7-1-2012

Feeding Ecology and Life History Strategies of White-faced Capuchin Monkeys

Elizabeth Eadie

Follow this and additional works at: http://digitalrepository.unm.edu/anth_etds

Part of the Anthropology Commons

Recommended Citation
Elizabeth C. Eadie

Candidate

Anthropology

Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

Jane B. Lancaster, Chairperson

Hillard Kaplan

Astrid Kodric-Brown

Susan Perry

Melissa Emery Thompson
FEEDING ECOLOGY AND LIFE HISTORY STRATEGIES OF WHITE-FACED CAPUCHIN MONKEYS (*CEBUS CAPUCINUS*)

by

ELIZABETH C. EADIE

B.S., Biology and Anthrozoology, University of Michigan, 2003
M.S., Anthropology, University of New Mexico, 2006

Dissertation

Submitted in Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy
Anthropology

The University of New Mexico
Albuquerque, New Mexico

August 2012
Dedication

For my mom, dad, James, and Yann
ACKNOWLEDGMENTS

There are many people who I would like to thank for their help with this dissertation. First, I would like to thank my advisor Jane Lancaster for all of her guidance and support throughout graduate school. Her levels of insight and knowledge are truly inspirational. I would also like to thank Jane and the rest of my committee members, Hillard Kaplan, Astrid Kodric-Brown, Susan Perry, and Melissa Emery Thompson, for helping me to refine this manuscript as well as my numerous funding proposals. Each of these people has provided me with invaluable advice and guidance.

I would like to thank my mother Deborah Eadie for reading and editing just about everything I ever wrote while in graduate school, including multiple revisions of each part of this dissertation. I would like to thank both my mother, father, and brother for all of their emotional and financial support throughout my many years of schooling. This support helped make school much more fun and less stressful than it otherwise would have been.

Yann Klimentidis is another person who has helped me with every part of my life throughout graduate school. I feel extremely lucky to have you in my life.

I had several amazing field assistants, without whom I could not have completed this project. My first field assistant, Laura Zdunek, helped me with huge parts of this project and was a wonderful and fun companion in the field. Karol Cano Comancho and Elodie Chaverou were also instrumental in completing important parts of this study. Kristin Sabbi made me laugh throughout the last two months of data collection in the field and was a perfect final field assistant for this project.
Dr. Nancy Conklin Brittain helped me with all steps of the nutritional analysis part of this project, from applying for permits, collection methods, training me to do the actual analyses, and interpreting the results. It was a joy to be trained by Nancy.

I owe a special thanks to several people associated with the Pacuare Nature Reserve. The director of the Pacuare Nature Reserve, Carlos Fernandez Alfaro, allowed me to conduct my field work there and made sure that I had everything that I needed. Along with Carlos, Arturo Fernandez Alfaro, Danilo, and Ana Garcia made my time in Costa Rica special.

I would like to thank Lisa Rapaport for comments and editing for Chapter 2. Megan Workman also read and commented on parts of this document, visited me in the field, brought much appreciated food entertainment, and has been an all-around amazing friend.

Glenn Stark, Yong Lin, David Reed, and Paul Hooper provided crucial help and advice with statistics.

The following sources provided funding for this project: The National Science Foundation: DIG-0925843, The Leakey Foundation Grant, and from a Sigma Xi Grants-in-Aid-of-Research: G200710101136267644, The University of New Mexico Office of Graduate Studies and Graduate Program Student Associations.

Lastly, thank you to my wonderful friends in Albuquerque and beyond for making these years so fun: Kendra Pesko and Dave Melius, Chris Brown, Susan Stevens and Brian Adams, Kristin Snopkowski, Kathryn Lenberg and Mike Petty, Bonnie Young, Meghan Healy, Helen Davis, and Teresa Hammer.
FEEDING ECOLOGY AND LIFE HISTORY STRATEGIES OF WHITE-FACED CAPUCHIN MONKEYS (*CEBUS CAPUCINUS*)

By

Elizabeth C. Eadie

B.S., Biology and Anthrozoology, University of Michigan, 2003

M.S., Anthropology, University of New Mexico, 2006

Ph.D., Anthropology, University of New Mexico, 2012

Abstract

Dietary niches have widespread effects on individuals’ life histories, behaviors, and morphologies. Capuchin monkeys inhabit a complex dietary niche that often entails hunting of relatively large vertebrate prey, tool-use, and extraction of embedded resources that other closely related and sympatric species do not exploit. In this dissertation I examine, a) how juvenile capuchins overcome the challenges of reliance on a difficult-to-acquire diet, b) at what age juveniles achieve maximum foraging return rates for difficult-to-acquire foods, and c) what nutritional benefits capuchins obtain from exploitation of these foods. In the process of addressing these questions I test two prominent hypotheses regarding reliance on a difficult-to-acquire diet. First, I test two predictions form the food scarcity/difficulty hypothesis which posits that species who rely more heavily on foods that are either rare or difficult to acquire should exhibit higher rates of food transfers, because juveniles in these species face greater foraging
challenges. Second, I test two predictions from the ecological complexity hypothesis which proposes that species that rely on more difficult-to-acquire foods require longer juvenile periods, in order to learn the skills necessary to exploit these foods. Foraging return rates and rates of food transfers were calculated for individuals in three groups of wild capuchin monkeys inhabiting the Pacuare Nature Reserve in Costa Rica. Foraging return rates were measured in terms of bites ingested per forage time. In addition, food items were analyzed for nutritional content which enabled calculations of nutrient return rates. The major results include: 1) food transfer rates were highest in infants, and food items that were more difficult to acquire and had more nonstructural carbohydrates were transferred more frequently; 2) juvenile foraging strategies for difficult-to-acquire foods can be distinguished from adult strategies; 3) maximum foraging efficiency was not achieved until well into adulthood for difficult-to-acquire fruits. These findings support the food difficulty hypothesis regarding food transfers and the ecological complexity hypothesis regarding long juvenile periods. A final goal for this study was to evaluate the benefits of foraging for difficult-to-acquire foods. Results imply the most likely benefit accrued from difficult-to-acquire foods is as a source of fallback nutrients.
# Table of Contents

Chapter 1: Introduction .................................................................................................................. 1

Feeding ecology and life history ................................................................................................. 1

Capuchins .................................................................................................................................... 2

Theoretical Background ............................................................................................................. 3

Study site ..................................................................................................................................... 8

Population .................................................................................................................................... 9

Outline of dissertation ............................................................................................................... 10

Chapter 2: Food transfers in capuchin monkeys (*Cebus capucinus*): a test of the food difficulty hypothesis .......................................................................................................................... 12

Abstract ....................................................................................................................................... 12

Introduction .................................................................................................................................. 13

Hypotheses and Predictions ........................................................................................................ 20

Methods ....................................................................................................................................... 21

Results .......................................................................................................................................... 32

Discussion .................................................................................................................................... 41

Chapter 3: Feeding strategies for difficult-to-acquire foods in juvenile capuchin monkeys (*Cebus capucinus*) ........................................................................................................................................ 44

Abstract ....................................................................................................................................... 44

Introduction .................................................................................................................................. 45
Hypotheses and Predictions ................................................................. 49
Methods ............................................................................................. 50
Results ............................................................................................... 55
Discussion .......................................................................................... 69

Chapter 4: A Test of the Ecological Complexity Model for Long Juvenile Periods in White-faced Capuchin Monkeys (Cebus capucinus) ............................................................. 73
Abstract ............................................................................................. 73
Introduction ....................................................................................... 74
Predictions ......................................................................................... 81
Methods ............................................................................................. 82
Results ............................................................................................... 88
Discussion .......................................................................................... 100

Abstract ............................................................................................. 105
Introduction ....................................................................................... 106
Hypotheses ......................................................................................... 109
Methods ............................................................................................. 110
Results ............................................................................................... 117
Discussion .......................................................................................... 130
Chapter 6: Conclusions ................................................................. 137
References .................................................................................. 142
List of Figures:

Figure 2.1: Food Transfer Recipient Rates by Age Class ................................................. 34
Figure 3.1: Proportion of Oil Palm Fruits Harvested from the Ground .............................. 56
Figure 3.2: Bite Rates from Tree Compared to Ground Harvesting ................................. 58
Figure 3.3a: Proximity for DtA Foods .................................................................................. 60
Figure 3.3b: Proximity for EtA Foods .................................................................................. 60
Figure 3.4a: Bite Rate for DtA Foods When In or Not In 1m Proximity of Other Individuals .............................................................. 63
Figure 3.4b: Bite Rate for EtA Foods When In or Not In 1m Proximity of Other Individuals ........................................................................................................ 63
Figure 3.5a: Proportion of Forage Scans Devoted to Easy Fruits by Sex and Age Class 66
Figure 3.5b: Proportion of Forage Scans Devoted to Medium Fruits by Sex and Age Class ........................................................................................................................................ 66
Figure 3.5c: Proportion of Forage Scans Devoted to Hard Fruits by Sex and Age Class 66
Figure 3.5d: Proportion of Forage Scans Devoted to Surface Insects by Sex and Age Class .......................................................................................................................................... 67
Figure 3.5e: Proportion of Forage Scans Devoted to Embedded Insects by Sex and Age Class ........................................................................................................................................ 67
Figure 4.1: Activity Budgets by Age Class .......................................................................... 89
Figure 4.2: Foraging Time Allocation by Sex and Age Class .............................................. 90
Figure 4.3a: Return Fates for DtA vs. EtA Fruits ................................................................. 92
Figure 4.3b: Hard Fruit Return Rates with Adult Age Classes .......................................... 92
Figure 4.4a: Return Rates for EtA Fruits ............................................................................ 94
Figure 4.4b: Easy Fruit Return Rates with Adult Age Classes................................................. 95
Figure 4.5a: Return Rates for Embedded Insects................................................................. 96
Figure 4.5b: Return Rates for Surface Insects ................................................................. 96
Figure 4.6: Correlation between Skill and Strength Levels for Fruits................................. 98
Figure 4.7: Return Rates for DtA Fruits: Adult Males, Adult Females, and Subadult Females .................................................................................................................................................................................. 99
Figure 5.0: Dry Weight by Difficulty Level ........................................................................... 118
Figure 5.1: Fruit Return Rates by Age Class and Difficulty Level .................................... 119
Figure 5.2: Insect Return Rates by Age Class ..................................................................... 121
Figure 5.3a: Adult Return Rates by Difficulty Level ............................................................ 123
Figure 5.3b: Juvenile Return Rates by Difficulty Level ......................................................... 123
Figure 5.4: Anti-Nutrient Content by Difficulty ................................................................. 127
Figure 5.5a: Fruit Availability ............................................................................................. 129
Figure 5.5b: Proportion of Forage Observations on Different Food Types by Month ... 129
List of Tables

