infants. 3) Small juveniles will display higher rates of more "inquisitive"

behaviors than independent infants, since the latter are somewhat restricted in their movements. 4) Small and large juveniles will have higher rates of VISUAL FORAGE than adults. They are less familiar with the food items in the habitat, and therefore need to invest more time in VISUAL FORAGE behavior than the older and more experienced age classes.

### Foods Eaten

Overall, food size will correspond to age class. 1) Smaller animals (i.e. independent infants and small juveniles) will have higher rates of eating SMALL FRUIT than larger animals (i.e. large juveniles and adults). 2) Larger animals will have higher rates of eating LARGE FRUIT than smaller animals. 3) Larger animals will have higher rates of eating MEDIUM INSECT and LARGE INSECT than smaller animals.

### Substrate Use

1) Larger animals will use more difficult substrates when looking for food items than smaller animals. "More difficult" substrates are those that require a lot of handling and processing (e.g. LARGE BRANCH and WASP NEST). 2) Independent infants will have higher rates of use of smaller substrate items than juveniles and adults. 3) Older individuals will explore substrates that include possible hidden food items at a greater frequency than younger animals. 4) Older individuals will have higher rates of using acacia substrates (thorns and branches) while foraging for acacia ant larvae than younger individuals, due to a greater efficiency in cracking

open the ACACIA THORNS, as well as knowing how to avoid effectively stings and bites from the ants.

### Location in Canopy

1) Smaller juveniles will use terminal branches more than larger animals. 2) Independent infants will be in "safer" areas at a higher frequency rate than other areas. "Safer" areas are defined here as those areas which afford more protection and cover in the form of natural structures from predator detection. Examples of these safer areas are: TREE CROTCH, INNER BRANCH, and VINES at all levels of the canopy (i.e. lower, middle, and higher). 3) Small juveniles will use a greater variety of locations than the other age classes, due to an excelerated exploration of the surrounding habitat. 4) Adults will have higher rates of utilizing the high location areas of the canopy, as well as the GROUND location, due to vigilance behavior. 5) Independent infants and small juveniles will occupy the lower and middle canopy locations at a higher rate than either the upper canopy or the GROUND.

## METHODS

### The Study Site:

Santa Rosa National Park is located in the Guanacaste province of Northwestern Costa Rica, adjacent to the PanAmerican Highway. It is 10,800 ha in size and most of the park is at an elevation of 280 m above sea level. As a result of the natural topography and past land-use practices, the vegetation is a mixture of grassland, dry deciduous forest, and semi-evergreen forest (Chapman, 1987).

There are two distinct seasons. The dry season is characterized by virtually no rainfall from mid-December to mid-May, and the wet season, from May until December, averages between 900 mm and 2400 mm of rain annually.

## The Study Subjects:

Data were taken on two social groups of capuchins: the Los Valles group (LV) and the Cerco de Piedra group (CP). In the wet season of 1992 group LV consisted of: 3 adult and subadult males, 5 adult females, 3 large juveniles, 5 small juveniles and 3 independent infants. In the dry season of 1993 group LV consisted of: 4-6 adult and subadult males, 5 adult females, 2 large juveniles, 8 small juveniles, and 2 independent infants. In the wet season of 1992 group CP consisted of: 2 adult and subadult males, 4 adult females, 3 large juveniles, 3 small juveniles and 1 independent infant. In the dry season of 1993 group CP consisted of: 4-6 adult and subadult males, 4-5 adult females, 2 large juveniles, 4 small juveniles, and 1-2 independent infants.

## Data Collection and Analysis:

Both social groups were habituated to human observers; observation distances of five to ten meters were common, with distances sometimes as close as 2-3 meters. Individuals were identified by size, characteristics of fur markings, brow hair length, and facial markings.

The fieldwork for this study was conducted during the rainy season months between April and September, 1992 and during the dry season months between January and April, 1993. Approximately 337 hours of frequency data were collected, using ten-minute instantaneous focal samples (Altmann, 1974; Fragaszy *et al.*, 1992). Behavior of the focal animal was noted every 60 seconds. Data were taken according to an ethogram modified for this study (see Appendix 1. Note: only foraging behaviors that are discussed here are listed). Although it was difficult on certain days to collect data on every individual in the group that was being followed (individuals not seen, individuals on periphery of group, etc.), a continuous record of the number of samples for each age class was kept to ensure that sampling between the age classes and individuals was evenly distributed.

Data were taken on recognized individuals categorized into five age classes: adult, large juvenile, small juvenile, independent infant, and dependent infant. However, only four age classes are analyzed here: adult, large juvenile, small juvenile, and independent infant. Dependent infants, aged 0-6 months, are not included in analyses because they spent most of their time on or near their mother. Independent infants are aged 6 months to 1 year, small juveniles are approximately 1-3 years old, large juveniles are approximately 3-4 years old for females, 3-5 years old for males (see Appendix 7).

Analyses were performed on the rates (frequencies per hour) of foraging on 13 feeding behaviors (Tables 2.1-2.2 and Appendix 1), 7-9 food types (Tables 2.3-2.4 and Appendix 2), using 19 substrate categories (a substrate is anything acted upon by an animal in seeking a food item) (Tables 2.5-2.6 and Appendix 3), in 13 location categories (Tables 2.7-2.8 and Appendix 4). The variables chosen in these categories represent the most commonly used items in the habitat by the capuchins in this study (see Appendices for descriptive information).

The relationships between the four components of foraging patterns (feeding behavior, food type, substrate, location) and the four age classes (adult, large juvenile, small juvenile, independent infant) and the two sexes were analyzed by repeated measures of analysis of variance (ANOVAs) and multiple analysis of variance (MANOVAs), using the Statistical Package for the Social Sciences (SPSS version 4.0) (Nie *et al.*, 1975). As the data were not normally distributed, proportional data were transformed using the arcsine method before analysis. Differences between the two study groups were not statistically significant at the $p < 0.05$ level. Therefore, individuals from both groups were lumped into their respective age-sex classes for the purposes of further statistical analyses. Although the focus of this study is on age differences, sex was included as a variable so that its contribution to variation in foraging patterns could be examined as well. The main effects and the main interactions were examined for significant differences at the $p < 0.05$ level by age, sex, and by age & sex (Table 2.9 & 2.10). MANOVA tests were run first and significant differences were noted at $p < .05$. ANOVA tests to look for the effects of age and then sex were then run on the individual categories (e.g., SMALL FRUIT, MEDIUM FRUIT, LARGE FRUIT) within each component of foraging patterns.

When examining differences in overall foraging patterns, the feeding behavior categories (Appendix 1) were found to be the most useful in determining age class differences, in that more interpretable trends were found between age class and behavior. Differences in food types eaten, substrates acted upon and location used in canopy are discussed as supplemental information to illuminate the differences and similarities between the age classes.

## RESULTS: FEEDING BEHAVIOR

Significant age effects on feeding behavior were found during the wet season (MANOVA WS Factor main effect: f = 5.11, df = 3, p <.01; main interaction: f = 4, df = 36, p <.01) (Table 2.9). Of 13 foraging behaviors analyzed, four behaviors were significantly different among age classes: EXPLORE, EAT, POKE and VISUAL FORAGE (Table 2.1). For example, there was a decrease in the frequency of EXPLORE and POKE as animals became older, but an increase in EAT and VISUAL FORAGE as animals matured. No significant sex effects on feeding behavior were found during the wet season.

Age significantly affected feeding behavior during the dry season (MANOVA WS Factor main effect: f = 4.56, df = 3, p <.05; main interaction: f = 2.83, df = 36, p <.01) (Table 2.10). Five individual feeding behavior categories, CARRY IN HANDS/MOUTH, PICK OUT WITH FINGERS/MOUTH, EAT, UNROLL and POKE, showed statistical significances in the analysis (Table 2.2). Only for UNROLL was there a clear trend with age, decreasing with increasing age. Overall, there were no significant sex effects on feeding behavior during the dry season; however, one individual feeding behavior, TAP, was found to be significant by sex, with females using the behavior with greater frequency than males.

## RESULTS: FOOD TYPE

Although overall, significant age effects on the category "food type" were found during the wet season, (MANOVA WS Factor main effect: f = 4.96, df = 3, p <.01) (Table 2.9), the individual food items within this category were not statistically significant according to tests (Table 2.3). No significant sex effects on food type were found during the wet season.

Overall, there were no significant age effects on food type during the dry season (MANOVA WS Factor main effect: f = .71, df = 3, p = .5; main interaction: f = 1.39, df = 18, p = .1). There were no significant sex effects on food type during the dry season (MANOVA WS Factor main effect: f = .88, df = 1, p = .4; main interaction: f = .5, df = 6, p = .8) (Table 2.10); however, two individual food type categories, MEDIUM INSECT and LARVAE, were found to be statistically significant.

## RESULTS: SUBSTRATE USE

Significant age effects on substrate use were found during the wet season (MANOVA WS Factor main effect: f = 10.49, df = 3, p <.01; main interaction: f = 3.47, df = 63, p <.01) (Table 2.9). Specifically, of 19 substrate categories analyzed, the following seven substrates were found to be significant by age (Table 2.5): SMALL DEAD BRANCH, MEDIUM DEAD BRANCH, BARK-SURFACE, SMALL LIVE BRANCH, GREEN LEAF, INNER BRANCH and TERMINAL BRANCH. The last five showed a decreasing trend with age, while the first two showed no consistent trend with age. Although the main effect of sex on substrate use during the wet season was not significant (p =

.3), the main interaction of sex by substrate was (p <.01) (Table 2.9). Specifically, two individual substrate categories, SMALL DEAD BRANCH and MEDIUM DEAD BRANCH, were found to be statistically significant.

Overall, there were significant age effects on substrates used during the dry season (MANOVA WS Factor main effect: f = 4.04, df = 3, p <.01; main interaction: f = 1.79, df = 54, p <.01) (Table 2.10), and five individual substrate categories were statistically significant: SMALL DEAD BRANCH, MEDIUM DEAD BRANCH, DEAD LEAF, TERMINAL BRANCH and INNER BRANCH. The first two shower higher rates in younger animals, the next two show a general decrease with age, while the last category shows a higher rate in independent infants. All categories tended to have a greater rate of use by younger age classes. There were no significant sex effects on substrates used during the dry season.

## RESULTS: LOCATION IN CANOPY

During the wet season, there were no significant age effects on location in canopy (MANOVA WS Factor main effect: f = 1.09, df = 3, p = .4; main interaction: f = .78, df = 36, p = .8) (Table 2.9); however, one individual location category, LOWER CANOPY TREE TRUNK, was found to have a significant age effect, with increased age. There were significant sex effects on location in canopy during the wet season (Table 2.9) for the categories of LOWER CANOPY TREE TRUNK and MIDDLE CANOPY VINES.

Overall, there were no significant age effects on location in canopy during the dry season. However, of the thirteen individual location categories that were analyzed, two had significant age effects during the dry season: LOWER CANOPY INNER BRANCH, which had lowest use by adults, and LOWER CANOPY TERMINAL BRANCH, for which use decreased with age. There were no significant sex effects on location during the dry season (MANOVA WS Factor main effect: f = 0.01, df = 1, p = .9; main interaction: f = 2.05, df = 12, p <.05) (Table 2.10).

## DISCUSSION

The results provide some support for the general hypothesis that individuals in different stages of development forage in different manners. The four age classes in the two capuchin study groups showed different rates of feeding behaviors, foods eaten, substrates used while foraging, and location in the canopy. These differences are interpreted below in light of developmental factors.

### Feeding Behavior

Capuchins are extremely active and inquisitive foragers, spending between fifty and eighty percent of their daily activity budget searching for food (Freese, 1983; Fedigan, 1993; Fedigan, pers. comm.). As their diet is omnivorous in character, they employ an opportunistic foraging strategy that enables them to maximize nutrient intake from a wide variety of food items. They are considered to be highly intelligent, primarily because of their dexterous manipulative abilities. This manipulative ability is apparent in their foraging behavior: they break open small and large branches, unroll palm fronds and other leaves for hidden insects and larvae, and reach into the holes and crevices of virtually any substrate (Gibson, 1986).

When an infant is independent, it is able to "try out" some of the activities first observed while on its mother. In addition to such observational learning, an individual may also employ a trial-and-error strategy when exploring its natural environment. Hence, individuals in different stages of development are expected to have different rates for different types of feeding behaviors. Adults, for example, should exhibit more "complex" feeding behaviors than either small juveniles or independent infants. Three of the 13 behaviors analyzed were considered to be complex (BREAK OPEN WITH HANDS AND/OR MOUTH, CARRY IN HANDS AND/OR MOUTH, and PROBE), that is, involving a series of steps or actions and often requiring a greater time investment by the foraging individual.