Table 1-1: Distribution of Study Individuals By Age Class And Group Age Class........ 10
Table 2.1: Glossary ........................................................................................................... 25
Table 2.2: Food Difficulty Levels....................................................................................... 30
Table 2.3a: Observation Numbers for Each Type of Scrounge Behavior .................. 32
Table 2.3b: Distribution of Scrounge Behaviors across Age Classes............................ 32
Table 2.4a: Food Transfer Recipient Rates by Age Class ........................................... 33
Table 2.4b: Scrounge rates by age class .......................................................................... 33
Table 2.5: Change in Odds That a Food Item is Scrounged With Change in Difficulty Level ........................................................................................................................................... 36
Table 2.6: Nutritional Content of Foods Taken by Capuchins ........................................ 38
Table 2.7: Odds That a Food Item Will Be Involved in a Food Transfer to an Infant Dependent on Nutrient Content ........................................................................................................... 40
Table 3.1: Proportion of Oil Palm Fruits Harvested From the Ground (PGS) for Each Age Class .......................................................................................................................................................... 57
Table 3.2: Oil Palm Bite Rates for Tree Compared to Ground Foraging ....................... 59
Table 2.3: Proportion of Focal Follows Spent Within 1 Meter of Another Individual by Age Class And Food Difficulty Level ........................................................................................................... 61
Table 3.4: Comparison of Bite Rates For DtA and Eta Foods When In or Not In 1m Proximity of Other Individuals ............................................................................................................................... 64
Table 3.5: Proportion of Scan Samples Spent on Each Food Type by Age Class........... 68
Table 4.1: Bite Rate versus Age Class for DtA (top) and EtA (bottom) Fruits .............. 91
Table 4.2: Bite Rate versus Age Classes with Adults Divided by Estimated Age For DtA (Top) And EtA (Bottom) Fruits ................................................................. 93
Table 4.3: Hard Fruit Bite Rate Predicted by Harvest (above) and Process (below) Strength and Skill Levels ............................................................................. 98
Table 5.0: Fruit Dry Weight by Difficulty Level ..................................................... 119
Table 5.1: Fruit Bite Rate by Age Class and Difficulty Level ................................. 120
Table 5.2: Insect Return Rates by Type .................................................................. 121
Table 5.3: Adult Nutrient Return Rates by Difficulty Level ................................. 124
Table 4.4: Juvenile Nutrient Return Rates by Difficulty Level ............................ 125
Table 5.5: Anti-Nutrient Concentrations for EtA, MtA, and DtA Fruits ............... 127
Table 5.6: Correlations between Food Availability and Foods Eaten ................. 130
Chapter 1: Introduction

Feeding Ecology and Life History

Ultimately, organisms that are best able to harvest energy from the environment and utilize it to pass on their genes are the most successful. Each species has different strategies to accomplish this feat. For example, while some species of mammals obtain nutrients from relatively abundant food sources such as grass and leaves, and have specialized digestive systems to enable this strategy, others rely on foods that are less abundant and more difficult-to-acquire, but easier to digest. Species that occupy feeding niches that are more complex and variable may require a long learning phase before reaching maximum foraging efficiency (Kaplan et al., 2000; van Noordwijk and van Schaik, 2005; Lonsdorf, 2006; Gunst et al., 2010). For example, once chimpanzees and orangutans start to use tools, it appears to take several years before they achieve maximum proficiency (Lonsdorf et al., 2004; van Noordwijk and van Schaik, 2005). In white-winged choughs, who forage for invertebrates on the ground in soil and leaf litter, foraging efficiency increases from fledging through at least the first five years of life (Heinsohn et al., 1988). Growth rates during this learning phase may be slow (Janson and van Schaik, 1993; Leigh, 1994). Slow growth rates lead to long juvenile periods (Charnov and Berrigan, 1993). It is hypothesized that many salient human traits, such as our large brains, long juvenile periods, and tool use, are adaptations to a complex foraging niche (Parker and Gibson, 1977; Kaplan et al., 2000; Rapaport and Brown, 2008). Numerous inter-species comparisons examine which characteristics are correlated with dietary complexity (Harvey and Clutton-Brock, 1985; Barton, 1996; Walker et al.,
2006; Kaplan et al., 2007). However, currently few studies assess whether specific traits, which are correlated with a complex foraging niche, are direct adaptations for that foraging niche.

**Capuchins**

Capuchins share many analogous life history characteristics with humans and chimpanzees. The lineages of New World Monkeys from which capuchins evolved, and that of Old World Monkeys, from which chimpanzees and humans evolved, diverged approximately 40 million years ago (Purvis, 1995). Given this long time span between a last common ancestor and the present, and the fact that many primates do not share the traits that distinguish capuchins, chimpanzees, and humans from other primates, the traits that capuchins share with chimpanzees and humans are likely to have arisen through parallel or convergent evolution, whereby similar ecological situations resulted in similar adaptations, rather than stem from a common ancestor. For this reason, capuchin monkeys provide a unique and especially useful model to study the environmental and social factors that have selected for many of the human and chimpanzee traits that distinguish us and our closest living relatives from most other mammals and primates.

Traits shared by capuchins, chimpanzees and humans include: long juvenile periods (Harvey and Clutton-Brock, 1985; Ross, 1991); a diet of high nutrient, easily digested foods with a correspondingly small gut (Milton, 1987; Janson and Boinski, 1992; Hakeem et al., 1996; Leonard and Robertson, 1997); a proportionally large brain (Fragaszy et al., 1990; Hakeem et al., 1996; Hartwig, 1996; Rilling and Insel, 1999); long life spans (Harvey and Clutton-Brock, 1985); tool use (Boinski et al., 2000; Ottoni and
Izar, 2008); hunting of relatively large vertebrate prey (Rose, 1997), relatively altricial young (Fragaszy, 1990); and substantial behavioral differences across sites for foraging behaviors (Chapman and Fedigan, 1990; Panger et al., 2002); and for social interactions and conventions (Perry et al., 2003; Perry, 2011).

The ecological factors that selected for these traits are still debated and not well-understood (Ross and Jones E., 1999; Deaner et al., 2003; Kappeler et al., 2003). This dissertation focuses on how a complex dietary niche affects capuchins, especially juveniles, by investigating whether certain life history, behavioral, and morphological adaptations could have evolved in response to this niche. Inhabitance of a complex dietary niche is likely to have an especially large impact on juveniles because they are weaker and have less experience than their adult counterparts (Janson and van Schaik, 1993; Altmann, 1998). Research on how individuals in this dietary niche acquire food at different ages will reveal which strategies enable juveniles to attain their nutrient requirements. Given the numerous life history, behavioral, and morphological parallels between humans and capuchins, the associations between a complex dietary niche with specific behaviors and adaptations in capuchins, are likely to have analogous forms in humans.

**Theoretical Background**

Although the ecological factors that have selected for the suite of traits shared by humans and capuchins are not well-understood, the theoretical bases for the correlations between some of these traits are well-established (Gadgil and Bossert, 1970; Charnov and Berrigan, 1993; Ross and Jones E., 1999). Life History Theory provides an explanation
for how and why many life history and morphological traits are likely to coevolve, based on the premise that organisms have a finite amount of energy to spend on three basic investments throughout life: growth, reproduction, and maintenance. Life History Theory describes how organisms maximize their fitness by adjusting the amount of energy put toward each of these three investments according to age and condition (Gadgil and Bossert, 1970). From this, Life History Theory proposes that life stage events such as the length of gestation, age at weaning, age at first birth, and lifespan, are timed to maximize an organism’s fitness. Since energy that is spent on one investment cannot be used for another, organisms face a series of tradeoffs for how to budget their energy.

The Embodied Capital Theory of Evolution expands on the three categories on which energy can be spent (growth, maintenance, and reproduction) to include skill and knowledge as components of an organism’s “embodied capital” (Kaplan et al., 2001). This addendum helps to clarify why species that live in more complex dietary niches may require longer juvenile periods: energy that is used to acquire skill and knowledge is energy that cannot be used for physical growth. In certain ecological contexts, greater levels of skill and knowledge can improve reproductive success by leading to higher energy capture rates, higher survival probabilities, and higher reproductive rates. The acquisition of skill and knowledge is especially important during the juvenile period when youngsters must learn how to become proficient adults.

The foraging ecologies of both humans and capuchins are likely to require more investment into learning and skill acquisition than that of other, closely-related species. Humans and capuchins are known to exploit a wide variety of dietary items that are difficult to obtain, and that other, closely related species do not eat (Kaplan et al., 2000;
Fragaszy et al., 2004 c). Often these are energy-rich food sources such as the storage and reproductive organs of plants that are protected in some manner (Fragaszy et al., 2004 c). For example, capuchin monkeys are known to frequently exploit foods with elaborate defense mechanisms such as items with spines or thorns, biting or stinging insects, or food encased in hard shells (Fragaszy et al., 2004 c). Two additional characteristics that distinguish capuchin foraging from many other nonhuman primates, but are common in humans and chimpanzees, are vertebrate predation and object or tool use (Boesch and Boesch, 1990; Rose, 1997; van Schaik et al., 1999; Ottoni and Mannu, 2001; Fragaszy et al., 2004 a). Hunting, tool-use, and extractive foraging are all behaviors that require more skill, and are hypothesized to entail a higher investment into learning, than more common primate foraging behaviors such as leaf-eating and non-extractive fruit foraging.

Several of the traits mentioned in the previous paragraphs are highly correlated (Harvey and Clutton-Brock, 1985; Charnov, 1991; Charnov and Berrigan, 1993). A large brain relative to body size is correlated with a high-quality diet (Clutton-Brock and Harvey, 1980; Aiello and Wheeler, 1995; Barton, 1996; Kaplan et al., 2007; Hartwig et al., 2011) and long juvenile periods are correlated with long life spans (Promislow and Harvey, 1990; Charnov and Berrigan, 1993). The juvenile period can be defined as the period from when a youngster first becomes nutritionally independent, until the onset of reproduction (Pagel and Harvey, 1993; Blurton Jones et al., 1999). During this time period a young monkey must be able to locate, harvest and process enough food to survive, acquire skills for adulthood, and grow to adult size. Ecological and phylogenetic differences will determine how energy allocation into each of these investments maximizes fitness. For example, organisms with short life spans and high adult mortality
will generally maximize their reproductive success by starting to reproduce at an early age (Reznick, 1990; Charnov and Berrigan, 1993; Ross and Jones E., 1999). In addition, organisms that do wait a long time to begin reproducing can often maximize fitness by investing more energy into growth and maintenance, thereby increasing the lifespan and allowing more time to reap the benefits of their earlier investment into somatic growth and embodied capital (Kaplan and Robson, 2002; Jones, 2011). These relationships help to explain the correlation between long juvenile periods and long lifespans. A consequence of this correlation is that insight on factors that select for long juvenile periods, simultaneously provide insight into factors that select for long lifespans (Charnov and Berrigan, 1993).

Another well-studied correlation is between diet quality and relative brain size. A high-quality diet can be defined as a diet that provides a large quantity of nutrients without requiring a long time or a large amount of energy to digest (Gaulin, 1979; Chivers and Hladik, 1980; Sailer et al., 1985). High-quality diets, thus, have high net nutrient return rates. Organisms with high-quality diets do not spend as much energy on digestion. Some of the energy that would have been spent on digestion may then be available for other things such as higher reproductive rates or extra brain tissue (Aiello and Wheeler, 1995). High-quality diets are probably necessary to provide steady sources of glucose in the quantities required for large brains (Fish and Lockwood, 2003; Milton, 2003).

Even with a high-quality diet, large brains are metabolically expensive and would only be expected to evolve in organisms where they provide an advantage in fitness that outweighs their high metabolic cost. High-quality foods are less abundant in the
environment than lower-quality foods (Gaulin, 1979) thus, larger organisms that rely on high-quality diets must either take advantage of high-quality foods that other species do not eat, travel further distances to acquire enough high-quality food, or both. Larger brains may enable more efficient foraging of the types of high-quality foods that other species cannot exploit efficiently, and could therefore provide a selective advantage in larger species who rely on high-quality diets for digestive reasons (Parker and Gibson, 1977; Byrne, 1999). On the other hand, small organisms relying on high-quality foods would not receive the same benefits from big brains because they do not need to procure large quantities of these foods. Smaller organisms also have higher weight-specific metabolisms (Kleiber, 1975) and thus, additional metabolic costs imposed by extra brain tissue would have proportionately greater costs. Given this cost/benefit profile of larger brains, smaller organisms may increase fitness more by spending extra energy afforded by a high-quality diet on higher reproductive rates.

In summary, larger organisms that rely on high-quality diets should benefit from larger brains if those brains help them meet their nutritional requirements. Across species, proportionately large brains are associated with long juvenile periods and reliance on a difficult-to-acquire diet (Clutton-Brock and Harvey, 1980; Harvey and Clutton-Brock, 1985; Barton, 1996). The energy that is used to fuel the growth and maintenance of a large brain is energy that cannot be used for the growth of the rest of the body. This shift in energy allocation may explain part of the reason why species that have large brains relative to their body size, also tend to have long juvenile periods. In addition, proportionately large brains are associated with difficult-to-acquire diets. Difficult-to-acquire diets are likely to require greater investments into skill and learning, further
resulting in a shift in energy away from body growth. A greater understanding of the energetic costs and benefits associated with reliance on a difficult-to-acquire diet is likely to unveil clues about the interrelationship between long juvenile periods, a large brain size, and a difficult-to-acquire diet.

**Study Site**

The Pacuare Nature Reserve is located in the Limón Province of Costa Rica, 25 km north of the province capital city, Puerto Limón (10°10’N, 83°14’W). The reserve is bordered on the east by the Atlantic Ocean and on the west by the Tortuguero canal. The reserve consists of 800 ha (1,977 acres) of primary and secondary, tropical wet, lowland forest. There is no dry season in this region, but the months of September and October typically receive less rain (≈160-200 mm), while November, December, and July usually receive the most rain (≈360-400mm) (Pool et al., 2007, www.weather-and-climate.com).

Three primate species inhabit the reserve: *Cebus capucinus*, *Alouatta palliata* (mantled howler monkeys), and *Ateles geoffroyi* (black-handed spider monkeys). The land is owned by the English Charity, *The Endangered Wildlife trust*. The reserve was established for the protection of endangered sea turtles which continues to be its main focus. The six kilometers of beach adjacent to the reserve (beaches are public property in Costa Rica) are an important nesting site for three species of sea turtles. The reserve has two research stations, one at the southern end and one at the northern end. The research stations are connected by a trail that runs through the forest, parallel to the beach. Between 2005 and 2010, I cut and maintained approximately five kilometers of smaller trails throughout the home ranges of the three capuchin study groups.
Population

There are between four and twelve recognized species of capuchins (Fragaszy et al., 2004 c; Lynch Alfaro et al., 2011). White-faced capuchin monkeys, Cebus capucinus, are the only species of capuchin found in Central America. The study population consisted of three groups of white-faced capuchin monkeys inhabiting the southern portion of the Pacuare Nature Reserve. I began to identify and habituate these monkeys in August of 2005. Prior to this, the group whose home range is located closest to the south research station, was somewhat habituated to human presence, but had not been formally studied. The other two groups had only seen humans when they happened to be near the main trail when a research assistant or guard passed by, and were not at all habituated. By the fall of 2009 I had spent approximately seven months on pilot studies, habituation, and identification, and most study individuals were comfortable with three-to-five meter observation distances. Data were collected on a total of 49 individuals between October of 2009 and August of 2010. The distribution of ages within each group is presented in Table I. 
Table I: Distribution of Study Individuals By Age Class And Group Age Class

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Infants (0-1 year)</th>
<th>Younger Juveniles (1-3 years)</th>
<th>Older Juveniles (3-5 years)</th>
<th>Subadults (5-7 years)</th>
<th>Adult Females (7+ years)</th>
<th>Adult Males (7+ years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>B</td>
<td>3*</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>6*</td>
</tr>
<tr>
<td>C</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>6</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>15</td>
<td>12</td>
</tr>
</tbody>
</table>

* Group B went through a takeover in May 2010 whereby two of the four adult males were replaced by two outside adult males. The other two adult males remained associated with group B. All three infants went missing at this time and were assumed victims of infanticide.

Outline of Dissertation

In this dissertation I will test predictions from the ecological complexity hypothesis and food difficulty/scarcity hypothesis. As is predicted by the ecological complexity and embodied capitol hypotheses, one goal of this study was to examine whether reliance on difficult-to-acquire foods could have selected for a long juvenile period, due to requiring long periods of skill development. Given that factors which select for a long juvenile periods will often co-select for a long lifespan, results from these analyses will have implications for both long juvenile periods and long lifespans.

The food scarcity/difficult hypothesis proposes that species relying on foods that are more difficult-to-acquire and/or rarer, will exhibit higher rates of food transfers, because in these species juveniles should have more trouble obtaining their own food. In a test of this hypothesis, I examine whether acquisition of food, through transfers from one individual to another, are associated with age and the level of difficulty that is required to obtain food items. A related goal of this study was to investigate the ontogeny
of foraging in capuchin monkeys. Specifically, I explore how immature individuals, who are weaker and less-experienced than adults, acquire nutrients within their complex dietary niche.

After examining the effects of reliance on difficult-to-acquire foods, I realized that another interesting topic has to do with why capuchins exploit these types of foods in the first place. Therefore, a final goal of this dissertation was to investigate how capuchins benefit from exploitation of difficult-to-acquire foods. Because reliance on a difficult-to-acquire diet is associated with a long juvenile periods and proportionately large brains, information on why capuchins eat difficult-to-acquire foods is also likely to shed light on why capuchins have long juvenile periods and large brains.

Chapters 1-3 examine adaptations and consequences of reliance on a difficult to acquire (DtA) diet. Chapters 1 and 2 examine the effect of reliance on a DtA diet on foraging ontogeny. Chapter 1 examines rates of food transfers in infant capuchin, while Chapter 2 focuses on the independent feeding strategies that juveniles use to acquire DtA foods, and how those strategies affect their return rates. Chapter 3 tests the ecological complexity hypothesis for long juvenile periods. Finally, Chapter 4 investigates four possible benefits of feeding on difficult-to-acquire foods.
Chapter 2: Food Transfers in Capuchin Monkeys (Cebus capucinus): A Test of the Food Difficulty Hypothesis

Abstract

Food transfers between primate mothers and infants are common, but transfers between other individuals are rare. Capuchins are one of the few exceptions in which this occurs. Capuchin monkeys inhabit a complex dietary niche that includes many difficult-to-acquire (DtA) dietary items, and they face high metabolic requirements which stem from proportionally large brains. This study examines whether infant capuchins use food transfers to overcome the challenges of their difficult-to-acquire diet and meet the high metabolic demands of a proportionately large brain. Although several studies of social tolerance and food transfers have been conducted on captive capuchins, few studies have looked at rates of food transfers in wild capuchins. This study will be the first to specifically test the food difficulty hypothesis in wild capuchin monkeys. It will be one of the first to look at rates of food transfers in wild capuchins, and is unique in that the majority of food transfers did not involve meat, as hunting of relatively large vertebrate prey was not observed. Instead, food transfers were observed for fruit and insect food items. In support of the food difficulty hypothesis, foods that were more difficult-to-acquire were transferred and scrounged more frequently. In support of the brain nutrient hypothesis, the nutrients that the brain requires in the largest quantities were positively associated with food transfer rates. Food transfers were common in infants (17% of foraging observations) but rare in all other age classes (less than 1% of observations).
These results support the hypothesis that increased rates of food transfers in capuchins help the proportionately large-brained infants to obtain essential DtA nutrients.

Introduction

Food sharing seems to occur whenever infants and young juveniles cannot obtain their own food in high enough quantities to sustain survival. Food sharing is common in taxa such as carnivores (Malcolm and Marten, 1982; Mech et al., 1999; Courchamp et al., 2002), meerkats (Doolan and Macdonald, 1999), and birds (De Kort et al., 2006). In all of these taxa, skill is required to obtain food. In many cases this skill involves physical coordination and strength for acquisition of mobile prey. The relative rarity of food sharing in primates may be a reflection of largely immobile diets.

Tolerated scrounging and/or food-sharing in primate species is usually restricted to the transfer of food from mother to infant (Feistner and McGrew, 1989; Feistner and Price, 1990). Primates in the following taxa are known to exhibit food transfers with greater frequency and/or between additional individuals: species in the Callitrichidae family (Feistner and McGrew, 1989; Rapaport and Brown, 2008), species in the Aotus and Callicebus genera (Wright, 1984), chimpanzees, and capuchin monkeys (Silk, 1978; de Waal et al., 1993; Perry and Rose, 1994). There appear to be two distinct ecological context in primates under which extended food transfers occur.