During the wet season, both small and large juveniles had the highest rate of BREAK OPEN WITH HANDS AND/OR MOUTH, and adults had the *lowest* rate. Interestingly, small juveniles and independent infants had the highest rates of CARRY IN HANDS AND/OR MOUTH. Neither BREAK OPEN WITH HANDS AND/OR MOUTH nor CARRY IN HANDS AND/OR MOUTH were significantly different by age during the wet season, but the behavior POKE was. However, it was the independent infants that displayed the greatest frequency of POKE. Again, this result is most likely due to the inquisitive nature of this age class, when, during this post-weaning developmental stage, the capuchins must acquire a vast amount of information about the food sources in their surrounding environment. Unexpectedly, during the dry season small juveniles had the *highest* rate of BREAK OPEN WITH HANDS AND/OR MOUTH; the other three age classes displayed lower, and quite similar, frequency rates. Small juveniles are extremely active members of the social groups and are constantly experimenting with objects in the surrounding environment. They may also have to spend more time working on substrates to extract the food items hidden within, thus increasing the frequency rates of this particular behavior. Large juveniles had the highest rate of CARRY IN HANDS AND/OR MOUTH, which was statistically significant for age. Adults were expected to have the highest rate of PROBE, as this behavior requires a concentrated effort to retrieve an embedded food item which is often hidden from view. However, small juveniles had the highest rate of PROBE, while independent infants had the lowest rate of this behavior.

By the time an infant is classified as "independent", it is no longer extensively carried by its mother. An independent infant still nurses, but most of its time is spent actively exploring the surrounding habitat and interacting with other group members. During this important period of development an individual must learn many factors crucial to its survival. Infants were expected to make more mistakes while foraging. That is, it was predicted that they would have higher rates of the behavior GRAB AND MISS, as well as lower rates of EAT than the other age classes. Indeed, during both seasons, independent infants had the highest rates of GRAB AND MISS, as well as the lowest rates of EAT, though only EAT in the wet season was significant. As independent infants still go back to nurse, they require fewer nutrients from the surrounding habitat.

During the developmental stage of small juvenile, an animal is no longer nursing from its mother and is actively exploring all the facets of the surrounding habitat. It was predicted, therefore, that small juveniles would have higher rates of "inquisitive" behaviors (here defined as EXPLORE, UNROLL, and VISUAL FORAGE) than independent infants, the latter being more restricted in their range of exploration. During the wet season, independent infants had an extremely high rate of EXPLORE, and in both seasons this behavior had a tendency to decrease ontogenetically. This may be a reflection of inefficiency in obtaining food items by younger animals. While an animal is exploring the substrates in its surroundings, it often comes into contact with different members of the social group. Independent infants and small juveniles must decode the intricacies of the social relationships which constitute the group in which it lives. Not only is this necessary for their survival, but it is also important for developing long-term relationships with individuals in the group. In addition, these individuals are now free to move among the other young animals in the social group who may be at or near the same stage of development (see following chapter). As Mitra *et al.* (1994) noted, young capuchins forage in a supportive social context, meaning that cohorts and known individuals in the group are always close by. Perhaps within this context, young capuchins are able to exploit a wide variety of materials during a developmental period of great foraging skill acquisition. During the dry season, independent infants had the highest rates of EXPLORE and UNROLL, while small juveniles had the highest rate of VISUAL FORAGE. Interestingly, independent infants had the lowest rate of

VISUAL FORAGE. Of these three behaviors, UNROLL and VISUAL FORAGE showed statistically significant age effects.

Predictably, adults had the lowest rate of EXPLORE. By the time an individual is an adult, its familiarity with the surrounding environment, particularly with different types of substrates, is at its highest level; the need to explore novel substrates and food items actively is markedly reduced. As predicted, small and large juveniles had higher rates of VISUAL FORAGE during the wet season, than adults. VISUAL FORAGE differs from EXPLORE, in that it is a *general* search for a food item where a specific substrate is not targeted for intensive searching (as for EXPLORE). It is likely that juveniles displayed higher rates of the former behavior due to less familiarity with food sources in the habitat (compared to adults). Independent infants had the lowest rate of VISUAL FORAGE. Although independent infants are off of their mothers by 6 months of age, they still go back to nurse and thus require less nutrients from the surrounding habitat. However, as noted earlier, they EXPLORE the surrounding environment to a greater degree than the other age classes. This is true for other *Cebus* species as well. As Fragaszy and Boinski note for *C. olivaceus* (in press), "Infants can be characterized as incidental foragers. Their foraging activity is exploratory in character, and except for fruit, results in negligible food intake." During the wet season, both EXPLORE and VISUAL FORAGE had statistically significant age effects.

Robinson (1981, 1984) defined differential niche exploitation within a group as a contributing factor to the overall group cohesiveness in the wedge-capped capuchin (*Cebus olivaceus*). He predicted that all age-sex classes would allocate more time to foraging when resources are scarce. As energy requirements scale approximately to body size, larger age-sex classes should consistently allocate more time to foraging. This was observed in both seasons of the present study, with small and large juveniles having higher frequency rates of VISUAL FORAGE than independent infants (Tables 2.1 and 2.2).

## Food

As capuchins are extremely active and inquisitive foragers, it is crucial that independent infants begin to learn which food types are accessible and most palatable. When an infant is still classified as "dependent", it seems very aware of what foods its mother is eating, often sniffing her mouth as she is ingesting food, or examining the food she carries in her hands. The infant is able to observe how she acquires different food types, how she processes these different food types, and which ones she prefers. Of course, while being carried on the mother's back, the dependent infant can observe other individuals in the social group doing these activities as well, especially those individuals in close proximity to its mother. By the time a young capuchin is foraging independently, it is familiar with many food types that can be eaten. A constraint, however, may be the size of the food item, as well as the degree of handling and processing that is required before eating. Thus, larger animals may be more adept and successful at handling larger food items.

Although the individual food categories were not statistically significant (Tables 2.3-2.4 and Appendix 2), there were some unexpected trends. During the wet season, independent infants ate no LARGE FRUIT during sampling time, but in the dry season, their rates of eating LARGE FRUIT were higher than that of the adults (independent infants = 5.85 times per hour, adults = 3.86 times per hour). This may reflect the fact that during the dry season there are more varieties of larger fruits (e.g. palm fruits, *Acrocomia vinifera*, are one of the large fruits available during the dry season but not in the wet season) and the rates for the independent infant, small juvenile, and large juvenile age classes are subsequently higher overall (Table 2.4). It seems more likely, though, that the individual's size or experience is not a factor when it comes to eating larger food items.

Similarly, I expected that independent infants and small juveniles would have higher rates of eating SMALL FRUIT than large juveniles and adults, based on the assumption that smaller fruits would be easier for smaller animals to handle. During the wet season small juveniles did have the highest rate (29.48 times per hour on average) of eating SMALL FRUIT, although it was similar to the rate for adults (27.55). However, during the dry season, there was no correlation between age class and SMALL FRUIT consumption. In fact, large juveniles had the highest rate of eating SMALL FRUIT (7.01 times per hour on average), and independent infants had the *lowest* rate (1.91 times per hour on average). Adults and small juveniles had similar rates (6.55 and 6.98, respectively).

Insects are an important part of capuchin diets (Freese, 1977; Freese and Oppenheimer, 1981; Freese, 1983; Robinson, 1984; Chapman, 1988). Medium and large insects, such as katydids, grasshoppers, tree cockroaches, walking sticks, etc., are desirable foods that are opportunistically caught, whenever possible. I predicted that larger animals would be able to catch these medium and large insects at a greater rate than smaller animals, due to quickness, larger body size and a greater dexterity in the capture of such prey. The wet season did show a trend: adults and large juveniles had higher rates of eating MEDIUM INSECT and LARGE INSECT than small juveniles and infants. Overall, there was a tendency for older animals to eat relatively more medium and large sized insects than small insects, except for adults during the wet season. During the dry season, however, there was no relationship between age class and the ingestion of medium sized insects (e.g. katydids); small juveniles, in fact, had the highest rate (8.25). Large juveniles did have the highest rate of eating LARGE INSECT (13.79), with adults (7.19), small juveniles (6.08), and infants (9.17) displaying frequency rates.

Insect larvae are an important source of protein for capuchins during the dry season in a highly seasonal habitat such as Santa Rosa (Freese, 1977; Chapman & Fedigan, 1990). In the long, rainless dry season, many tree species lose their leaves and do not fruit. During this period invertebrate and vertebrate prey become more important in the diet. Insect larvae, especially acacia ant larvae, is another vital part of the capuchin diet during this time (Freese, 1976). Although age class did not have a significant effect on the ingestion of LARVAE in either season, all age classes showed a dramatic increase in insect LARVAE ingestion during the dry season

(Table 2.4), with small and large juveniles having the highest rates (41.53 and 43.04, respectively), as they did during the wet season.

## Substrates Used

While foraging for food, capuchins utilize a great variety of substrates and almost every element of the environment is subject to an inquisitive poke, bite, or tearing apart . During the wet season, the rates of BARK-UNDER by small juveniles, large juveniles and adults were remarkable similar, and small juveniles had the *highest* rate of working on the substrate TREE HOLE. Small juveniles, large juveniles and adults all used WASP NEST as a substrate. The greater number of wasp nests during the wet season may be the reason that all age classes, except independent infants, used this substrate. As predicted, during the dry season larger animals used more "difficult" substrates than the smaller individuals in the social groups. Specifically, large juveniles had the highest rates of substrate category BARK-UNDER and TREE HOLE, although neither are significant. Adults were the only age class to use the substrate category WASP NEST.

As with food items, it was predicted that smaller animals, specifically independent infants, would use smaller substrates at a higher rate than the other age classes. During the wet season, both SMALL LIVE BRANCH and GREEN LEAF showed significant age effects, with independent infants having the highest rates. Independent infants also had high rates on SMALL DEAD BRANCH, but were second to large juveniles in terms of frequency rates. During the dry season, two small substrates, SMALL DEAD BRANCH and DEAD LEAF, supported this prediction and were statistically significant by age. Small juveniles had the highest rate of utilizing SMALL LIVE BRANCH (however, independent infants had the lowest rate and adults had the second highest rate), and independent infants and large juveniles had similar rates on GREEN LEAF. In some instances, then, body size was correlated with substrate size, while in other instances it was not as exclusive.

Interestingly, the 5 substrate categories that were statistically significant by age during the dry season, SMALL DEAD BRANCH, MEDIUM DEAD BRANCH, DEAD LEAF, INNER BRANCH and TERMINAL BRANCH, all had *independent infants* showing the highest rates (Table 2.6). Again, as with feeding behaviors, independent infants are learning what to utilize in the environment, and are exploring all of the different substrates they may come across, whether or not they hold any food items. A more experienced (and thus, older) individual, would probably bypass a LARGE LIVE BRANCH, for example, in order to concentrate on a more likely source of food.

Substrates that might contain hidden food items (e.g. BARK-UNDER) were predicted to be used at a greater rate by older, more experienced individuals. During the wet season, there appeared to be no relationship with these substrate categories and age class. (Table 2.5). However, during the dry season this was somewhat supported, with large juveniles having the highest rates in those substrate categories (although the age effects were not statistically significant).

A final prediction for substrate use considers the relationship between age class and acacia tree substrates; specifically, the thorns and branches that are broken open in the search for a favorite food item, acacia ant larvae. Acacia trees have low levels of secondary compounds for chemical defense against predators; instead, they are fiercely protected by the acacia ants which raise their larvae in the plant's thorns. As the capuchins feed on ant acacia larvae, speed and efficiency are required when breaking open the thorns (in order to minimize the effects of the biting and stinging ants). In the wet season, independent infants had the *highest* rate of using ACACIA THORNS, although, as discussed earlier, they also had the lowest rate of actually eating LARVAE of all kinds (including acacia ant larvae). Perhaps during this stage of development, independent infants are less successful foragers: they spend more time handling ACACIA THORNS, but have lower rates of actual larvae consumption. During the dry season, the time of greatest acacia ant larvae predation by the capuchins (Freese, 1976), there was no relationship between the use of acacia substrates and age class.

### Location

As capuchins forage they utilize many different areas of the canopy, from thin terminal branches to more sturdy tree trunks. In addition to varying types of canopy locations, the use of canopy height also varies: GROUND level, LOWER CANOPY (<3m), MIDDLE CANOPY (3-10m), and UPPER CANOPY (>10m).

I predicted that smaller juveniles would use terminal branches at a greater rate than larger animals, due to weight restrictions on larger animals. During the wet season, small juveniles used the LOWER CANOPY TERMINAL BRANCH location at the highest rate.

Independent infants used the LOWER CANOPY TERMINAL BRANCH location at the lowest rate, but used the MIDDLE CANOPY TERMINAL BRANCH location at the highest rate (Table 2.7). The UPPER CANOPY TERMINAL BRANCH location, however, was used by adults at a higher rate than the other age classes. This may be due to vigilance behavior on the part of the adults. As Rose and Fedigan (1995) found, adult males in particular direct their vigilance outwards and during this time may be peripheral to the social group. During the wet season, when visibility is reduced, these vigilant adults need to be up high and out on the terminal limbs in order to monitor what is going on outside of the social group. During the dry season, independent infants occupied the LOWER CANOPY TERMINAL BRANCH location at a statistically significant higher rate than the other age classes (Table 2.8), as predicted. Adults occupied both the MIDDLE CANOPY TERMINAL BRANCH and UPPER CANOPY TERMINAL BRANCH locations at the highest rates, although the small juvenile rate in the MIDDLE CANOPY TERMINAL BRANCH location was similar to that of the adults (36.08 and 38.14 times per hour on average, respectively).