Within the small New World monkeys (Callitrichidae, Aotus, and Callicebus) it is hypothesized that a combination of traits makes allocare and food-sharing a necessity. These traits include: a high infant/maternal weight ratio; lactation periods that are energetically expensive relative to other primate species (due to high birth rates and
growth rates); and carrying rather than caching of infants (Wright, 1990; Garber and Leigh, 1997; Leigh, 2004). Rapid growth and reproductive rates are likely a response to increased predation pressure. Predation may be higher in callitrichids because their small size makes them more vulnerable to predators and because small bodies have higher weight-specific metabolic requirements, necessitating more foraging, which could also increase their vulnerability (Rylands, 1996). In callitrichids, when infants transition from milk to solid foods they receive a large proportion of their food from helpers (Ruiz-Miranda et al., 1999; Feistner and Price, 2000). The process of weaning decreases the amount of nutrients that infants obtain from milk. Older individuals obtain some of these nutrients from large insects, small vertebrates, and relatively DtA fruits. However the acquisition of these items requires skills that weanlings have not mastered, which leaves them dependent on older group members for some proportion of their nutrients (Feistner and Price, 1990; Ruiz-Miranda et al., 1999).

Chimpanzees and capuchins do not exhibit rapid growth and are less heavily provisioned as juveniles compared with callitrichids, Aotus, and Callicebus (Fragaszy and Bard, 1997; Rose, 1997). Yet, as noted by de Waal et. al. (1993), capuchins and chimpanzees both rely on a high-quality, more difficult-to-acquire diet relative to other primate species. It has been proposed that among species relying on foods that are rare and/or require more skill to obtain, there should be higher levels of food transfers from adults to juveniles (Silk, 1978; de Waal et al., 1993; Jaeggi and van Schaik, 2011). Food transfers are hypothesized to enable juveniles to obtain difficult-to-acquire and/or rare food items to which they would otherwise have little access. Therefore, higher frequencies of food transfers are hypothesized to reflect the greater challenges faced by
juveniles in the acquisition of difficult and/or rare food items. Fragaszy et al. (2004) refer
to this as the food scarcity/difficulty hypothesis. One goal of this paper is to test the
difficulty part of the food scarcity/difficulty hypothesis for infant capuchin monkeys.

The diet of capuchin monkeys, like that of chimpanzees, includes many food
items that are difficult-to-acquire (DtA) relative to the dietary items of most nonhuman
primates (Izawa, 1979; Fragaszy et al., 1990, 2004 c; Janson and Boinski, 1992; Fragaszy
and Boinski, 1995). Capuchins commonly open hard-shelled fruits (Izawa, 1979), catch
and eat vertebrate prey such as lizards, frogs, birds, squirrels, and coati pups (Izawa,
1978; Rose, 1997), and in some populations carry heavy rocks to appropriate anvil stones
in order to smash open palm nuts (Ottoni and Mannu, 2001). These foraging behaviors
entail a high degree of skill, strength, or both, compared with more common primate
foraging activities of plucking fruits or young leaves and ingesting them as found. In
many primates it may be beneficial for infants to acquire much of their food
independently: it gives infants a chance to gain valuable foraging experience at a time
when they are still provisioned with milk and thus not responsible for all of their
nutritional requirements, and mothers do not pay a cost from sharing their food when
they are already burdened with the energetic demands of lactation. In addition to the
challenges of acquiring DtA food items, chimpanzees and capuchins both have relatively
large brains for their body size (Rilling and Insel, 1999), which pose high metabolic
demands that will be elaborated on in the next several paragraphs. The combination of
reliance on foods that are more difficult to acquire and high metabolic demands, is
hypothesized to increase the benefits of food transfers in capuchins and chimpanzees, and
thereby increase the rates of food transfers.
The next several paragraphs will discuss which nutrients should be important for the growth and maintenance of proportionately large brains in infants. Although, across mammals, proportionally large brains do not seem to be correlated with higher basal metabolic rates (BMRs) (Armstrong, 1983; Leonard and Robertson, 1994; Aiello and Wheeler, 1995; but see Isler and Van Schaik, 2006), they require that the percentage of total bodily energy that is spent on brain tissue is greater (Armstrong 1983; Leonard and Robertson 1994) and coincide with higher daily metabolic rates (Milton and May 1976). In addition, within primates, there is some evidence that relative brain size is correlated with BMR (Isler and Van Schaik, 2006).

Higher daily metabolic requirements stem from characteristics that are unique to the brain. Unlike other organs, the brain requires that a portion of its energy (as low as 30% in humans) be in the form of glucose, even under starvation conditions (Cunnane 2005; Holliday 1986). A consequence of this characteristic is that the more brain tissue an organism has, the higher its daily glucose requirement (Holliday 1986). Smaller individuals such as juveniles and infants, who have higher brain-to-body mass ratios than adults, have proportionately higher glucose requirements (Holliday 1986). Thus, the diet of an organism with a proportionally large brain, and to an even greater extent the diet of a juvenile in this species, must contain large amounts of the types of food from which glucose can be obtained.

Glucose can come in three basic forms: sugars, starches, and fiber. Sugars and starches are known as nonstructural carbohydrates (NSC) and provide capuchins with a net positive quantity of glucose and calories (National Research Council’s Committee on Animal Nutrition, 2003). Alternatively, fiber (also referred to as structural carbohydrates)
does not provide a sustainable quantity of nutrients for capuchins because they do not have a digestive system that is designed to extract a net positive quantity of calories from structural carbohydrates (Milton, 1987; Lambert, 1998). Instead, for species such as capuchins, a greater quantity of fiber will increase passage rates and decrease calorie absorption (Lambert, 1998).

Capuchins, like most primates, rely on fruits for their source of glucose. Compared with unripe fruits, ripe fruits generally have higher contents of energy, carbohydrates, lipids, and sometimes protein, (Schaefer et al., 2003). Not surprisingly, capuchins seem to have a strong preference for ripe fruits (Izawa, 1979; Robinson, 1986). Ripe fruits, however, are more dispersed in time and space than are leaves or unripe fruits (Milton, 1980). Organisms that rely on a greater quantity of ripe fruits in their diet must travel greater distances (Milton and May, 1976), leading to higher daily metabolic rates characteristic of big-brained species such as capuchins (Leonard and Robertson, 1992). Thus, if brain metabolism is an important factor that limits growth rates, glucose should be in high demand and highly valued.

Two additional macronutrients that could potentially influence infant foraging decisions are protein and fat. Although protein is required for growth and survival, the relatively slow growth rates of primates lead to low protein requirements compared with other mammals (Oftedal et al., 1991). Compared with adults, captive juvenile Cebus monkeys require more protein per kg of body mass, but less protein as a percentage of their daily energy requirements (Oftedal et al., 1991). Another factor to consider is that juvenile capuchins do not maintain a higher proportion of protein for their body weights compared with adults (Ausman et al., 1982). If juvenile return rates/daily requirements
for protein are proportional to their return rates/daily requirements for calories, given that juvenile and adult capuchins have largely similar diets (Fragaszy and Boinski, 1995; MacKinnon, 2006), juvenile capuchins should meet their protein requirements if they are able to eat enough food to sustain their energy requirements. Infants, who by definition still receive nutrients from breast milk which is a good source of protein and fat (Milligan, 2010), and obtain some additional protein from insect foraging, are unlikely to be protein deficient.

Fat is an especially important macronutrient for brain maintenance and development (Cunnane and Crawford, 2003). Brain myelination, part of neural development that requires brain lipids, continues into adulthood in rats and at least through the first decade in humans (Insel, 1995). Capuchin monkeys are known to undergo more postnatal brain growth relative to other New World monkeys (Hartwig, 1996). Given that capuchins have proportionally large brains and an extended period of postnatal brain growth, it is likely that juvenile capuchins have high fat requirements. These requirements, in turn, should influence juvenile capuchins’ affinity for high-fat food items. However, infants may fulfill much of their lipid requirements through nursing. Therefore, nutrients that should be in high demand in infant capuchins include sugar and starch (sources of glucose), but not necessarily protein or fat. Foods with lower fiber and secondary metabolite content should be preferred because these compounds inhibit the absorption of nutrients.

Several characteristics suggest that food transfers could play a role in providing access to DtA food items for infant capuchins. First, both wild and captive capuchin
monkeys are very tolerant of the close presence of other capuchins, especially infants and juveniles, while foraging (Izawa, 1980; de Waal et al., 1993). Second, capuchins are particularly messy eaters, frequently dropping pieces of food around themselves during ingestion (Fragaszy et al., 2004 c). Infant capuchins therefore have opportunities to scrounge food items. Third, capuchins show more interest in conspecific foraging behavior when the focal individual is foraging for rare food items and food items that require more steps to process (Perry and Ordoñez, 2006). This suggests that young capuchins recognize food items that are less accessible and/or can detect the value of a food from cues made by older individuals. Lastly, in captive situations, capuchins have a tendency to move toward other group members while they themselves are foraging, thus, providing a context that is ideal for a scrounger (de Waal, 2000). In captive contexts, it is not uncommon for individuals possessing food items to allow other individuals to pick up pieces of the food that have fallen nearby (Fragaszy et al., 1997).

Rapaport and Brown (2008) provide a detailed description of “social food-acquisition” patterns across primates. Immature primates are found to co-feed and beg for food items more often when they involve difficult-to-acquire, difficult-to-process, or rare food items. These behaviors may result in nutritional benefits for difficult-to-acquire foods (Rapaport and Brown, 2008). In capuchins, Boinski et al. (2000) found that in foraging contexts that involved the use of substrates, one to several immature capuchins would frequently “closely and persistently monitor” the foragers’ actions. Similarly, O’Malley and Fedigan (2005) found that juvenile capuchins watch the food processing behaviors of adults more often than the other way around. Thus immature individuals may have the opportunity to obtain pieces of DtA food items, however, Boinski et al.
(2000) note that no instances of food sharing or tolerated scrounging were observed during their study, while O’Malley and Fedigan (2005) explain that observers would engage in begging or scrounging attempts only with prized food items such as vertebrate prey, eggs, or wasp nests, but not with fruits that required processing. Thus whether infants obtain food or just information from proximity to complex foraging behaviors needs further exploration.

From a cost/benefit perspective, both reliance on a DtA diet, and high metabolic demands from a proportionately large brain should increase the benefits that infants obtain through food transfers. The costs to adult capuchins from the loss of food through food transfers may be higher than in taxa with proportionately smaller brains. But adult demands should not increase as much as the benefits to juveniles for two reasons: the metabolic demands of a large brain are proportionately higher for smaller-bodied juveniles, and adults have many years of additional foraging experience. Therefore the combination of proportionately large brains and a reliance on a DtA diet is hypothesized to select for higher rates of food transfer in capuchin monkeys.

**Hypotheses and Predictions**

I tested two hypotheses proposed to explain food transfers in capuchin monkeys. The first hypothesis could apply to infants and juveniles, while the second, in this form, only applies to infants who are likely to have distinct nutritional requirements from juveniles due to their acquisition of nutrients through breast-feeding.