I also predicted that independent infants would be found more often in "safer" areas, that is, areas in which there is more protection and cover in the form of natural structures from predator detection. Examples of "safer" areas are: TREE CROTCH, INNER BRANCH, and VINES (see Appendix 4 for definitions). During the wet season, independent infants were not found in these so-called "safer" areas at a greater rate than the other age classes. Surprisingly, infants had the highest frequency rate of being on the GROUND (13.03 times per hour), a location which most researchers agree is quite dangerous due to terrestrial predators (e.g. felids, canids, tayras, boas, etc.). During the wet season, independent infants, small juveniles, and large juveniles appear to spend more time playing on the ground, both in "rough and tumble", as well as "chase" play. This may be a factor in the higher rates of GROUND use by independent infants. Independent infants had low rates in TREE CROTCH locations and had the lowest rates in INNER BRANCH and vine locations (Table 2.7). During the dry season, independent infants did have the highest rates of occupying middle canopy inner branches, but they also had the low rates of occupying TREE CROTCH, VINE and other INNER BRANCH locations (Table 2.8).

It was predicted that small juveniles would utilize a greater variety of locations (i.e. have high frequency rates in many location categories) than the other age classes, due to curiosity, greater activity levels, and an accelerated learning period in regard to their environment. During the wet season, small juveniles did display the highest rates of occupying four locations: LOWER CANOPY TERMINAL BRANCH, lower canopy VINES, MIDDLE CANOPY TREE TRUNK, and UPPER CANOPY INNER BRANCH. Adults however, had the highest rates in five location categories: LOWER CANOPY INNER BRANCH, LOWER CANOPY TREE CROTCH, LOWER CANOPY TREE TRUNK, MIDDLE CANOPY TREE CROTCH and UPPER CANOPY TERMINAL BRANCH (Table 2.7). This finding suggests that although small juveniles may be more inquisitive than adult individuals (e.g. EXPLORE), adults appear to be in more places in the canopy more often. Small juveniles may not be making use of a greater variety of locations in the canopy. During the dry season, small juveniles had the highest rates in four locations: LOWER CANOPY INNER BRANCH, LOWER CANOPY TREE CROTCH, LOWER CANOPY TREE TRUNK and MIDDLE CANOPY TREE TRUNK. Large juveniles also had the highest rates in four location categories: GROUND, LOWER CANOPY VINES, MIDDLE CANOPY TREE CROTCH and MIDDLE CANOPY VINES. Compared to the wet season, then, small and large juveniles appear to utilize more levels of the canopy at a greater rate during the dry season.

I predicted that adults would have the highest rates of occupying the upper levels of the canopy (>10m), as well as the GROUND location, due to vigilance and surveillance activities. During the wet season, adults did display the highest rates of utilizing the UPPER CANOPY TERMINAL BRANCH location, but contrary to prediction, independent infants had the highest frequency rates of occupying the GROUND level of the forest. During the dry season, however, adults had the highest rates of using the UPPER CANOPY INNER BRANCH location, but not the UPPER CANOPY TERMINAL BRANCH location. This may be due to an increased visibility due to the deciduous trees losing their leaves: there is no need for an individual to go out onto the terminal branches for a good view. Large juveniles had the highest rate of occupying the GROUND, followed closely by independent infants (29.51 and 25.05 times per hour on average, respectively).

Finally, I predicted that independent infants and small juveniles would occupy the LOWER and MIDDLE CANOPY locations at a higher rate than either the UPPER CANOPY or the GROUND. This prediction was supported by small juveniles during the wet season, when they had the highest rates of occupying LOWER CANOPY TERMINAL BRANCH, LOWER CANOPY VINES, and MIDDLE CANOPY TREE TRUNK. Contrary to this prediction though, independent infants had the highest rate of using the GROUND (as noted previously), as well as the highest rate of using the MIDDLE CANOPY TERMINAL BRANCH location. During the dry season, small juveniles had the highest rates of occupying four LOWER and MIDDLE CANOPY locations (as discussed above), while independent infants had the highest rates in two MIDDLE and LOWER CANOPY locations (LOWER CANOPY TERMINAL BRANCH and MIDDLE CANOPY INNER BRANCH), supporting the prediction.

Developmental factors might explain the differences in foraging behavior discussed in this chapter. In feeding behavior, for example, independent infants had an extremely high rate of EXPLORE during the wet season, and in both seasons this behavior had a tendency to decrease ontogenetically. In addition, infants made more mistakes while foraging (e.g. GRAB AND MISS) during both seasons, as well as having the lowest rates of EAT. Fragaszy and Boinski (Boinski & Fragaszy, 1989; Fragaszy & Boinski, in press) suggested that experience may influence foraging success, in that older individuals should be more efficient than younger (and smaller) individuals.

In terms of complex behaviors, however, the data did not support the initial prediction. For example, during the dry season small juveniles had the highest rate of BREAK OPEN WITH HANDS AND/OR MOUTH. Also, adults and small juveniles had virtually identical rates of PROBE. In addition, in the wet season small juveniles and independent infants had the highest rates of CARRY IN HANDS AND/OR MOUTH and small juveniles displayed the greatest frequency of PROBE. As noted by Parker and Gibson (1977), complex object manipulation would be expected in a habitat with highly seasonal food sources. In addition, as Byrne & Suomi (1995) reported for *C. apella*, complex manipulation of food and objects first begins at 3-4 months and increases to stable levels in the second half of the first year. *Cebus* display highly manipulative foraging behaviors as well as some degree of tool use (Izawa & Mizuno, 1977; D'Amato *et al.*, 1985; Antinucci & Visalberghi, 1986; Fernandez, 1991).

Where food sources were concerned, in the dry season there was no correlation between age class and SMALL FRUIT consumption. During the wet season small juveniles did have the highest rate of eating SMALL FRUIT (although, as noted earlier, it was extremely close to the rate of adults), and independent infants ate no LARGE FRUIT during sampling time, but overall there seems to be little support for the initial prediction of age class correlating with food size.

As with food items, body size was sometimes related to substrate size, while in other instances it was not. For example, in the dry season larger animals used more "difficult" substrates than the smaller individuals in the social groups (e.g. BARK-UNDER, TREE HOLE and WASP NEST). As Fragaszy and Boinski (in press) note, size largely predicts strength in manipulating food-bearing substrates, and therefore access to desired resources. However, contrary to this prediction, in the wet season small juveniles had the highest rate of working on the substrate TREE HOLE. This is most likely due to the highly inquisitive nature of juvenile capuchins.

During the wet season, some of the initial predictions regarding location use were supported. For example, adults did display the highest rates of utilizing the UPPER CANOPY TERMINAL BRANCH location, small juveniles utilized LOWER CANOPY TERMINAL BRANCH location at the highest rate, and independent infants utilized the MIDDLE CANOPY TERMINAL BRANCH location at the highest rate. Contrary to what was predicted, independent infants had the highest frequency rates of occupying the GROUND level of the forest. Developmental factors may explain some of these differences, however the exact borderlines are often unclear. Also, as Fragaszy (1990) notes, "it is not evident that capuchin infants face greater risk during independent locomotion than do infants of the other genera" (p. 125). However, she goes on to argue that "although the infants of chimpanzees and capuchins can manipulate objects at young ages, their opportunities to interact with the environment are more constrained by postural limitations than those of squirrel monkeys, baboons or macaques" (p. 125). With regard to the white-faced capuchins in this study, however, such developmental constraints (e.g. size and immature locomotor skills) appear not to be limiting factors in the exploration and use of varying locations in the habitat.

## CONCLUSION

The main question I addressed in the present study was, are there age class differences in the foraging behavior of the capuchin study groups at Santa Rosa, and if so, can developmental factors be applied to explain these differences?

*Cebus* monkeys living in the same social group exhibit great variation across age and sex classes in activity budgets and foraging behavior (Fragaszy, 1986; Rose, 1994a; Fragaszy & Boinski, in press). The ability of *Cebus* to exploit a wide variety of food items derives in part from their manipulative abilities. They display a dexterity in handling objects that is not seen in other Neotropical primates (Fragaszy, *et al.*, 1990). Developmental factors, such as size limitation and immature foraging skills, appear to explain the original predictions outlined for age class differences in *C. capucinus* foraging behavior (although, social and ecological factors undoubtedly play a supporting role). Seasonal variation may occur, as there were significant differences between the age classes in location use during the dry season, but not in the wet season.

| Feeding Behavior | Adult (n=14) | Large Juv (n=6) | Small Juv (n=8) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Break Open With Hands/Mth | 4.66 | 12.69 | 9.05 | 6.31 | 0.12 |
| Carry in Hands/Mth | 0.38 | 0.31 | 1.12 | 1.10 | 0.97 |
| Eat | 33.84 | 31.42 | 35.76 | 17.51 | 0.02 |
| Explore | 5.86 | 10.04 | 10.09 | 23.85 | <0.01 |
| Grab | 3.08 | 6.70 | 3.21 | 1.08 | 0.15 |
| Grab and Miss | 0.09 | 0.23 | 0.03 | 0.31 | 0.26 |
| Pick Out With Fingers/Mth | 4.07 | 7.76 | 7.84 | 3.17 | 0.21 |
| Poke | 0.22 | 0.11 | 1.27 | 1.42 | 0.00 |
| Probe | 0.87 | 0.81 | 2.23 | 0.25 | 0.50 |
| Smell | 0.70 | 0.46 | 0.46 | 0.08 | 0.89 |
| Tap | 0.43 | 0.74 | 0.21 | 0.00 | 0.35 |
| Unroll | 1.04 | 0.83 | 1.33 | 1.25 | 0.94 |
| Visual Forage | 29.11 | 39.92 | 37.30 | 13.79 | 0.00 |

**Table 2.1.** Mean frequency rates and ANOVA P-values for feeding behaviors of individuals in both social groups during the wet season.

| Feeding Behavior | Adult (n=17) | Large Juv (n=4) | Small Juv (n=12) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Break Open With Hands/Mth | 6.12 | 6.48 | 10.28 | 6.76 | 0.13 |
| Carry in Hands/Mth | 0.23 | 1.10 | 0.85 | 0.53 | 0.00 |
| Eat | 20.26 | 27.53 | 32.85 | 12.21 | 0.12 |
| Explore | 1.43 | 2.89 | 2.89 | 3.92 | 0.17 |
| Grab | 1.10 | 1.86 | 1.83 | 0.72 | 0.37 |
| Grab and Miss | 0.01 | 0.04 | 0.11 | 0.29 | 0.05 |
| Pick Out With Fingers/Mth | 2.11 | 3.82 | 4.66 | 2.87 | 0.04 |
| Poke | 0.00 | 0.04 | 0.00 | 0.08 | 0.01 |
| Probe | 1.14 | 0.86 | 1.13 | 0.00 | 0.49 |
| Smell | 0.13 | 0.20 | 0.11 | 0.06 | 0.67 |
| Tap | 0.10 | 0.23 | 0.08 | 0.00 | 0.09 |
| Unroll | 0.07 | 0.04 | 0.10 | 0.53 | 0.00 |
| Visual Forage | 17.73 | 21.03 | 24.57 | 17.46 | 0.01 |

**Table 2.2.** Mean frequency rates and ANOVA P-values for feeding behaviors of individuals in both social groups during the dry season.

| Food Items | Adult (n=14) | Large Juv (n=6) | Small Juv (n=8) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Small Fruit | 27.55 | 11.84 | 29.48 | 18.42 | 0.75 |
| Medium Fruit | 1.20 | 0.33 | 1.58 | 0.43 | 0.98 |
| Large Fruit | 5.20 | 7.97 | 4.41 | 0.00 | 0.61 |
| Small Insect | 6.45 | 5.53 | 4.95 | 3.32 | 0.20 |
| Medium Insect | 0.40 | 1.01 | 0.23 | 0.06 | 0.66 |
| Large Insect | 1.70 | 6.53 | 0.37 | 0.24 | 0.30 |
| Larvae | 5.41 | 10.22 | 7.14 | 2.48 | 0.44 |
| Caterpillar | 15.82 | 18.37 | 10.64 | 3.47 | 0.20 |
| Acorn | 2.13 | 2.51 | 7.62 | 6.73 | 0.62 |

**Table 2.3.** Mean frequency rates and ANOVA P-values for food items eaten by individuals in both social groups during the wet season.

| Food Items | Adult (n=17) | Large Juv (n=4) | Small Juv (n=12) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Small Fruit | 6.55 | 7.01 | 6.98 | 1.91 | 0.44 |
| Medium Fruit | 3.60 | 2.39 | 6.84 | 1.05 | 0.46 |
| Large Fruit | 3.86 | 10.93 | 8.51 | 5.85 | 0.18 |
| Small Insect | 12.57 | 19.04 | 14.64 | 32.33 | 0.13 |
| Medium Insect | 7.50 | 6.04 | 8.25 | 6.33 | 0.85 |
| Large Insect | 7.19 | 13.79 | 6.03 | 9.17 | 0.39 |
| Larvae | 29.53 | 43.04 | 41.53 | 32.17 | 0.82 |

**Table 2.4.** Mean frequency rates and ANOVA P-values for food items eaten by individuals in both social groups during the dry season.

| Substrates Used | Adult (n=14) | Large Juv (n=6) | Small Juv (n=8) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Acacia Branch | 0.12 | 0.09 | 0.54 | 0.44 | 0.13 |
| Acacia Thorn | 0.30 | 0.51 | 1.39 | 2.54 | 0.12 |
| Bark-Surface | 1.23 | 1.91 | 4.39 | 4.18 | 0.02 |
| Bark-Under | 0.43 | 0.42 | 0.44 | 0.06 | 0.29 |
| Small Dead Branch | 2.13 | 9.48 | 5.14 | 8.25 | <0.01 |
| Medium Dead Branch | 1.40 | 9.01 | 2.44 | 1.27 | <0.01 |
| Large Dead Branch | 0.41 | 0.13 | 0.53 | 0.87 | 0.97 |
| Small Live Branch | 2.63 | 4.98 | 5.64 | 8.14 | <0.01 |
| Medium Live Branch | 2.33 | 1.01 | 1.68 | 1.28 | 0.82 |
| Large Live Branch | 0.08 | 0.12 | 0.35 | 0.41 | 0.41 |
| Dead Leaf | 3.16 | 3.86 | 6.43 | 5.05 | 0.50 |
| Green Leaf | 2.25 | 2.59 | 3.62 | 6.09 | <0.01 |
| Inner Branch | 0.00 | 0.06 | 0.10 | 2.48 | <0.01 |
| Terminal Branch | 0.00 | 0.00 | 0.88 | 7.90 | <0.01 |
| Leaf litter | 0.38 | 0.46 | 0.47 | 0.29 | 0.97 |
| Tree Crotch | 0.60 | 0.32 | 0.70 | 0.06 | 0.41 |
| Tree Hole | 0.83 | 1.03 | 3.23 | 0.06 | 0.14 |
| Tree Trunk | 0.36 | 0.40 | 0.62 | 1.09 | 0.51 |
| Wasp Nest | 0.65 | 0.20 | 0.55 | 0.00 | 0.74 |

Table 2.5. Mean frequency rates and ANOVA P-values for substrates used by individuals in both social groups during the wet season.

| Substrates Used | Adult (n=17) | Large Juv (n=4) | Small Juv (n=12) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Acacia Branch | 0.72 | 0.42 | 0.98 | 0.26 | 0.62 |
| Acacia Thorn | 1.75 | 1.94 | 1.88 | 0.95 | 0.89 |
| Bark-Surface | 0.35 | 1.25 | 0.47 | 0.99 | 0.09 |
| Bark-Under | 0.09 | 0.40 | 0.03 | 0.00 | 0.12 |
| Small Dead Branch | 2.11 | 2.34 | 7.21 | 7.96 | <0.01 |
| Medium Dead Branch | 0.18 | 0.60 | 0.33 | 1.52 | <0.01 |
| Large Dead Branch | 0.31 | 0.21 | 0.69 | 0.00 | 0.57 |
| Small Live Branch | 2.15 | 0.86 | 3.30 | 0.70 | 0.74 |
| Medium Live Branch | 0.03 | 0.00 | 0.00 | 0.00 | 0.93 |
| Large Live Branch | 0.00 | 0.00 | 0.00 | 0.00 | N/A |
| Dead Leaf | 0.24 | 0.39 | 0.88 | 2.24 | <0.01 |
| Green Leaf | 0.11 | 0.45 | 0.25 | 0.42 | 0.40 |
| Inner Branch | 0.11 | 0.00 | 0.09 | 1.72 | <0.01 |
| Terminal Branch | 0.00 | 0.00 | 0.30 | 0.90 | 0.01 |
| Leaf litter | 0.50 | 1.07 | 0.56 | 0.90 | 0.90 |
| Tree Crotch | 0.15 | 0.30 | 0.44 | 0.03 | 0.47 |
| Tree Hole | 0.52 | 1.37 | 0.98 | 0.00 | 0.06 |
| Tree Trunk | 0.31 | 1.18 | 0.59 | 0.04 | 0.07 |
| Wasp Nest | 0.13 | 0.00 | 0.00 | 0.00 | 0.35 |

Table 2.6. Mean frequency rates and ANOVA P-values for substrates used by individuals in both social groups during the dry season.

| Locations Used | Adult (n=14) | Large Juv (n=6) | Small Juv (n=8) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Ground | 6.76 | 5.60 | 9.90 | 13.03 | 0.86 |
| Lower Canopy-Inner Branch | 1.97 | 1.69 | 0.98 | 0.18 | 0.37 |
| Lower canopy-Terminal Branch | 1.71 | 0.71 | 3.53 | 0.30 | 0.31 |
| Lower Canopy-Tree Crotch | 0.14 | 0.05 | 0.00 | 0.00 | 0.84 |
| Lower Canopy-Tree Trunk | 1.96 | 0.51 | 0.59 | 0.23 | 0.02 |
| Lower Canopy-Vines | 4.99 | 4.45 | 12.08 | 0.14 | 0.31 |
| Middle Canopy-Inner Branch | 50.26 | 50.97 | 48.31 | 40.18 | 0.84 |
| Middle Canopy-Terminal Branch | 71.60 | 71.90 | 71.34 | 74.82 | 0.94 |
| Middle Canopy-Tree Crotch | 3.02 | 0.11 | 0.77 | 0.77 | 0.21 |
| Middle Canopy-Tree Trunk | 2.68 | 2.81 | 9.78 | 1.11 | 0.14 |
| Middle Canopy-Vines | 20.77 | 44.91 | 23.77 | 33.47 | 0.08 |
| Upper Canopy-Inner Branch | 0.74 | 0.93 | 2.79 | 0.84 | 0.46 |
| Upper Canopy-Terminal Branch | 5.98 | 1.01 | 3.03 | 0.16 | 0.20 |

Table 2.7. Mean frequency rates and ANOVA P-values for locations in the canopy used by individuals in both social groups during the wet season.

| Locations Used | Adult (n=17) | Large Juv (n=4) | Small Juv (n=12) | Ind Inf (n=4) | ANOVA P-Value |
|---|---|---|---|---|---|
| Ground | 13.15 | 29.51 | 15.87 | 25.04 | 0.41 |
| Lower Canopy-Inner Branch | 13.34 | 26.02 | 27.34 | 26.41 | 0.01 |
| Lower canopy-Terminal Branch | 0.56 | 1.14 | 2.20 | 4.05 | 0.00 |
| Lower Canopy-Tree Crotch | 0.07 | 0.00 | 0.92 | 0.05 | 0.39 |
| Lower Canopy-Tree Trunk | 0.21 | 0.33 | 0.74 | 0.13 | 0.55 |
| Lower Canopy-Vines | 0.00 | 0.24 | 0.00 | 0.00 | 0.06 |
| Middle Canopy-Inner Branch | 42.02 | 32.27 | 39.35 | 48.12 | 0.36 |
| Middle Canopy-Terminal Branch | 38.14 | 18.07 | 36.08 | 19.87 | 0.27 |
| Middle Canopy-Tree Crotch | 0.22 | 1.18 | 0.35 | 0.00 | 0.30 |
| Middle Canopy-Tree Trunk | 0.38 | 0.00 | 0.70 | 0.16 | 0.57 |
| Middle Canopy-Vines | 0.00 | 0.55 | 0.00 | 0.00 | 0.06 |
| Upper Canopy-Inner Branch | 0.14 | 0.00 | 0.00 | 0.00 | 0.60 |
| Upper Canopy-Terminal Branch | 0.78 | 1.43 | 0.00 | 0.00 | 0.19 |

Table 2.8. Mean frequency rates and ANOVA P-values for locations in canopy used by individuals in both social groups during the dry season.

| **Main effects: Behavior** | **F** | **DF** | **P** |
|---|---|---|---|
| sex | 1.65 | 1 | 0.21 |
| age | 5.11 | 3 | 0.01 |
| sex by age | 2.19 | 3 | 0.11 |

| **Interactions: Behavior** | **F** | **DF** | **P** |
|---|---|---|---|
| sex by beh | 1.31 | 12 | 0.21 |
| age by beh | 4.00 | 36 | <0.01 |
| sex by age by beh | 1.04 | 36 | 0.42 |

| **Main effects: Food** | **F** | **DF** | **P** |
|---|---|---|---|
| sex | 0.14 | 1 | 0.71 |
| age | 4.96 | 3 | 0.01 |
| sex by age | 0.39 | 3 | 0.76 |

| **Interactions: Food** | **F** | **DF** | **P** |
|---|---|---|---|
| sex by food | 0.67 | 8 | 0.72 |
| age by food | 0.73 | 24 | 0.82 |
| sex by age by food | 0.71 | 24 | 0.84 |

| **Main effects: Substrate** | **F** | **DF** | **P** |
|---|---|---|---|
| sex | 1.18 | 1 | 0.29 |
| age | 10.49 | 3 | <0.01 |
| sex by age | 2.01 | 3 | 0.14 |

| **Interactions: Substrate** | **F** | **DF** | **P** |
|---|---|---|---|
| sex by subst | 3.51 | 21 | <0.01 |
| age by subst | 3.47 | 63 | <0.01 |
| sex by age by subst | 1.88 | 63 | <0.01 |

| **Main effects: Location** | **F** | **DF** | **P** |
|---|---|---|---|
| sex | 1.05 | 1 | 0.32 |
| age | 1.09 | 3 | 0.37 |
| sex by age | 0.64 | 3 | 0.60 |

| **Interactions: Location** | **F** | **DF** | **P** |
|---|---|---|---|
| sex by loc | 2.47 | 12 | 0.00 |
| age by loc | 0.78 | 36 | 0.82 |
| sex by age by loc | 0.82 | 36 | 0.58 |

**Table 2.9.** Multiple analysis of variance for feeding behaviors, food items, substrates used, and location in canopy, in both social groups during the wet season.

| **Main effects: Behavior** | F | DF | P |
|---|---|---|---|
| sex | 0.03 | 1 | 0.58 |
| age | 4.56 | 3 | 0.01 |
| sex by age | 0.70 | 2 | 0.51 |

| **Interactions: Behavior** | F | DF | P |
|---|---|---|---|
| sex by beh | 1.18 | 12 | 0.30 |
| age by beh | 2.83 | 36 | <0.01 |
| sex by age by beh | 0.75 | 24 | 0.80 |

| **Main effects: Food** | F | DF | P |
|---|---|---|---|
| sex | 0.88 | 1 | 0.36 |
| age | 0.71 | 3 | 0.55 |
| sex by age | 0.44 | 2 | 0.65 |

| **Interactions: Food** | F | DF | P |
|---|---|---|---|
| sex by food | 0.50 | 6 | 0.81 |
| age by food | 1.39 | 18 | 0.14 |
| sex by age by food | 0.72 | 12 | 0.73 |

| **Main effects: Substrate** | F | DF | P |
|---|---|---|---|
| sex | 0.18 | 1 | 0.68 |
| age | 4.04 | 3 | 0.02 |
| sex by age | 0.67 | 2 | 0.52 |

| **Interactions: Substrate** | F | DF | P |
|---|---|---|---|
| sex by subst | 1.30 | 18 | 0.18 |
| age by subst | 1.79 | 54 | <0.01 |
| sex by age by subst | 1.49 | 36 | 0.03 |

| **Main effects: Location** | F | DF | P |
|---|---|---|---|
| sex | 0.01 | 1 | 0.94 |
| age | 1.64 | 3 | 0.20 |
| sex by age | 0.98 | 2 | 0.39 |

| **Interactions: Location** | F | DF | P |
|---|---|---|---|
| sex by loc | 2.05 | 12 | 0.02 |
| age by loc | 1.11 | 36 | 0.31 |
| sex by age by loc | 1.21 | 24 | 0.23 |

Table 2.10. Multiple analysis of variance for feeding behaviors, food items, substrates used, and location in canopy, in both social groups during the dry season.

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# CHAPTER 3

## Age class Spatial Association Patterns of *Cebus capucinus* at Santa Rosa National Park, Costa Rica

## INTRODUCTION

Most primate infants and juveniles seem to be attracted to other members of the same age class, particularly for social activities such as play (Cheney, 1978; Fairbanks, 1993; O'Brien & Robinson, 1993; van Noordwijk *et al.*, 1993). Peer groups are an important context in which infants and juveniles are socialized within the larger group; through peer groups, immatures come into contact with non-related group members, and learn their position and function within the social group (Fedigan, 1982). In many social mammals, offspring are spatially separated from adult members of the social group (e.g. bovids: Lawrence, 1990; Lazo, 1994); in some species, these peer affiliative bonds enable the infants and juveniles to exploit dietary niches that allow them adequate nutritional intake (e.g. rats: Galef & Wright, 1995). This may be accomplished through the acquisition by juveniles of a novel feeding behavior in a social context (e.g. humpback whales: Weinrich *et al.*, 1992). This is also true in many reptile species (e.g. garter snakes: Burghardt, 1983), where both diet and familiarity play a part in patterns of aggregation (Lyman-Henley & Burghardt, 1995). In capuchin monkeys (*Cebus spp.*), Visalberghi and Fragaszy (1995) have demonstrated that attraction to and ingestion of novel food items is socially facilitated. That is, when individuals are in social groups they are more likely to try a new food item than when they are alone.