**Food difficulty hypothesis:** Higher levels of food transfers between individuals will occur for foods that are rare and/or require skill to obtain.

- Prediction 1: food transfers occur more frequently with foods that are more difficult to acquire.
• Prediction 2: food transfers occur more frequently to younger, less skilled foragers.

**Brain nutrient hypothesis:** Food transfers help infant capuchins to acquire nutrients that are important for the growth and maintenance of proportionately large brains.

• Prediction 3: A greater quantity of simple sugars and/or NSCs, which are nutrients that are easily converted to glucose for the brain, should be especially valuable to young juveniles, and thus, should be stronger predictors of food transfers than other nutrients.

• Prediction 4: Fiber content will show an inverse relationship with food transfer frequency because it hinders calorie absorption rather than providing a net positive number of calories.

• Prediction 5: Lipid content should be a weaker predictor of food transfers in infants than NSC and simple sugar content because although lipids are important for brain development, infants are likely to acquire a significant amount of fat from breast milk.

• Prediction 6: Protein content will be the least significant predictor of food transfers in infants because infants do not have particularly high protein demands compared with older individuals and are likely to acquire a significant proportion of their protein requirements from breast milk.

**Methods**

**Study site:** Observations took place at the Pacuare Nature Reserve in the Limón Province of Costa Rica. The site is located 25 km north of the capital Puerto Limón,
between the Tortuguero Canals and the Caribbean Sea (10°10’N, 83°14W). The reserve contains 800 ha of mixed primary and secondary, tropical, wet, lowland forest. The three study groups have territories in the southern portion of the reserve. Their habitat consists of secondary, primary, and swamp lowland forest habitats.

Study groups: The three study groups (“A”, ”B” and “C”) had been studied intermittently by the author since 2005. Individuals were recognized by their body size, sex, and unique physical features such as cap line irregularities, head shape, and scars. Identities were well established by the author prior to the start of this study. Data were collected on 49 individuals within the three study groups. Subjects included 6 infants (age 0-1 year), 5 younger juveniles (ages 1-3 years), 5 older juveniles (ages 3-5 years), 6 subadults (ages 5-7 years) and 27 adults (older than 7 years). Age classes were defined as in similar studies involving foraging in juvenile capuchins (MacKinnon, 2006; Gunst et al., 2008, 2010) and are designed to reflect differences in tolerance, experience, size, and reproductive activity. Younger juveniles receive higher tolerance in feeding contexts (Janson, 1985; Janson, 1990a), and in captivity are between 50 and 80% of an adult female body weight (Fragaszy and Bard, 1997). Older juveniles receive an intermediate amount of aggression in foraging contexts and still have some growth left to do. Subadult females have reached or are close to adult size, but have generally not started to reproduce (Di Bitetti and Janson, 2001). Subadult and adult males receive the most aggression from the alpha male and are the least tolerated at preferred feeding sites (Janson, 1985). By 7 years most males have emigrated from their natal groups (Jack and Fedigan, 2004).
Data collection: Data were collected from October 2009 through August 2010. Along with a field assistant, I conducted scan samples (Altmann, 1974) every 30 minutes while in the presence of a study group. Scan samples lasted for 5 minutes during which time the first behavior observed for each individual positively identified over the interval was recorded. Between scan samples we conducted focal follows (Altmann, 1974) on individuals engaging in foraging activities. Focal follows lasted for the duration of a foraging event on one food type; if the focal individual stopped foraging or changed to a different food item the focal follow was ended. Subjects were chosen based on visibility and the food item being foraged, such that, each individual was not followed more than once per day for each food item. During focal follows, I narrated behaviors while my field assistant recorded them in real time on an HP iPaq using Noldus Observer 8.0 and Pocket Observer 3.1 behavioral data collection software (Noldus Information Technology, Wageningen, Netherlands).

Tolerated scrounge and forage-related behaviors are defined in Table 2.1. As recommended by Feistner and McGrew (1989) in order to standardize language, sharing behaviors involve the transfer of defensible food items and are distinguished from theft. Passive share and passive take involve sharing behaviors in which one individual is allowed to take food from the possession of another individual who, in turn, does not express any sign of irritation in the form of an open-mouth threat, scream, or hit. The word “passive” is used to differentiate these behaviors from active sharing in which the individual in possession of the food item actively transfers that food item to another individual. Active sharing was not observed in any of the scan samples during the study period so is not included in the definitions. Forceful take is similar to passive take but
coincides with a display of aggression on the part of the original possessor of the food item. Picking up dropped food items involves a lesser degree of social tolerance and little cost to the original possessor. A behavior was recorded as collect dropped near (CDN) if the individual who dropped the food item was present when the dropped food item was retrieved. For simplicity, from here on the behaviors: passive take, forceful take, and CDN will be referred to collectively as scrounge behaviors because they indicate situations where an individual obtains food through non-independent means. Passive take and forceful take will be referred to as receive food transfer behaviors, and passive take, forceful take, passive share, and taken from will be referred to as food transfers because in these cases food is directly transferred from the possession of one individual to another. Tolerated scrounge events between all individuals, including mothers and infants, were included in the analysis.
Table 2.1: Glossary

<table>
<thead>
<tr>
<th>Foraging Behaviors</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Search</td>
<td>Investigation of potential food sites.</td>
</tr>
<tr>
<td>Harvest</td>
<td>Removal of a food item from a substrate.</td>
</tr>
<tr>
<td>Process</td>
<td>Manipulation of a food item that an individual already has in his/her possession in order to improve ingestion or digestibility. (E.g. removal of a shell or exoskeleton).</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Scrounge Behaviors</th>
<th>Definitions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Passive share</td>
<td>The focal individual allows another individual to take food from his/her possession without reprimanding that individual in anyway (such as with a hit or scream).</td>
</tr>
<tr>
<td>Passive take</td>
<td>The focal individual removes food from the possession of another individual without receiving negative repercussions.</td>
</tr>
<tr>
<td>Forceful take</td>
<td>The focal individual removes food from the possession of another individual but receives aggression, (in the form of an open-mouth threat, scream, or hit) in response</td>
</tr>
<tr>
<td>Taken from</td>
<td>The focal individual has food taken from his/her possession and responds with aggression (in the form of an open-mouth threat, scream, or hit)</td>
</tr>
<tr>
<td>Collect dropped Near (CDN)</td>
<td>Foraging for a food that another individual has dropped, in the presence of that individual</td>
</tr>
</tbody>
</table>

*Food difficulty levels:* Food items were assigned a difficulty level for each of the different components of foraging: search, harvest, and process. In order to distinguish difficulty due to strength from difficulty due to skill these categories were assigned separately according to two sets of criteria. Strength levels were categorized by whether no (“1”), moderate (“2”), or intense (“3”) force was necessary to complete the behavior. Intense force was defined as force that required leveraging using body positions or use of an object by older juveniles, subadults, and/or adults. Examples of foraging behaviors that require intense force include tearing apart canes in search of embedded larvae or pounding open a hard-shelled fruit on a branch. A moderately forceful manipulation was defined as one that required solely manual pressure by older juveniles, subadults, and/or...
adults. Examples include removing a fruit from a thick stem or removal of a thin, hard shell. For skill, the difficulty classification was based on whether zero (“1”), one (“2”), or greater than one (“3”) skillful manipulation was necessary to complete the behavior. A skillful manipulation was defined as an action that requires one of the following: a dexterous manipulation, sequence-specific, condition-specific, or location-specific action. Examples include avoiding defense systems such as thorns or spikes, and locating larvae within canes. The values for total strength and total skill levels were computed by taking the sum of the difficulty levels for search, harvest, and process. All food items in this dataset were successfully acquired by each age-sex category and, thus, strength levels are designed to reflect the extra time it might take a weaker individual to acquire a food item, rather than whether an individual is likely to obtain a particular food item at all. Total difficulty is equal to the sum of total strength and total skill.

*Nutritional Analysis*: I collected samples of 23 plant food items in the field and processed then for future nutritional analysis. Following the protocols used by Conklin-Brittain et al. (2006), processing consisted of weighing each food item to determine the wet weight, dividing items into the parts that were eaten versus the parts that were not eaten, reweighing each part, drying samples in an electronic food dehydrator, weighing the dried samples, and lastly, packing the samples into zip-lock bags with silica packs. I transported dried samples to the Primate Nutritional Ecology Laboratory at Harvard University where I was trained to analyze each sample for the following macronutrients: protein, lipids, free simple sugars (water-soluble sugars), total NSC, total fiber (equal to the sum of: cellulose, hemicellulose, and lignins), and tannins. Kilocalories (KCAL) were calculated from the quantities of NSC, protein, and fat: $\text{KCAL} = 4\times\text{NSC} + 4\times\text{protein} + $
9*lipid. The methods used to analyze food items for this project followed the methods described in Conklin and Wrangham (1994). Water content was calculated as the difference between wet field weight and dry weight. “Dry weight” as discussed in the analysis refers to the dry weight of the edible portion of the food item. All nutrient percentages are calculated as a proportion of dry matter except for tannins which are reported as a percentage of quebracho units. Quebracho is the common name for several plants with high levels of condensed tannins. Quebracho units reflect the spectrophotometric absorbance level of a known quantity of condensed tannin extracted from a quebracho species (Wisdom et al., 1987).

Statistics: I carried out all statistical analyses in R v. 2.11.1 (R Development Team 2010). Scrounge rates were calculated for both scan samples and focal follows. For both scan samples and focal follows I calculated the number of samples that each individual engaged in a scrounge event out of the total number of samples where that individual engaged in any forage behavior. I also computed the number of samples where a food item was involved in a scrounge event out of the total number of samples where that food was involved in a forage behavior. Initially, I carried out all analyses separately for each data set. The results were very similar in each case. I therefore combined the datasets whenever appropriate for the final analyses in order to maximize power.

Forty-three food items that were observed eaten during scan samples and/or focal follows were used in the analysis of the scrounge rates versus difficulty levels. Each food item was assigned a difficulty level according to the methods described above (see Table 2.2). The dependent variable for these analyses was either the proportion of food transfers or the proportion of scrounge observations (“PSO” from here on). This consisted of the
number of observations where a food item was involved in either food transfer or scrounging behaviors, out of the total number of observations in which that food item was observed eaten or foraged for. Food transfer rates and PSO were regressed against food difficulty levels and the individual food difficulty components: total difficulty, total skill, total strength, search skill, harvest skill, process skill, search strength, harvest strength, and process strength. Again the proportional data were fit using a GLM with a quasi-binomial error distribution.