Ecological variables, such as intra-group competition for food sources, are also important in structuring spatial associations within social groups (Wrangham, 1980; Terborgh & Janson, 1986). The pattern of intra- and inter-group food competition, for example, has been used to explain the nature of social relationships within the group (Wrangham, 1980; Vehrencamp, 1983), and some researchers feel that the importance of food competition in structuring social behavior has been underestimated (e.g. Janson & van Schaik, 1988). It might be expected that in social groups of white-faced capuchins (*Cebus capucinus*), where adults typically rank over immatures (Fragaszy, 1986; Fedigan, 1993), independent infants and juveniles would either avoid or be supplanted from the vicinity of foraging adults, thus leading to age class subgroups.

Spatial association patterns have been examined in several Old World monkey species in the wild, for example, the toque macaque (*Macaca sinica*, e.g. Dittus, 1977), and yellow baboons (*Papio cynocephalus*, e.g. Rhine, 1975; Altmann, 1979). In New World monkeys, previous studies of spatial association patterns for the genus *Cebus* have focused on the wedge-capped capuchin (*C. olivaceus*) in Venezuela (e.g. Robinson, 1981 & 1986), and on the brown capuchin (*C. apella*) in Peru (e.g. Janson, 1990a & 1990b). These studies have documented the variable use of time and space within primate species, and have helped to explain the causes for spatial structuring within primate social groups. For example, Robinson (1981) found that *C. olivaceus* groups are organized in consistent and predictable configurations, based on age-sex classes. The results of his study suggest that class-specific characteristics (i.e. physical capabilities) influence how animals weigh the relative importance of foraging success and risk of predation (Robinson, 1981).

The objective of the present study is to relate spatial association patterns across age classes in *C. capucinus* to social and ecological explanations, and to compare these findings with those of past *Cebus* studies. Nearest neighbor data are examined to determine if there are any differences between age classes in spatial association patterns in the *C. capucinus* study groups. The following questions are addressed: Do independent infants and juveniles associate more frequently with members of their own age classes than with adults? Do juveniles, specifically small juveniles, form peer groups? And finally, what is the ontogeny of spatial association patterns within the social groups?

## Spatial Association Pattern Hypothesis and Predictions:

As mentioned above, the objective of the present study is to relate spatial association pattern changes across age classes in *C. capucinus* to social and ecological theoretical explanations. My general hypothesis is that due to both competitive and affiliative patterns, individuals of the same age class are more likely to be found in spatial proximity to each other, than to members of different age classes.

Based upon this hypothesis of age class differences in spatial association patterns of white-faced capuchins, I predict that:

Individuals will associate most with members of their own age class. In addition to determining the basic association patterns within the capuchin groups, the ontogeny of affiliative patterns will be examined. Specifically, the following question will be addressed: with what age class do individuals in the social group associate more often at different stages of their development?

## METHODS

### The Study Site:

Santa Rosa National Park is located in the Guanacaste province of Northwestern Costa Rica, adjacent to the PanAmerican Highway. It is 10,800 ha in size and most of the park is at an elevation of 280 m above sea level. As a result of the natural topography and past land-use practices, the vegetation is a mixture of grassland, dry deciduous forest, and semi-evergreen forest (Chapman, 1988). There are two distinct seasons. The dry season is characterized by virtually no rainfall from mid-December to mid-May, and the wet season, from May until December, averages between 900 mm and 2400 mm annually.

### The Study Subjects:

Data were taken on two social groups of capuchins: the Los Valles group (LV) and the Cerco de Piedra group (CP). In the wet season of 1992 group LV consisted of: 3 adult and subadult males, 5 adult females, 3 large juveniles, 5 small juveniles and 3 independent infants. In the dry season of 1993 group LV consisted of: 4-6 adult and subadult males, 5 adult females, 2 large juveniles, 8 small juveniles, and 2 independent infants. In the wet season of 1992 group CP consisted of: 2 adult and subadult males, 4 adult females, 3 large juveniles, 3 small juveniles and 1 independent infant. In the dry season of 1993 group CP consisted of: 4-6 adult and subadult males, 4-5 adult females, 2 large juveniles, 4 small juveniles, and 1-2 independent infants.

## Data Collection and Analysis:

Both social groups were habituated to human observers; observation distances of five to ten meters were common, with distances sometimes as close as 2-3 meters. Individuals were identified by size, characteristics of fur markings, brow hair length, and facial markings.

The fieldwork for this study was conducted during the rainy season months between April and September, 1992 and during the dry season months between January and April, 1993. Approximately 337 hours of frequency data were collected during the wet season in 1992 and during the dry season in 1993, using ten-minute instantaneous focal samples. Individuals in proximity to the focal animal were noted at the beginning and end of each ten-minute sample in the following manner: contact, less than 3 meters, 3-10 meters, and greater than 10 meters. However, for the purposes of the present study, only "nearest neighbor" animals at a distance of up to 3 meters (from the focal animal) at the beginning of each ten-minute focal sample, are analyzed and reported.

Proximity data were taken on individuals from the five age classes: adult, large juvenile, small juvenile, independent infant, and dependent infants. Dependent infants are aged birth to 6 months, independent infants are aged 6 months to 1 year, small juveniles are aged 1-3 years approximately, and large juveniles are aged approximately 3-4 years for females, 3-5 years for males (see Appendix 7). Since dependent infants spend most of their time on or near their mother, they were not included in the analyses for the present study.

Data were analyzed to determine whether individuals of the same age class (independent infant, small juvenile, large juvenile, adult) were more likely to be found in proximity to one another than to members of other age classes. To determine the "best neighbor" (the most likely nearest neighbor, given the age class representation in the group), I tallied the number of individuals found in contact to 3 meters of the focal animal by age class for each proximity scan. I then divided the number of proximal individuals in a given age class by the total number of potential neighbors available for that age class. The "best neighbor" for each proximity scan was defined as the age class with the highest ratio of observed to potential proximity scores. Thus, a "best neighbor" could be determined even if that age class was underrepresented or overrepresented in the social group. If the "best neighbor" was in the same age class as the focal animal, it would suggest a peer group formation. If there was a tie in the resulting ratios, that proximity scan was discarded. Chi-square tests were performed on the scan data collected at the beginning of each focal session. One test was performed for each of the two seasons (wet and dry) and for each of the two study groups (CP and LV), on each age class as focal animal, resulting in a total of 16 goodness of fit chi-square tests. Statistical significance was noted at $p < 0.05$.

Percentages of proximity scans, in which each age class category was found to be best neighbor, were evaluated in order to document the ontogeny of proximity patterns (Figs. 3.1-3.4).

## RESULTS: INDEPENDENT INFANTS (Fig. 3.1)

For the CP Group during the wet season (chi-square: df = 3, $X^2 = 21.38$, $p < .001$), independent infants were in proximity for a greater percentage of proximity scans with adults than with any other age class.

For the LV Group during the wet season (chi-square: df = 3, $X^2 = 36.59$, $p < .001$), independent infants were in proximity for a greater percentage of proximity scans with independent infants than with any other age class.

For the CP Group during the dry season (chi-square: df = 3, $X^2 = 1$, $p = .8$), independent infants were in proximity with independent infants and small juveniles for the same proportion of proximity scans.

For the LV Group during the dry season (chi-square: df = 3, $X^2 = 19.33$, $p < .001$), independent infants were in proximity for a greater percentage of proximity scans with adults than with any other age class.

## RESULTS: SMALL JUVENILES (Fig. 3.2)

For the CP Group during the wet season (chi-square: df = 3, $X^2 = 14$, $p < .01$), small juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

For the LV Group during the wet season (chi-square: df = 3, $X^2 = 6.42$, $p = .09$), small juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

For the CP Group during the dry season (chi-square: df = 3, $X^2 = 1.62$, $p = .7$), small juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

For the LV Group during the dry season (chi-square: df = 3, $X^2 = 19.63$, $p < .001$), small juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

## RESULTS: LARGE JUVENILES (Fig. 3.3)

For the CP Group during the wet season (chi-square: df = 3, $X^2 = 4.3$, $p = .2$), large juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

For the LV Group during the wet season (chi-square: df = 3, $X^2 = 3.6$, $p = .3$), large juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

For the CP Group during the dry season (chi-square: df = 3, $X^2$ = 8.52, $p < .05$), large juveniles were in proximity for a greater percentage of proximity scans with adults than with any other age class.

For the LV Group during the dry season (chi-square: df = 3, $X^2$ = 5.4, $p = .1$), large juveniles were in proximity for a greater percentage of proximity scans with small juveniles than with any other age class.

**RESULTS: ADULTS** (Fig. 3.4)

For the CP Group during the wet season (chi-square: df = 3, $X^2$ = 15.23, $p < .01$), adults were in proximity for a greater percentage of proximity scans with adults than with any other age class.

For the LV Group during the wet season (chi-square: df = 3, $X^2$ = 9.05, $p < .05$), adults were in proximity for a greater percentage of proximity scans with adults than with any other age class.

For the CP Group during the dry season (chi-square: df = 3, $X^2$ = 27.08, $p < .001$), adults were in proximity for a greater percentage of proximity scans with adults than with any other age class.

For the LV Group during the dry season (chi-square: df = 3, $X^2$ = 33.54, $p < .001$), adults were in proximity for a greater percentage of proximity scans with adults than with any other age class.

## DISCUSSION

In the present study, individuals of certain developmental stages showed consistent age preferences of association by age class. Several distinct patterns are present. For example, it was predicted that independent infants would associate more frequently with members of their own age class than with other social group members. This was true only in the LV group during the wet season (Fig. 3.1). During this time the LV group had the highest number of independent infants of any group or season, with 3 individuals. Thus, the independent infants had a greater number of individuals to choose from, within their own age class. This is apparent in other *Cebus* species as well. For example, Robinson (1981) found that wedge-capped capuchin infants of both sexes were found together, forming a little "subgroup" high in the trees in the back of the social group. In the present study, however, in groups and during seasons where there were only one or two independent infants, the independent infants associated with members of other age classes more often, particularly adults. An additional explanation may be that independent infants associate more frequently with older age classes in order to acquire the foraging and social skills needed for survival. As Avery (1994) found for red-winged blackbirds, "naive" flock members benefited by foraging with experienced birds. Interestingly, the benefit was in learning where to forage, not where to avoid. In some primate species (e.g. squirrel monkeys, *Saimiri oerstedi*), individual experience appears to be more important than social experience in the acquisition of certain foraging skills (Boinski

& Fragaszy, 1989). In fact, Milton (1993) found that species-typical foraging behavior in spider monkeys (*Ateles geoffroyi*) can develop in the absence of opportunities to observe and interact with more experienced individuals in the social group. However, squirrel monkey infants observing other infants and adults having problems handling difficult prey items, suggests that avoidance of certain noxious prey items could be transmitted socially (Boinski & Fragaszy, 1989).

It was predicted that small juveniles would associate more frequently with members of their own age class than with other social group members. This was found to be consistently true in both social groups and in both seasons (Fig. 3.2). This preference for peer group affiliation is also true for other monkey species, as O'Brien and Robinson (1993) note for the wedge-capped capuchin (*C. olivaceus*), and van Noordwijk *et al.* (1993) note for long-tailed macaques (*Macaca fascicularis*). As mentioned in the introduction, factors used to explain such peer group affiliations generally fall into two categories: ecological and social.

Ecological constraints may include both direct and indirect food competition within group members. Intra-group direct competition occurs when aggressive interactions between group members leads to a reduced food intake for some individuals (Robinson, 1981). Suggested correlates for direct competition are a high variability in the dispersion of food patches, a higher-than-average density of feeding animals, a scarcity of alternative foods, a small food patch area, etc. (Janson & van Schaik, 1988). Thus, direct competition results in a lower energy intake for some individuals. For example, Janson (1985, 1988) found that food intake of individual subordinate brown capuchins was directly affected by aggression: the greater the rate of aggression in a food tree, the lower the subordinate feeding rates were relative to the dominant individual feeding rates. Intra-group indirect competition is subtle, and occurs when some individuals remove limited food supplies from an area before other group members have a chance to feed.

According to this theory, food competition should be especially intense when food occurs in discrete patches, when such patches are rare, when travel costs between patches are high, and when group members overlap in foraging areas (Altmann, 1974). However, since capuchins are opportunistic omnivorous feeders, their food types cannot be characterized as occurring in rare and discrete patches. When food sources are limited, though (as is possible during the dry season), the foraging efficiency of the individual may be maximized by the formation of foraging subgroups. These smaller groups of individuals may be able to exploit the foraging habitat successfully with a reduced chance of aggressive encounters from other group members. Thus, an optimal level of nutrient intake may be maintained, while energy expenditure is minimized (Pyke *et al.*, 1977). Indirect food competition may also result in an increase in time spent foraging, as individuals try to compensate for a lower energy intake (Janson & van Schaik, 1988). Thus, in theory, peer affiliative bonds may enable juveniles to exploit a dietary niche that is untouched by the larger, faster, and more efficient adults in the social group: While adults may be in one area of the group foraging for large arboreal insects (i.e. cicadas, cockroaches, etc.), smaller juveniles may be more peripheralized, foraging in smaller substrates for invertebrates (i.e. insect larvae). In the previous chapter, however, this was not always the case (see Chapter 2).

There may also be distinct spatial association patterns among the individuals in different age classes due to dietary preferences and food types available. Fragaszy (1986) suggests that dietary differences between nursing infants and independently foraging juveniles must be very large, given the range of items obtained by juveniles which are essentially unexploited by dependent infants. Although dependent infants were excluded from analyses in the present study, independent infants and small juveniles did have different dietary profiles in both wet and dry seasons (Tables 2.3-2.4).

Social factors are also used to explain peer group affiliations. For example, Fragaszy and Visalberghi (1990) examined the social processes that affect the appearance of innovative behaviors in capuchins. Juveniles foraging together are exposed to new aspects of the habitat when an individual in the group discovers a new possible food item. The social processes that support the spread of innovative behaviors include a social enhancement of interest in the objects and in the area around the activity. Whereas social processes that inhibit the display of innovative behaviors include situations in which dominant individuals restrict access and/or force subordinates to maintain active vigilance (Fragaszy & Visalberghi, 1990). The authors also found that differences in innovative behavior patterns and the extent of interest in a new item vary between and within age groups. In a later study, the same authors discuss how social influences affect individual responsiveness to key features of the environment, including food. They observed that individuals were more interested in another individual's food when foods were novel than when they were familiar (although actual food consumption was not affected) (Visalberghi & Fragaszy, 1995). Thus, social facilitation can have a role in broadening the dietary repertoire of capuchins, particularly during the exploratory developmental stage of small juvenile.

The third prediction, that large juveniles would associate more frequently with members of their own age class than with other social group members, was not supported. Contrary to the prediction, the preferred age class association of nearest neighbor for the large juveniles was the age class of small juvenile. Only one exception to this occurred: In the CP group during the dry season, when large juveniles were found in closest proximity to adults (Fig. 3.3). This supports other studies of juvenile primates, where "young" (i.e. small) juveniles form more cohesive cohorts than do "old" (i.e. large) juveniles (e.g. baboons: Pereira, 1988).

The final prediction of spatial association patterns, was that adults would associate more frequently with members of their own age class than with other social group members. This was found to be true in both groups and in both seasons (Fig. 3.4). Adults in other social species of New World monkeys also show preference for associating with other adults. As Strier (1993) observed in a study of spatial relations in the woolly spider monkey (*Brachyteles arachnoides*), adults preferred nearest neighbor associations with other adults over other age classes for a greater percentage of scan samples. In the present study, independent infants were the second most preferred age class. As noted earlier, independent infants still return to their mothers to nurse, and so during this time are in closer proximity to adults.

## Development of "nearest neighbor" associations:

Several factors facilitate the developmental changes in nearest neighbor associations in white faced capuchins. For example, independent infants leave the exclusive care of their mothers and begin to explore the surrounding habitat around 6 months of age. This is followed by the typical (though not exclusive) primate characteristic of an extended juvenile period before sexual maturation. Finally, large juvenile and subadult males (in the case of capuchins) emigrate from their natal groups and immigrate into others, although subadult females do, on occasion, emigrate as well. There appears to be a generalized trend in the development of age association patterns: independent infants are found in close proximity more often with independent infants and small juveniles when these age classes are sufficiently represented in the social groups (e.g. LV during the wet season and CP during the dry season) but in the absence of sufficient numbers of same-age cohorts, independent infants are found in close proximity more often with the adults of the social group (e.g. CP during the wet season and LV during the dry season). Small juveniles were always found in closer proximity to other small juveniles for a greater percentage of the observed proximity scans, and large juveniles were found in closer proximity to either small juveniles (e.g. LV during both seasons) or to adults (e.g. CP during both seasons). Finally, adults were always found in closer proximity to other adults (after dependent infants were removed from the analyses).

As individuals mature from infancy, there appears to be a shifting away from associating with the adult members of the group, to associating with individuals closer to the same age and developmental stage. There are interesting differences in each developmental stage when social groups and seasons are compared, suggesting that ecological and social factors are the controlling processes in spatial association preferences.

Preferences of independent infants showed a wide variation between groups and seasons (Fig. 3.1). As mentioned earlier, when there were limited same-age cohorts in the social group, as was the case with LV during the dry season and CP during the wet season, independent infants spent the greatest amount of scan samples in close proximity to adults. At this developmental stage, this association is not unexpected, as independent infants go back to their mothers to nurse, and are often in the center of a resting group of adults. However, when there were more same-age cohorts available for interaction, independent infants preferred to associate with those individuals (e.g. LV in the wet season). Small juveniles were the nearest neighbor to independent infants for roughly the same percentage in both groups and seasons (21.28% to 31.25%), suggesting that seasonal differences were not a factor in this association pattern. Overall, large juveniles were not the preferred nearest neighbor, however, in the CP group during the dry season, independent infants associated with large juveniles the greatest percentage of proximity scan samples (18.75%). In fact, independent infants associated with large juveniles and adults for the same percentage of samples. Due to the differences in association patterns across groups and seasons, it seems likely that both ecological and social factors influence nearest neighbor associations. However, since both the LV and CP groups differed within the same season, ecological factors (e.g. food competition during times of food stress) may not have a strong effect on preferred nearest neighbors. Therefore, it appears that social factors (e.g. how many individuals in an age class are present to interact with) have more of an influence on spatial association patterns during this developmental stage.

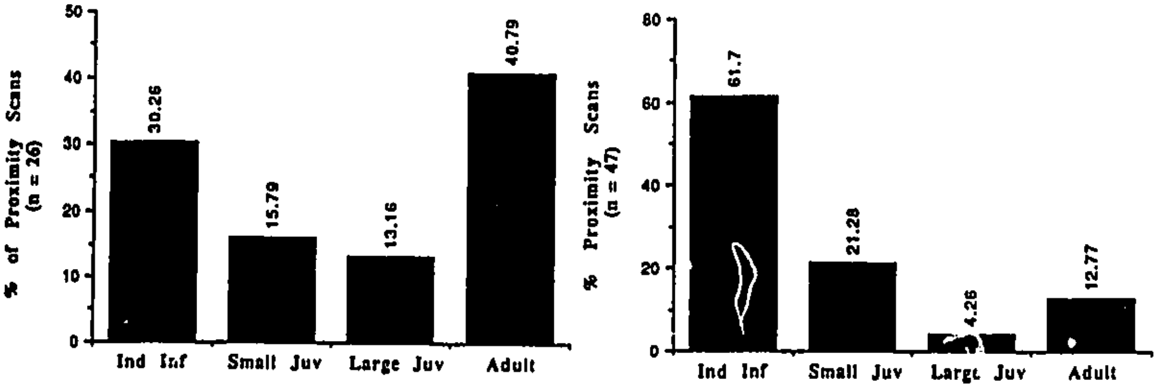
Preferences of small juveniles, on the other hand, showed a remarkable similarity across groups and seasons. During this developmental stage, small juveniles were always the preferred nearest neighbor of other small juveniles in both social groups (Fig. 3.2). In some instances, small juveniles comprised over half of the total percentage of proximity scan samples (e.g. 53.33% for the CP group in the wet season) (Fig. 3.2). Similarly, the age class that was the nearest neighbor for the second highest percentage of scan samples, was always independent infant. Therefore, since seasonal differences were not apparent, small juveniles prefer to associate with other small juveniles for social reasons, such as peer group formations. Such peer groups are most likely beneficial in situations where observational learning occurs (i.e. foraging and social interactions). As individuals mature, it appears that the focus of an individual's attention is shifted away from the mother and other adults in the social group, and towards individuals at the same developmental stage.

Nearest neighbor preferences of large juveniles were extremely similar in both groups during the wet season, with small juveniles making up the largest percentage of scan samples (Fig. 3.3). Small juveniles were also the preferred nearest neighbor in the LV group during the dry season. However, during the dry season in the CP group, adults were the nearest neighbor to large juveniles for almost half of the proximity scans (42.86%). This disparity between seasons may be explained by social factors. During the wet season the capuchin social groups are, for the most part, more relaxed due to an abundance of food items. They are thus able to spend more time on social activities such as play. This was observed in the study groups, with large juveniles frequently joining small juveniles in "chase" play and "rough and tumble" play sessions. During the dry season, when food items are not as evenly distributed, nor abundant, bouts of play diminished in frequency and duration. The high association of large juveniles to adults in the CP group during the dry season is most likely because large juveniles, being closer in size and weight to adults, have similar nutritional and metabolic requirements, and thus forage on similar substrates and food items as well as travel in similar areas of the canopy (see chapter 2).

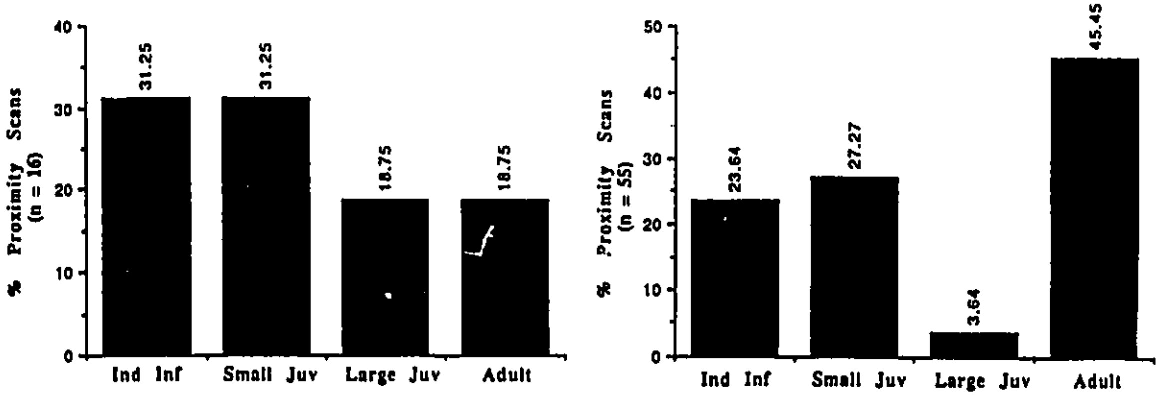
By the time individuals are fully mature and considered adults, nearest neighbor preferences were highly similar in both groups and seasons (Fig. 3.4). During periods of rest, adults cluster into grooming groups surrounded by dependent infants. These "core" groups are usually composed of adult females, their dependent young, and the alpha male. Other adult males may be in proximity as well, especially if the social group is relatively large in size. Independent infants and juveniles generally rest less during this time, spending energy on play and exploration. Also, when dependent infants are removed from analyses, it seems likely that adults will have other adults as nearest neighbors in the proximity scans based on the affiliative behaviors mentioned above.

## CONCLUSION

Overall, there is a pattern of development in terms of spatial association preferences among the age classes. Specifically, it appears that small juveniles and adults prefer to associate with members of their own age classes for a greater percentage of proximity scans than independent infants and large juveniles. These strong preferences seem to be more socially than ecologically motivated, particularly with small juveniles forming peer groups. There was also no apparent change in pattern of spatial association preferences between the seasons for small juveniles and adults, suggesting that ecological changes do not affect the choice for a nearest neighbor. These findings are consistent with past studies of spatial association patterns in capuchins. As Janson (1990a) found, neighbor-specific factors reflect the diverse behavior that make individuals prefer to be near or to avoid certain other group members. In addition, he found that ecological pressures tend to influence position-specific factors within the social group, not neighbor-specific factors. Robinson (1981) and O'Brien and Robinson (1993) discuss a pattern of nearest neighbor associations during foraging based on like-age associations in the wedge-capped capuchin. Particularly, they found that juvenile males strongly associate with one another and with subadult males, and that juvenile females associate with one another. These findings, along with the findings of the present study, suggest that the formation of peer groups, particularly among the juvenile age classes, may be found in all four species of *Cebus*.