To examine the effect of age on proportion of forage events that involved receiving food through food transfers or through scrounge behaviors, the proportion of observations where an individual received food through a food transfer or through scrounge behaviors was computed for each study individual. This consisted of the number of scans and focal follows during which an individual was observed to receive food through food transfers (passive take or forceful take), or through scrounge behaviors (passive take, forceful take, CDN), out of the total number of scans where the individual was observed to engage in forage-related behaviors (including: search, harvest, process, bite and chew) plus the total number of focal follows for that individual. The proportions were not normally distributed and did not exhibit homogeneity of variances (as can be expected with proportion data). To analyze the data, I used generalized linear models (GLMs) with a quasi-binomial distribution. The quasi-binomial distribution was used to correct for over- and under-dispersion (Crawley 2007) which was present for all data subsets. An analysis of deviance was conducted on this model to test whether there were significant differences in scrounging rates for different age classes.
GLMs were used to examine the effect of nutrient content on the frequency of food transfers. The response variable was the number of samples where infants received food through food transfers for a particular food item, out of the total number of samples where that food was ingested or foraged. This was regressed against each nutrient of interest separately to determine which nutrients were the strongest predictors. Dry weight of the edible portion of the food item, the percent fiber in the food item, and the total difficulty score were added to each model as controls. The nutrients of interest included: KCALs, NSCs, free simple sugars, lipid, protein, and condensed tannins.
Table 2.2: Food Difficulty Levels

<table>
<thead>
<tr>
<th>Food Item</th>
<th>Scientific name</th>
<th>Family</th>
<th>Difficulty ID</th>
<th>Search Strength</th>
<th>Harvest Strength</th>
<th>Total Strength</th>
<th>Search Skill</th>
<th>Harvest Skill</th>
<th>Process Skill</th>
<th>Total Skill</th>
<th>Total Difficulty</th>
<th>Total Observations</th>
<th>Total CDN Observations</th>
<th>Total Food transfer observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>burio</td>
<td><em>Hampea appendiculata</em></td>
<td>Malvaceae</td>
<td>2</td>
<td>1</td>
<td>1.5</td>
<td>3.5</td>
<td>1.5</td>
<td>1</td>
<td>2</td>
<td>4.5</td>
<td>8</td>
<td>43</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>monkey chocolate</td>
<td><em>Herrania purpurea</em></td>
<td>Sterculiaceae</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>2</td>
<td>7</td>
<td>13</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>caimito</td>
<td><em>Chrysophyllum cainito</em></td>
<td>Sapotaceae</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>8</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>cativo</td>
<td><em>Prioria copaifera</em></td>
<td>Fabaceae</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>7</td>
<td>12</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>higueron</td>
<td><em>Ficus insipida</em></td>
<td>Moraceae</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3.5</td>
<td>1</td>
<td>1</td>
<td>3.5</td>
<td>6.5</td>
<td>40</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>inga pod</td>
<td><em>Inga vera subsp. vera</em></td>
<td>Fabaceae</td>
<td>8</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>9</td>
<td>53</td>
<td>0</td>
</tr>
<tr>
<td>guaiatil ground</td>
<td><em>Genipa americana</em></td>
<td>Rubiaceae</td>
<td>10</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>105</td>
<td>0</td>
</tr>
<tr>
<td>guayaba</td>
<td><em>Psidium guajava</em></td>
<td>Myrtaceae</td>
<td>11</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>34</td>
<td>2</td>
<td>13</td>
</tr>
<tr>
<td>guayaba de mono</td>
<td><em>Posoqueria latifolia</em></td>
<td>Rubiaceae</td>
<td>12</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2.5</td>
<td>5.5</td>
<td>9.5</td>
<td>13</td>
<td>0</td>
</tr>
<tr>
<td>hat berries</td>
<td><em>Siparuna sp.</em></td>
<td>Monimiaceae</td>
<td>13</td>
<td>1</td>
<td>1</td>
<td>1.5</td>
<td>3.5</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>7.5</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
<td>huevo de mono</td>
<td><em>Tabemaemontana alba</em></td>
<td>Apocynaceae</td>
<td>15</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>8</td>
<td>79</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>jicaro de playa</td>
<td><em>Amphitecna latifolia</em></td>
<td>Bignoniaceae</td>
<td>16</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>7</td>
<td>12</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>jobo</td>
<td><em>Spondias mombin</em></td>
<td>Anacardiaceae</td>
<td>17</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>lemon gatorade</td>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>berries (lgb)</td>
<td></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>neea</td>
<td><em>Neea sp.</em></td>
<td>Nyctanginaceae</td>
<td>19</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>noni</td>
<td><em>Morinda citrifolia</em></td>
<td>Rubiaceae</td>
<td>20</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>37</td>
<td>0</td>
</tr>
<tr>
<td>oil palm tree</td>
<td><em>Elaeis oleifera</em></td>
<td>Aracaceae</td>
<td>21</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>7</td>
<td>12</td>
<td>427</td>
<td>0</td>
</tr>
<tr>
<td>opossum grapes</td>
<td><em>Vitis tiliifolia</em></td>
<td>Vitaceae</td>
<td>22</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>13</td>
<td>6</td>
</tr>
<tr>
<td>palm heart</td>
<td><em>Aracaceae</em></td>
<td><strong>Total</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>palma real</td>
<td><em>Attalea rostrata</em></td>
<td>Aracaceae</td>
<td>24</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>2.5</td>
<td>6.5</td>
<td>12.5</td>
<td>2</td>
</tr>
<tr>
<td>panama hat</td>
<td>Carludovica rotundifolia</td>
<td>Cyclanthaceae</td>
<td>25</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>135</td>
<td>0</td>
</tr>
<tr>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>pejibaye</td>
<td>Bactris gasipeas</td>
<td>Arecaeeae</td>
<td>26</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>8</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>piperaceae</td>
<td>Piper sp.</td>
<td>Piperaceae</td>
<td>27</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>psychotria marginata</td>
<td>Psychotria marginata</td>
<td>Rubiaceae</td>
<td>28</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>tropical almond</td>
<td>Terminalia catappa</td>
<td>Combretaceae</td>
<td>29</td>
<td>1</td>
<td>1</td>
<td>1.5</td>
<td>3.5</td>
<td>2</td>
<td>1</td>
<td>1.5</td>
<td>4.5</td>
<td>8</td>
<td>139</td>
<td>0</td>
</tr>
<tr>
<td>yolillo</td>
<td>Raphia taedigera</td>
<td>Arecaeeae</td>
<td>30</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>7</td>
<td>12</td>
<td>33</td>
<td>0</td>
</tr>
<tr>
<td>guaitil tree</td>
<td>Genipa americana</td>
<td>Rubiaceae</td>
<td>31</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>6</td>
<td>11</td>
<td>67</td>
<td>0</td>
</tr>
<tr>
<td>oil palm ground</td>
<td>Elaeis oleifera</td>
<td>Araceaeae</td>
<td>33</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>112</td>
<td>0</td>
</tr>
<tr>
<td>surface insect</td>
<td></td>
<td></td>
<td>34</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>7</td>
<td>913</td>
<td>0</td>
</tr>
<tr>
<td>embedded insect</td>
<td></td>
<td></td>
<td>35</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>7</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>6</td>
<td>13</td>
<td>221</td>
<td>0</td>
</tr>
<tr>
<td>lengua de gato</td>
<td>Conostegia sp.</td>
<td>Melastomataceae</td>
<td>36</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>coconut</td>
<td>Cocos nucifera</td>
<td>Arecaeeae</td>
<td>37</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td>3</td>
<td>7</td>
<td>13</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>banana</td>
<td>Musa acuminata</td>
<td>Musaceae</td>
<td>38</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>bejuco de agua</td>
<td></td>
<td></td>
<td>39</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1.5</td>
<td>3.5</td>
<td>6.5</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>berries</td>
<td>(unkown species)</td>
<td></td>
<td>40</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>48</td>
<td>0</td>
</tr>
<tr>
<td>mano de tigre</td>
<td>Monostera deliciousa</td>
<td>Araceae</td>
<td>41</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>5</td>
<td>9</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>banana heart</td>
<td>Musa acuminata</td>
<td>Musaceae</td>
<td>43</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>9</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>lengua de vaca flower</td>
<td>Pentagonia monocaulis</td>
<td>Rubiaceae</td>
<td>44</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>snails</td>
<td></td>
<td></td>
<td>45</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>5</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>11</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>pop pod fruits</td>
<td>Dialium sp.</td>
<td>Leguminoseae</td>
<td>46</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>wild guava</td>
<td>Alibertia edulis</td>
<td>Rubiaceae</td>
<td>47</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>8</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>pipa</td>
<td>Cocos nucifera</td>
<td>Arecaeeae</td>
<td>48</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>5</td>
<td>10</td>
<td>5</td>
<td>0</td>
</tr>
</tbody>
</table>
**Results**

Scrounge rates: The observed numbers of each type of scrounging behavior are presented in table 2.3a. The average rate of tolerated scrounging events in scans was 1 out of every 71 foraging behaviors. For focal follows the rate was 1 out of every 40.3 focal follows.

<table>
<thead>
<tr>
<th>Scrounge Behavior</th>
<th>Total Number of Observations</th>
<th>Passive Share</th>
<th>Passive Take</th>
<th>CDN</th>
<th>Forceful take</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scan Samples*</td>
<td>18/1260</td>
<td>6†</td>
<td>6†</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>Focal Follows</td>
<td>29/1168</td>
<td>10</td>
<td>8</td>
<td>9</td>
<td>2</td>
</tr>
</tbody>
</table>

*These numbers reflect the number of scans where foraging took place

†Out of the 6 passive take and 6 passive share events from scans, 4 of these were reciprocal. Thus, there were a total of 8 scrounge events involving passive share and passive take behaviors.

**Table 2.3b: Distribution of Scrounge Behaviors across Age Classes**

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Individuals</th>
<th>Number who engaged in scrounge behaviors</th>
<th>Passive Take Obs.</th>
<th>Active Take Obs.</th>
<th>CDN Obs.</th>
<th>Total Obs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infants</td>
<td>3</td>
<td>3</td>
<td>9</td>
<td>1</td>
<td>14</td>
<td>58</td>
</tr>
<tr>
<td>Younger Juveniles</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>415</td>
</tr>
<tr>
<td>Older Juveniles</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>327</td>
</tr>
<tr>
<td>Subadults</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>353</td>
</tr>
<tr>
<td>Adults</td>
<td>28</td>
<td>5</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>1258</td>
</tr>
</tbody>
</table>

Food transfer and scrounge rates by age class: The distribution of food transfer and scrounge observations across age classes is illustrated in Table 2.3b. Analysis of deviance revealed that there are significant differences in rates of both food transfers and
scrounging between adults and infants but not between adults and any other age class (see Table 2.4a and 2.4b). Figure 2.1 illustrates the rate that each age class received food transfers as predicted by the statistical model. The predicted proportion of scrounge events for infants was 28.4%, for young juveniles was 0.7%, for older juveniles and subadults was 0.3%, and for adults was 0.5%. The predicted proportion of forage observations where food is received through food transfers is 14.7% for infants, 0.5% for younger juveniles, 0.3% for older juveniles, 0% for subadults and 0.4% for adults.