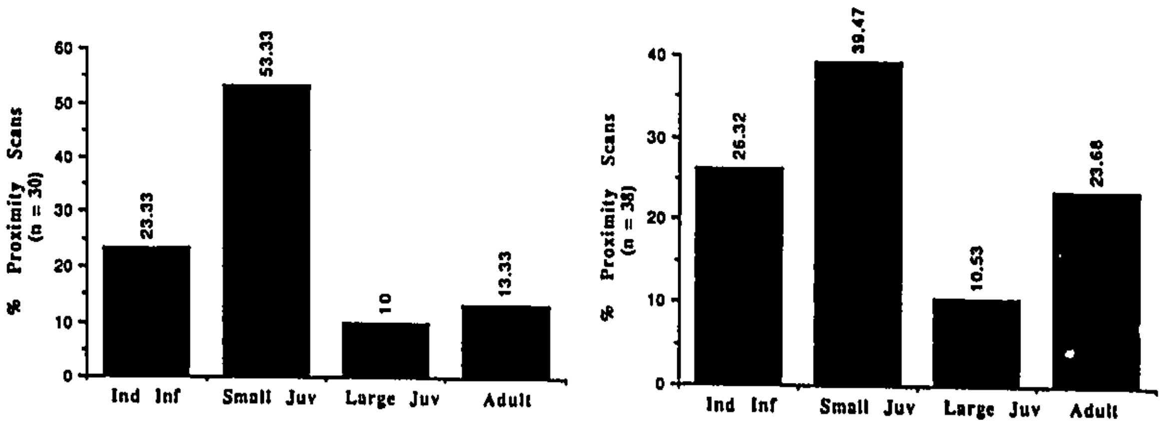


CP Group: Wet Season LV Group: Wet Season



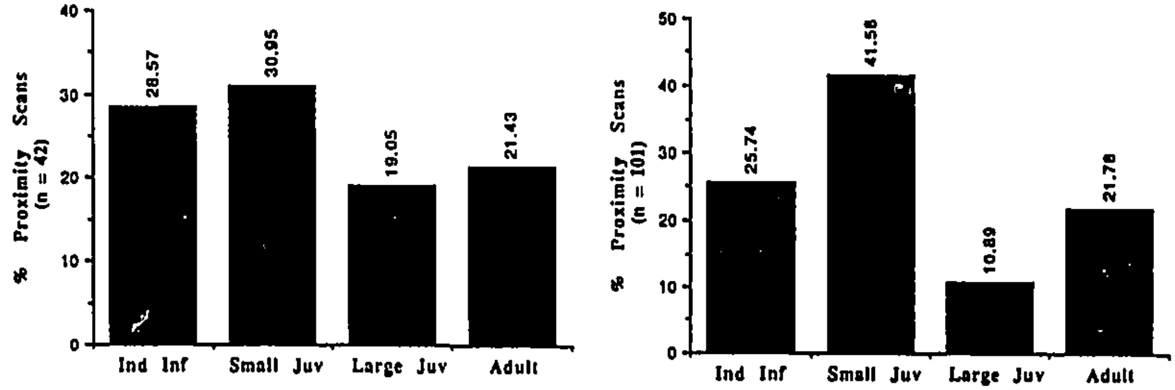
CP Group: Dry Season LV Group: Dry Season

**Fig. 3.1. Independent Infants as Focal Animals**
Distribution of nearest neighbors by age class when independent infant individuals are the focal animal. Data are taken from proximity scans at the beginning of each ten-minute focal sample. The number of observations for each social group and season are given in parentheses along the y-axis of each bar graph. Dependent infants were excluded due to closer proximity to their mothers.



CP Group: Wet Season

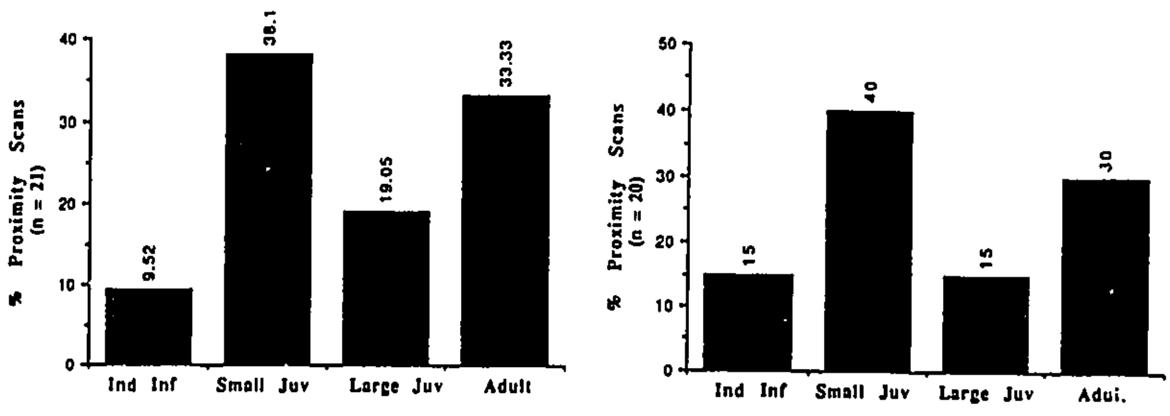
LV Group: Wet Season



CP Group: Dry Season

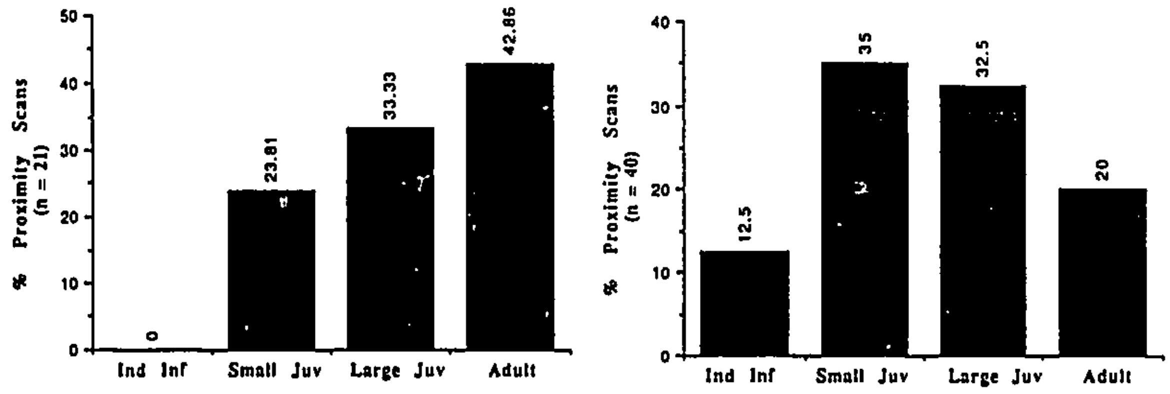
LV Group: Dry Season

Fig. 3.2. Small Juveniles as Focal Animals
Distribution of nearest neighbors by age class when small juvenile individuals are the focal animal. Data are taken from proximity scans at the beginning of each ten-minute focal sample. The number of observations for each social group and season are given in parentheses along the y-axis of each bar graph. Dependent infants were excluded due to closer proximity to their mothers.



CP Group: Wet Season

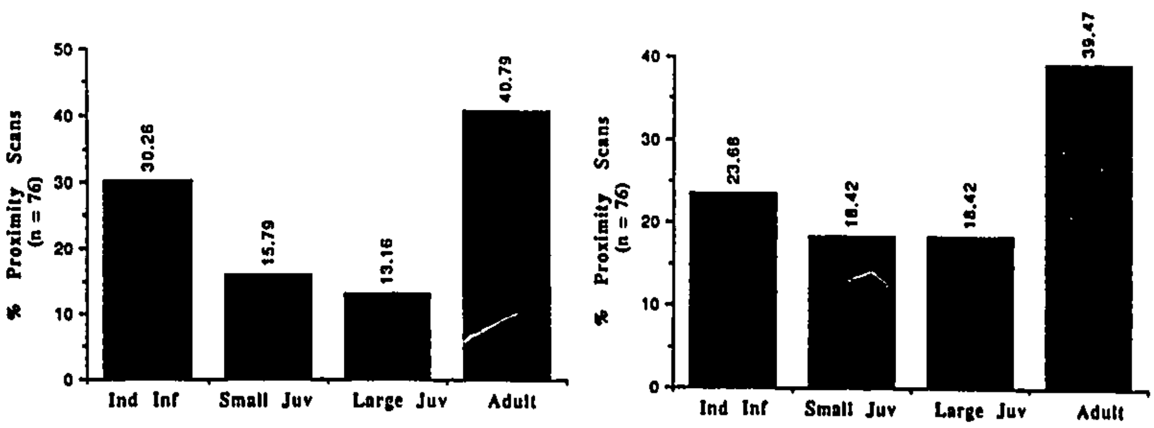
LV Group: Wet Season



CP Group: Dry Season

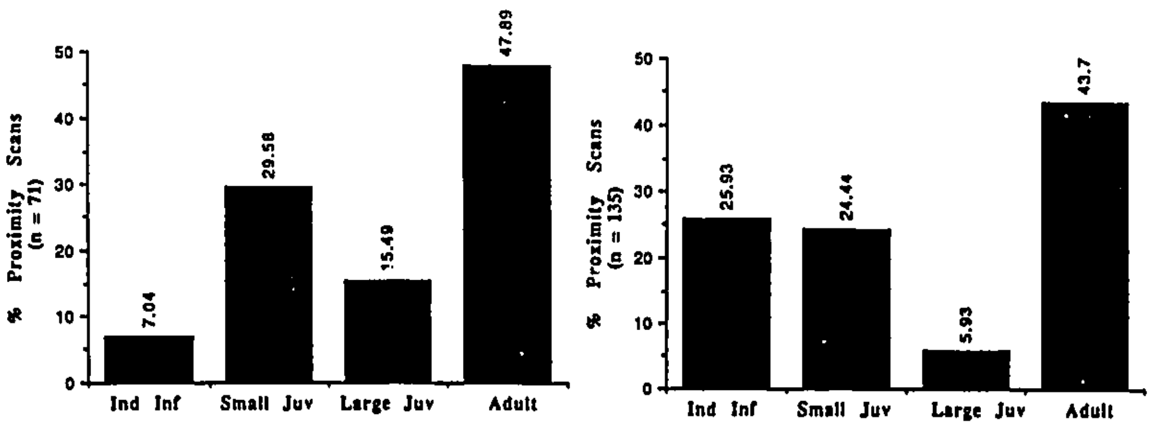
LV Group: Dry Season

Fig. 3.3. Large Juveniles as Focal Animals
Distribution of nearest neighbors by age class when large juvenile individuals are the focal animal. Data are taken from proximity scans at the beginning of each ten-minute focal sample. The number of observations for each social group and season are given in parentheses along the y-axis of each bar graph. Dependent infants were excluded due to closer proximity to their mothers.



CP Group: Wet Season

LV Group: Wet Season



CP Group: Dry Season

LV Group: Dry Season

Fig. 3.4. Adults as Focal Animals
Distribution of nearest neighbors by age class when adult individuals are the focal animal. Data are taken from proximity scans at the beginning of each ten-minute focal sample. The number of observations for each social group and season are given in parentheses along the y-axis of each bar graph. Dependent infants were excluded due to closer proximity to their mothers.

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# CHAPTER 4

## Discussion and Conclusion

In this thesis, I examine two aspects of the behavioral ecology of white-faced capuchin monkeys. First, I discuss age differences in foraging in terms of feeding behaviors, foods eaten, substrates used, and location in canopy. Foraging behavior is broken down into these four categories, so that the effects of age class differences can be examined more closely. Second, I look at the age class spatial association patterns of the two study groups, with particular attention to how nearest neighbor preferences change as individuals grow older. The overall conclusion of this thesis is that individuals in the four age classes (independent infant, small juvenile, large juvenile and adult) act differently, and associate with members of the group differently, due to varying levels of development and skill.

Chapter two presents evidence that some differences in foraging behavior can best be explained by developmental factors. Specifically, the frequency rates of the feeding behavior EXPLORE showed a tendency to decrease ontogenetically from independent infant to adult. Also, infants had a tendency to make more mistakes while foraging (e.g. higher rates of GRAB AND MISS and lower rates of EAT), suggesting that efficient foraging skills do not become fully developed until older age class stages. Other behaviors, however, were contradictory to the initial predictions. For example, complex behaviors were not always performed more often by older and more experienced individuals (e.g. BREAK OPEN WITH HANDS AND/OR MOUTH, PROBE, AND CARRY IN HANDS AND/OR MOUTH). Do individuals develop these complex foraging skills along a consistently straight trajectory? The findings from this study suggest not. Rather, an accumulation of varying foraging skills is most likely acquired through inconsistent "trial and error" as well as observational learning. These findings also suggest that *Cebus capucinus* juveniles are complex foragers from a young age, even if certain behaviors are not yet refined (e.g. PROBE).

In chapter three I examine the differences in spatial association patterns across the four age classes (independent infant, small juvenile, large juvenile and adult), and consider the reasons for preferred nearest neighbors, based on age class. Based on initial subjective observations, I predicted that individuals would congregate with same-age group members, forming "peer groups". This was found to be true with small juveniles and adults in the present study. As trends in seasonal differences were not found, I looked to social factors to explain this preference. After dependent infants were excluded from analyses, adults had other adults as nearest neighbors more often than the other age classes. In a "female-bonded" species, such as capuchins (Wrangham, 1980), long-term relationships are formed and maintained between the adult females of the social group. Males and females also form long-term relationships, and the alpha male is usually a preferred grooming and resting partner.

Small juveniles congregated with same-age group members in both groups and both seasons. Young individuals in the social group are attracted to each other for play bouts, resting sessions, and foraging activities, and the small juveniles in this study were consistently within nearest neighbor range to other small juveniles more often than to other age classes. This finding is consistent with past studies of another *Cebus* species (e.g. *Cebus olivaceus*, Fragaszy, 1986; Robinson, 1981; O'Brien and Robinson, 1993).

This study suggests that age class differences are apparent in certain aspects of foraging behavior and spatial association patterns present in white-faced capuchins. Some interesting questions arise from these results: What role do individual differences play in the acquisition of foraging skills? How do local conditions affect the rates of food types eaten, substrates used, and locations used in the canopy? How do individual preference and past relationship history affect the nearest neighbor associations? How do the spatial association patterns differ in varying contexts? Further research is needed to address these issues.

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## APPENDIX 1. Definitions of Feeding Behavior Categories

**Break Open With Hands/Mouth** = An animal breaks open a twig, branch, seed, pod, etc. with its hands or mouth, in order to look for, and possible eat, a food item inside.

**Carry in Hands/Mouth** = An animal carries an object in hands or mouth while moving from one location to another.

**Eat** = An animal ingests a food item or other solid material.

**Explore** = The focused, deliberate and intense searching of a specific substrate for a potential food item.

**Grab** = An animal reaches out and manually takes a food item from a substrate with a rapid movement of the hands. Usually done when capturing insects or other rapidly moving prey items.

**Grab and Miss** = The same initial behavioral sequence as "grab", except that the intended prey is missed and not captured.

**Pick Out With Fingers/Mouth** = An animal uses its fingers or mouth to pick out an embedded food item to eat, such as larvae inside a branch or insects within a tree crevice.

**Poke** = An animal pokes an extended finger at an object, usually touching the object.

**Probe** = An animal uses its fingers or hands to search for a potential food item. This is often done by putting fingers, hands or arms up into tree holes and cervices to search for bird nests, tree cockroaches, etc.

**Smell** = An animal smells a food item by moving its head to the item or by bringing the item to the nose by hand.

**Tap** = An animal uses its finger/s to tap against some part of the substrate. This is usually done on dead branches, where the animal is presumably looking for hollow areas with larvae inside (similar to the aye-aye).

**Unroll** = An animal unrolls leaves with its hands, looking for insects or larvae to eat.

**Visual Forage** = An animal visually inspects the habitat. This may include some body movement and turning of the head.

## APPENDIX 2. Definitions of Food Type Categories

**Small Fruit** = A fruit that requires no processing before eating; up to 3 cm in length.

**Medium Fruit** = A fruit that requires some processing before eating; up to 6 cm in length.

**Large Fruit** = A fruit that requires processing before eating; larger than 6 cm in length. Usually requiring both hands to carry and/or process.

**Small Insect** = An insect that is quickly procured and eaten, usually with one hand. Size: roughly to 3 cm in length (e.g. ant, termite).

**Medium Insect** = An insect that is larger than "small insect" and smaller than "large insect". Size: roughly 3-6 cm (e.g. katydid, cricket).

**Large Insect** = An insect that often requires both hands to capture and process. Size roughly larger than 6 cm (e.g. tree cockroach, walking stick).

**Larvae** = Insect larvae of any kind; usually embedded in a substrate (e.g. dead branch).

**Acorns** = The acorns from oak trees (*Quercus oleoides*) during the wet season.

**Caterpillars** = A favorite capuchin food item during the (caterpillar) population explosions during the wet season.

## APPENDIX 3. Definitions of Substrate Categories

**Acacia Branch** = Branches of *Acacia collinsii* or *A. cornigera.*

**Acacia Thorns** = The thorns of *A. collinsii* or *A. cornigera,* housing acacia ant larvae.

**Bark-Surface** = The surface area of bark on tree trunks or branches.

**Bark-Under** = Underneath the surface area of bark on tree trunks or branches.

**Small Dead Branch** = A section of a dead branch smaller in circumference than the forearm of the focal animal.

**Medium Dead Branch** = A section of a dead branch roughly equal in circumference than the forearm of the focal animal.

**Large Dead Branch** = A section of a dead branch larger in circumference than the forearm of the focal animal.

**Small Live Branch** = A section of a live branch smaller in circumference than the forearm of the focal animal.

**Medium Live Branch** = A section of a live branch roughly equal in circumference than the forearm of the focal animal.

**Large Live Branch** = A section of a live branch larger in circumference than the forearm of the focal animal.

**Dead Leaf** = A dead leaf, brown in color, dry, and often curled up.

**Green Leaf** = A living leaf, green in color.

**Inner Branch** = The first 1/2 of a tree branch extending from the tree.

**Terminal Branch** = The second 1/2 of a tree branch extending from the tree.

**Leaf Litter** = The carpet of leaves and debris on the forest floor, composed mostly of dead leaves.

**Tree Crotch** = Where two main branches come together at the trunk of a tree.

**Tree Hole** = A hole or hollowed out area on a tree branch or trunk, often containing something hidden from view.

**Tree Trunk** = The trunk of a tree.

**Wasp Nest** = The nest of a social wasp colony, usually containing larvae.

## APPENDIX 4. Definitions of Location Categories

**Ground** = On the forest floor.

**Lower Canopy-Inner Branch** = The first 1/2 of a tree branch extending from the tree, <3 m in height.

**Lower Canopy-Terminal Branch** = The second 1/2 of a tree branch extending from the tree, <3 m in height.

**Lower Canopy-Tree Crotch** = The point where two main branches come together at the trunk of a tree, <3m in height.

**Lower Canopy-Tree Trunk** = The trunk of a tree, <3m in height.

**Lower Canopy-Vines** = A cluster of vines, <3m in height.

**Middle Canopy-Inner Branch** = The first 1/2 of a tree branch extending from the tree, 3-10 m in height.

**Middle Canopy-Terminal Branch** = The second 1/2 of a tree branch extending from the tree, 3-10 m in height.

**Middle Canopy-Tree Crotch** = The point where two main branches come together at the trunk of a tree, 3-10 m in height.

**Middle Canopy-Tree Trunk** = The trunk of a tree, 3-10 m in height.

**Middle Canopy-Vines** = A cluster of vines, 3-10 m in height.

**Upper Canopy-Inner Branch** = The first 1/2 of a tree branch extending from the tree, >10 m in height.

**Upper Canopy-Terminal Branch** = The second 1/2 of a tree branch extending from the tree, >10 m in height.

## APPENDIX 5. Identified Food Items Eaten By the Study Groups During Feb. & Apr.-Sept. 1992

| FAMILY | SPECIES | PART EATEN |
|---|---|---|
| Anacardiaceae | *Spondias mombin* | fruit |
| Annonaceae | *Annona purperea* | fruit |
| Apocynaceae | *Stemmadenia obovata* | seeds |
| Araliaceae | *Sciadodendron excelsum* | fruit |
| Bignoniaceae | *Tabebuia ochracea* | seeds |
| Bromeliaceae | *Bromelia pinguin* | fruit/apicle meristem |
| Burseraceae | *Bursera simaruba* | larvae in branches |
| Cactaceae | *Hylocerius costaricense* | fruit/seeds |
| Cochlospermaceae | *Cochlospermum vitifolium* | flowers |
| Combretaceae | *Combretum farinosum* | flowers |
| Dilleniaceae | *Curatella americana* | fruit/seeds |
| Elaeocarpaceae | *Muntingia calabura* | fruit |
| Erythroxylaceae | *Erythroxylon havanense* | fruit |
| Euphorbiaceae | *Margaritaria nobilis* | fruit/seeds |
| Fabaceae | *Gliricidia sepium*<br>*Lonchocarpus sp.* | stems<br>fruit |
| Fagaceae | *Quercus oleoides* | fruit (acorns) |
| Flacourtiaceae | *Zuelania guidonia* | fruit |

| FAMILY | SPECIES | PART EATEN |
|---|---|---|
| Gramineae | ? | seeds |
| Malphigiaceae | *Bunchosia biosellata* | fruit |
| | *Byrsonima crassifolia* | fruit |
| Mimosaceae | *Acacia collinsii* | ant larvae (in thorns)/ fruit |
| | *Acacia cornigera* | ant larvae (in thorns)/ fruit |
| Moraceae | *Ficus sp.* | fruit |
| | *Chlorophora tinctoria* | fruit |
| Palmae | *Acrocomia vinifera* | fruit |
| Passifloraceae | *Passiflora vitifolia* | fruit |
| Rubiaceae | *Alibertia edullis* | fruit |
| | *Chomelia spinosa* | fruit/seeds |
| | *Genipa americana* | fruit |
| | *Guettarda macrosperma* | fruit |
| | *Psychotria carthaginensis* | fruit |
| Sapindaceae | *Dipterodendron costaricensus* | fruit |
| Sapotaceae | *Manilkara zapota* | fruit |
| Simaroubaceae | *Simarouba glauca* | fruit |
| Solanaceae | *Solanum hazenii* | fruit |
| Theophracinaceae | *Jacquinia pungens* | fruit |
| Tiliaceae | *Apeiba tibourbou* | fruit |
| | *Luehea candida* | seeds |
| | *Luehea speciosa* | seeds |
| Ulmaceae | *Trema micrantha* | fruit |

OTHER:

Anole lizard (*Norops sp.*)

Ant larvae from *Acacia collinsii* and *Acacia cornigera*

Ants (from a ground nest)

Caterpillars

Common ground dove (*Columbina passerina*)

Crickets

Giant tree cockroaches (*Blaberus giganteus*)

Grasshoppers

Guanacaste walking sticks (*Calynda bicuspis*)

Katydids

Large insects (unidentified)

Larvae from dead branches

Larvae from live terminal branches (i.e. *Bursera simarouba*)

Pacific screech owl (*Otus cooperi*)

Scorpions

Small insects (unidentified)

Tree squirrel (*Sciurus variegatoides*)

Tree snail

Wasp larvae from nests (i.e. paper wasps: *Polistes sp.*)

White-throated magpie jay eggs (*Calocitta formosa*)

## APPENDIX 6. Identified Food Items Eaten By the Study Groups During Jan.-Apr. 1993

| FAMILY | SPECIES | PART EATEN |
|---|---|---|
| Anacardiaceae | *Spondias radlkoferi* | fruit |
| | *Spondias purperea* | fruit |
| Annonaceae | *Annona reticulata* | fruit |
| | *Annona purperea* | fruit |
| Burseraceae | *Bursera simaruba* | fruit |
| Caesalpinaceae | *Cassia biflora* | flower |
| | *Cassia farnesia* | fruit/ seeds |
| Combretaceae | *Combretum farinosum* | flowers |
| Dilleniaceae | *Curatella americana* | fruit/ seeds |
| Elaeocarpaceae | *Muntingia calabura* | fruit |
| | *Slonea terniflora* | fruit |
| Fabaceae | *Enterolobium cyclocarpum* | insect larvae in fruit |
| Gramineae | ? | seeds |
| Meleaceae | *Cedrella mexicana* | seeds |
| Mimosaceae | *Acacia collinsii* | fruit/ ant larvae |
| | *Acacia cornigera* | fruit/ ant larvae |
| Moraceae | *Ficus sp.* | fruit |
| Palmae | *Acroconia vinifera* | fruit |

| FAMILY | SPECIES | PART EATEN |
|---|---|---|
| Rubiaceae | *Alibertia edullis* | fruit |
| | *Randia echinocarpa* | fruit |
| Sapindaceae | *Dipterodendron costaricensus* | fruit |
| Simaroubaceae | *Simarouba glauca* | fruit |
| Theophracinaceae | *Jacquinia pungens* | fruit |
| Tiliaceae | *Luehea candida* | seeds |
| | *Luehea speciosa* | seeds |
| Verbenaceae | *Lantana camara* | fruit |
| | *Psidium guajava* | fruit |
| | *Karwinskia calderoni* | fruit |
| | *Lysiloma sp.* | fruit |

OTHER:

Ant larvae from *Acacia collinsii* and *Acacia cornigera*

Ants (from a ground nest)

Caterpillars

Climbing rat (*Ototylomys phyllotis*)

Crickets

Giant tree cockroaches (*Blaberus giganteus*)

Grasshoppers

Guanacaste walking sticks (*Calynda bicuspis*)

Katydids

Large insects (unidentified)

Larvae from dead branches

OTHER:

Larvae from live terminal branches (i.e. *Bursera simarouba*)

Roadside hawk eggs from nest (*Buteo magnirostris*)

Scorpions

Small insects (unidentified)

Spiny pocket mouse (*Liomys salvini*)

Tree squirrel (*Sciurus variegatoides*)

Tree snail

Wasp larvae from nests (i.e. paper wasps: *Polistes sp.*)

White-throated magpie jay hen (*Calocitta formosa*)

## APPENDIX 7. Definitions of *Cebus capucinus* Age Classes

**Dependent Infant** = Individuals aged birth to 6 months; the smallest members in the social group. For the first two months of life, the infant's coat color is dark overall, without the sharp contrast of dark and light fur that characterizes this species. During this period, the infant is carried by it's mother and is dependent on her for food, travel, etc. The infant may crawl off of her, explore its surroundings, and interact with other group members (infants are often carried by other individuals in the social group).

**Independent Infant** = Individuals aged six months to one year. Larger than dependent infants, but smaller than small juveniles. Independent infants are no longer dependent on their mothers for food and travel, although they often return to nurse. During this stage, individuals begin to actively explore the surrounding environment (in terms of social interactions as well as in a foraging context). Their faces are usually light in color and free of marks, scars, discolorations, etc.

**Small Juvenile** = Individuals aged one to three years. Larger than independent infants, but smaller than large juveniles. These individuals are extremely active and curious, and are able to obtain all of their nutritional requirements from the surrounding habitat. Like independent infants, small juveniles usually lack the distinguishing facial marks that are commonly seen in older individuals (i.e. scars, discoloration, etc.).

**Large Juvenile** = Individuals aged three to five years. Larger than small juveniles, yet lacking the robust body morphology of fully matue adults (thus, limbs appear disproportionally long).

**Adults** = Individuals aged five years and older. Adults are the largest animals in the social group, with a robust body morphology. At this stage differences between the sexes are extremely apparent (i.e. adult females often have noticible hairs on their brows and foreheads, while adult males are filled out and slightly more muscular). Distinguishing facial characteristics are also apparent.