### Table 2.4a: Food Transfer Recipient Rates by Age Class

| Age Class      | FTRR | Estimate | Std. Error | z value | Pr(>|z|) |
|----------------|------|----------|------------|---------|---------|
| Adults         | 0.004| -5.53    | 0.48       | N/A     | N/A     |
| Subadults      | 0.000| -22.67   | 2896.04    | -0.01   | 0.995   |
| Older Juveniles| 0.003| -5.79    | 1.08       | -0.22   | 0.825   |
| Younger Juveniles | 0.005| -5.34    | 0.76       | 0.21    | 0.832   |
| Infants        | 0.147| -1.76    | 0.37       | 6.23    | <0.001  |

### Table 2.4b: Scrounge rates by age class

| Age Class      | PSO  | Estimate | Std. Error | z value | Pr(>|z|) |
|----------------|------|----------|------------|---------|---------|
| Adults         | 0.005| -5.346   | 0.308      | -17.381 | <0.001  |
| Subadults      | 0.003| -5.867   | 0.753      | -0.641  | 0.525   |
| Older Juveniles| 0.003| -5.790   | 0.753      | -0.547  | 0.588   |
| Younger Juveniles | 0.007| -4.930   | 0.436      | 0.780   | 0.440   |
| Infants        | 0.284| -0.925   | 0.185      | 12.313  | <0.001* |

Model Output interpretation: 4a: Estimates are equal to the log of the predicted proportion of observations where an individual is a food transfer recipient (FTRR). FTRR=1/(1+1/e^Estimate). P-values for adults indicate the probability that the adult FTRR is significantly different from e^0 (=1) and is thus not meaningful for this study. P-values for the other age classes indicate the probability that the FTRR for the respective age class is the same as the FTRR for adults. *indicates significance at an α=0.05 level.

4b: FRTT are replaced by the probability that an individual engages in a scrounge behavior out of all forage-related observations (PSO).
Figure 2.1: Food Transfer Recipient Rates by Age Class

Figure 2.1: Proportion of observations where an individual is a food transfer recipient (FTRR) for each age class. FTRR data combined from scan samples and focal follows. Bars indicated 95% confidence intervals.

Individuals involved: Out of the 47 total scrounge and scrounge from events, 17 involved transfer of food from mother to infant and an additional 4 involved transfer from a mother to a young juvenile. Another 7 scrounge events involved the transfer of food from a non-mother adult female to an infant. The remaining 19 events occurred between adults (2), between juveniles (6), from an adult other than the mother to a juvenile (6), involved adults taking food from infants or juveniles (4), or from an unidentified individual to an adult (1). An analysis of deviance revealed that age class was not a
significant predictor of an individual’s probability of being scrounged from (p=0.237, GLM, quasi-binomial model).

Scrounge rates vs. difficulty levels: Similar patterns were apparent for food transfer rates and PSO. However, the only difficulty level component that was a significant predictor of food transfer rates was process strength, whereas when CDNs were added to the data, many of the difficulty level components were significant predictors. Total difficulty, total skill, and total strength were all significant predictors of PSO (see Table 2.5). In addition, four of the components of total difficulty: search skill, process skill, harvest strength, and process strength were significant predictors of PSO. While it is possible that significant relationships for the difficulty components reflect especially important aspects of independent foraging, it is also possible that these difficulty components reflect the greatest challenges of this particular set of food items.
Table 2.5: Change in Odds That a Food Item is Scrounged With Change in Difficulty Level

| Difficulty          | Odds | Estimate | Std. Error | z value | Pr(>|z|) |
|---------------------|------|----------|------------|---------|---------|
| Total Difficulty    | 1.34 | 0.30     | 0.12       | 2.47    | 0.02*   |
| Total Skill         | 1.72 | 0.54     | 0.24       | 2.25    | 0.03*   |
| Total Strength      | 1.54 | 0.43     | 0.18       | 2.34    | 0.02*   |
| Search Skill        | 2.32 | 0.84     | 0.42       | 2.02    | 0.05*   |
| Harvest Skill       | 1.22 | 0.20     | 0.48       | 0.42    | 0.68    |
| Process Skill       | 5.33 | 1.67     | 0.40       | 4.22    | <0.001* |
| Search Strength     | <0.01| -8.42    | 1436.91    | -0.01   | 1.00    |
| Harvest Strength    | 2.28 | 0.82     | 0.33       | 2.52    | 0.02*   |
| Process Strength    | 2.72 | 1.00     | 0.42       | 2.37    | 0.02*   |

Odds are the factor by which the likelihood that infants and younger juveniles acquire food through scrounge behaviors increases for each 1 unit increase in difficulty level. For example, a 1 unit increase in total difficulty increases the likelihood that a food item will be scrounged by 34%. * indicates significance at an α=0.05 level. N=43 food items. Single predictor models: glm(PSO~difficult, quasibinomial

Food transfer rate vs. nutrient content: the food items that were analyzed for nutrients are listed with their nutrient composition in Table 2.6. In support of the brain nutrition hypothesis, free simple sugars and nonstructural carbohydrate content were the nutrients with the strongest positive association with food transfers when controlling for fiber content, dry weight, and difficulty level: for every additional percent of NSCs in a food item the proportion of observations where a food is involved in a food transfer increases by 5% (see Table 2.7). The increase was 10% for free simple sugars. As predicted, fiber content was negatively associated with food transfers: for each additional percent of fiber, the odds of a food transfer are between 75-93% compared with a food with 1% less fiber. In support of prediction 6, lipid content did not exhibit a significant positive relationship with food transfers. However, somewhat surprisingly, lipid content exhibited a significant negative association with food transfers. Protein content was also negatively associated with food transfers but this relationship was not significant. Due to the negative relationships between food transfers with lipid and protein content, the
relationship between KCAL/100g and food transfers was also negative. A final relationship between condensed tannins and food transfers was also negative. Condensed tannins can inhibit the absorption of protein (Oftedal et al., 1991) and can therefore be considered an anti-nutrient, similar to fiber.
### Table 2.6: Nutritional Content of Foods Taken by Capuchins

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>plant part</th>
<th>% DM ND F</th>
<th>% DM AD F</th>
<th>% D M</th>
<th>% D M Ls</th>
<th>% D M lip</th>
<th>% D M FS</th>
<th>% D M CP</th>
<th>% DQ U CT</th>
<th>% DQ U RD</th>
<th>% D M ash</th>
<th>% OM total NS C</th>
<th>KCA L/100g OM</th>
<th>Avg. DM for edible portion</th>
<th>Avg. OM for edible portion</th>
<th>bites / item</th>
<th>g DM/bite</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Herrania purpurea</em></td>
<td>pulp</td>
<td>22.3</td>
<td>10.4</td>
<td>12.1</td>
<td>3.5</td>
<td>6.7</td>
<td>1.4</td>
<td>42.2</td>
<td>6.3</td>
<td>0.2</td>
<td>0.0</td>
<td>5.0</td>
<td>68.4</td>
<td>313</td>
<td>1.20</td>
<td>1.15</td>
<td></td>
</tr>
<tr>
<td><em>Chrysophyllum cainito</em></td>
<td>pulp</td>
<td>34.9</td>
<td>16.4</td>
<td>18.6</td>
<td>8.1</td>
<td>8.4</td>
<td>22.4</td>
<td>18.1</td>
<td>5.6</td>
<td>2.2</td>
<td>2.9</td>
<td>35.1</td>
<td></td>
<td>372</td>
<td>1.51</td>
<td>1.47</td>
<td>33.0</td>
</tr>
<tr>
<td><em>Ficus insipida</em></td>
<td>pulp</td>
<td>49.3</td>
<td>40.1</td>
<td>9.2</td>
<td>20.1</td>
<td>20.0</td>
<td>4.2</td>
<td>11.9</td>
<td>4.9</td>
<td>32.9</td>
<td>6.0</td>
<td>5.2</td>
<td>38.5</td>
<td>214</td>
<td>0.83</td>
<td>0.79</td>
<td>3.3</td>
</tr>
<tr>
<td><em>Inga vera subsp. vera</em></td>
<td>pulp+seeds</td>
<td>47.7</td>
<td>4.9</td>
<td>42.8</td>
<td>1.2</td>
<td>3.8</td>
<td>1.5</td>
<td>14.7</td>
<td>15.7</td>
<td>0.6</td>
<td>0.6</td>
<td>2.4</td>
<td>33.6</td>
<td>539</td>
<td>1.73</td>
<td>1.70</td>
<td>20.0</td>
</tr>
<tr>
<td><em>Psidium guajava</em></td>
<td>pulp</td>
<td>54.1</td>
<td>42.7</td>
<td>11.4</td>
<td>13.2</td>
<td>29.5</td>
<td>0.9</td>
<td>18.0</td>
<td>3.2</td>
<td>10.6</td>
<td>6.0</td>
<td>4.5</td>
<td>39.1</td>
<td>178</td>
<td>5.03</td>
<td>4.81</td>
<td>63.1</td>
</tr>
<tr>
<td><em>Posoqueria latifolia</em></td>
<td>pulp</td>
<td>13.8</td>
<td>9.7</td>
<td>4.1</td>
<td>0.5</td>
<td>9.2</td>
<td>1.0</td>
<td>41.8</td>
<td>8.3</td>
<td>0.1</td>
<td>0.0</td>
<td>8.1</td>
<td>74.8</td>
<td>346</td>
<td>1.10</td>
<td>1.02</td>
<td>23.4</td>
</tr>
<tr>
<td><em>Siparuna sp.</em></td>
<td>pulp</td>
<td>9.7</td>
<td>7.8</td>
<td>1.9</td>
<td>3.5</td>
<td>4.2</td>
<td>39.0</td>
<td>13.9</td>
<td>17.5</td>
<td>4.9</td>
<td>0.8</td>
<td>3.2</td>
<td>31.6</td>
<td>561</td>
<td>0.01</td>
<td>0.01</td>
<td>4.0</td>
</tr>
<tr>
<td><em>Heliconia mathiasiae</em></td>
<td>pulp+seed</td>
<td>43.6</td>
<td>34.2</td>
<td>9.4</td>
<td>24.3</td>
<td>9.9</td>
<td>18.3</td>
<td>13.3</td>
<td>10.3</td>
<td>0.8</td>
<td>2.9</td>
<td>17.0</td>
<td>12.3</td>
<td>303</td>
<td>1.89</td>
<td>1.58</td>
<td></td>
</tr>
<tr>
<td><em>Tabemaeontana alba</em></td>
<td>pulp</td>
<td>13.8</td>
<td>7.3</td>
<td>6.5</td>
<td>2.4</td>
<td>4.9</td>
<td>22.8</td>
<td>28.8</td>
<td>10.0</td>
<td>0.8</td>
<td>0.0</td>
<td>7.4</td>
<td>49.8</td>
<td>464</td>
<td>0.28</td>
<td>0.26</td>
<td>10.5</td>
</tr>
<tr>
<td><em>Amphitecna latifolia</em></td>
<td>pulp</td>
<td>16.4</td>
<td>12.5</td>
<td>3.9</td>
<td>6.2</td>
<td>6.3</td>
<td>0.8</td>
<td>33.6</td>
<td>6.6</td>
<td>1.5</td>
<td>0.0</td>
<td>4.3</td>
<td>75.1</td>
<td>335</td>
<td>3.26</td>
<td>3.13</td>
<td>88.0</td>
</tr>
<tr>
<td><em>Lemon gatorade berries (a Myrtaceae sp.)</em></td>
<td>pulp</td>
<td>37.3</td>
<td>34.7</td>
<td>2.6</td>
<td>17.4</td>
<td>17.2</td>
<td>1.5</td>
<td>35.7</td>
<td>3.8</td>
<td>5.9</td>
<td>5.3</td>
<td>3.6</td>
<td>55.9</td>
<td>253</td>
<td>0.09</td>
<td>0.09</td>
<td>1.0</td>
</tr>
<tr>
<td><em>Morinda citrofolia</em></td>
<td>pulp</td>
<td>19.4</td>
<td>16.8</td>
<td>2.7</td>
<td>3.2</td>
<td>13.5</td>
<td>1.7</td>
<td>30.9</td>
<td>8.7</td>
<td>4.1</td>
<td>0.0</td>
<td>8.7</td>
<td>67.4</td>
<td>324</td>
<td>1.52</td>
<td>1.40</td>
<td>26.5</td>
</tr>
</tbody>
</table>

38
<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>NDF</th>
<th>ADF</th>
<th>HC</th>
<th>Ls</th>
<th>Cs</th>
<th>Lipid</th>
<th>FSS</th>
<th>CP</th>
<th>RD</th>
<th>Ash</th>
<th>NSC</th>
<th>OM</th>
<th>DM</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elaeis oleifera</td>
<td>pulp</td>
<td>21.4</td>
<td>11.4</td>
<td>10.0</td>
<td>4.4</td>
<td>7.0</td>
<td>62.6</td>
<td>8.2</td>
<td>2.5</td>
<td>0.7</td>
<td>0.0</td>
<td>2.0</td>
<td>11.7</td>
<td>632</td>
</tr>
<tr>
<td>Vitis tiliifolia</td>
<td>pulp</td>
<td>17.9</td>
<td>16.5</td>
<td>1.4</td>
<td>10.1</td>
<td>6.4</td>
<td>1.7</td>
<td>30.4</td>
<td>4.6</td>
<td>4.0</td>
<td>7.1</td>
<td>5.3</td>
<td>74.5</td>
<td>334</td>
</tr>
<tr>
<td>Aracaceae sp. (Pith)</td>
<td>pulp</td>
<td>23.6</td>
<td>12.0</td>
<td>11.7</td>
<td>0.2</td>
<td>11.8</td>
<td>3.1</td>
<td>23.6</td>
<td>25.0</td>
<td>0.2</td>
<td>0.0</td>
<td>11.1</td>
<td>41.3</td>
<td>311</td>
</tr>
<tr>
<td>Carladovica rotundifolia</td>
<td>pulp</td>
<td>23.8</td>
<td>13.4</td>
<td>10.5</td>
<td>5.6</td>
<td>7.8</td>
<td>11.3</td>
<td>42.7</td>
<td>10.4</td>
<td>1.1</td>
<td>0.0</td>
<td>7.0</td>
<td>51.0</td>
<td>358</td>
</tr>
<tr>
<td>Bactris gasipes</td>
<td>pulp</td>
<td>32.8</td>
<td>13.9</td>
<td>19.0</td>
<td>0.5</td>
<td>13.4</td>
<td>1.9</td>
<td>31.2</td>
<td>18.1</td>
<td>0.3</td>
<td>0.0</td>
<td>6.4</td>
<td>43.5</td>
<td>270</td>
</tr>
<tr>
<td>Piper sp.</td>
<td>pulp</td>
<td>29.5</td>
<td>17.0</td>
<td>12.3</td>
<td>9.0</td>
<td>8.2</td>
<td>3.5</td>
<td>32.3</td>
<td>11.7</td>
<td>0.6</td>
<td>0.0</td>
<td>5.9</td>
<td>52.5</td>
<td>293</td>
</tr>
<tr>
<td>Psychotria marginata</td>
<td>pulp</td>
<td>7.3</td>
<td>6.3</td>
<td>1.0</td>
<td>2.4</td>
<td>3.9</td>
<td>1.9</td>
<td>40.7</td>
<td>5.9</td>
<td>0.1</td>
<td>7.2</td>
<td>9.9</td>
<td>83.3</td>
<td>378</td>
</tr>
<tr>
<td>Terminalia catappa</td>
<td>pulp</td>
<td>20.2</td>
<td>16.7</td>
<td>3.5</td>
<td>7.1</td>
<td>9.5</td>
<td>0.9</td>
<td>35.9</td>
<td>4.0</td>
<td>6.9</td>
<td>21.4</td>
<td>6.7</td>
<td>73.1</td>
<td>318</td>
</tr>
<tr>
<td>Raphia taedigera</td>
<td>pulp</td>
<td>16.4</td>
<td>12.5</td>
<td>3.8</td>
<td>6.2</td>
<td>6.3</td>
<td>54.5</td>
<td>6.2</td>
<td>6.1</td>
<td>6.8</td>
<td>8.7</td>
<td>2.1</td>
<td>21.4</td>
<td>611</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Details:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acronyms: NDF=neutral detergent fiber fraction; ADF=acid detergent fiber fraction; HC=hemicellulose; Cs=cellulose; Ls=lignins; FSS=fraction sugars, CP=crude protein; DQU=Quebracho dry matter units; CT=condensed tannins; RD=radial diffusion; NSC=nonstructural carbohydrates; OM=organic matter; DM=dry matter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>The following percentages were calculated from nutritional analyses, methods described in Conklin-Brittain et al. 2006: NDF, ADF, HC, Ls, Cs, Lipid, FSS, CP, OM, RD, Ash. Percentage values refer to the percent of the dry weight for the edible portion of the food item.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Calculations:</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>%OM total NSC=100-%OM NDF-%OM lipid-%OM CP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kcal/100 g OM=4*%OM FSS + 4*%OM CP + 9*%OM lipid</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>grams DM per bite=DM/bites per food item</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>grams of nutrient per bite=grams DM per bite*((% nutrient)/100), for each of the following nutrients: NDF, lipid, CP, FSS, NSC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kcal per bite=grams DM per bite*((Kcal/100g)/100)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>grams nutrient per item=DM*% nutrient, for each nutrient</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2.7: Odds That a Food Item Will Be Involved in a Food Transfer to an Infant Dependent on Nutrient Content

| Summary table | Odds Ratio | Estimate | Std. Error | z value | Pr(>|z|) |
|---------------|------------|----------|------------|---------|---------|
| Model: glm(# transfers to infants/total # samples~dry weight + KCAL/100g + %fiber + total difficulty level), family=quasibinomial | Intercept 0.12 | -2.09 | 1.33 | -1.57 | N/A |
| | Dry weight 1.18 | 0.17 | 0.07 | 2.29 | 0.036* |
| | KCAL/100g 0.99 | -0.01 | 0.00 | -5.12 | 0.000* |
| | % Fiber 0.84 | -0.17 | 0.05 | -3.21 | 0.005* |
| | Total Difficulty Level 1.53 | 0.43 | 0.14 | 3.11 | 0.007* |
| Model: glm(# transfers to infants/total # samples~dry weight + NSC/100g + %fiber + total difficulty level), family=quasibinomial | Intercept 0.00 | -10.74 | 1.99 | -5.40 | N/A |
| | Dry weight 1.13 | 0.12 | 0.07 | 1.71 | 0.106 |
| | % NSC 1.05 | 0.05 | 0.01 | 5.91 | 0.000* |
| | % Fiber 0.93 | -0.08 | 0.05 | -1.43 | 0.172 |
| | Total Difficulty Level 1.61 | 0.48 | 0.12 | 3.88 | 0.001* |
| Model: glm(# transfers to infants/total # samples~dry weight + %FSS + %fiber + total difficulty level), family=quasibinomial | Intercept 0.00 | -10.75 | 2.09 | -5.13 | N/A |
| | Dry weight 1.26 | 0.23 | 0.07 | 3.58 | 0.002* |
| | % Free Simple Sugars 1.10 | 0.10 | 0.02 | 5.76 | 0.000* |
| | % Fiber 0.91 | -0.09 | 0.05 | -1.66 | 0.117 |
| | Total Difficulty Level 1.60 | 0.47 | 0.13 | 3.73 | 0.002* |
| Model: glm(# transfers to infants/total # samples~dry weight + %lipid + %fiber + total difficulty level), family=quasibinomial | Intercept 0.00 | -5.70 | 1.52 | -3.76 | N/A |
| | Dry weight 1.18 | 0.17 | 0.07 | 2.28 | 0.037* |
| | % Lipid 0.96 | -0.05 | 0.01 | -5.11 | 0.000* |
| | % Fiber 0.88 | -0.13 | 0.05 | -2.43 | 0.027* |
| | Total Difficulty Level 1.54 | 0.43 | 0.14 | 3.12 | 0.007* |
| Model: glm(# transfers to infants/total # samples~dry weight + %protein + %fiber + total difficulty level), family=quasibinomial | Intercept 35.16 | 3.56 | 2.44 | 1.46 | N/A |
| | Dry weight 1.31 | 0.27 | 0.10 | 2.63 | 0.018* |
| | % Protein 0.77 | -0.27 | 0.13 | -2.06 | 0.056 |
| | % Fiber 0.75 | -0.29 | 0.09 | -3.05 | 0.008* |
| | Total Difficulty Level 0.82 | -0.19 | 0.17 | -1.13 | 0.276 |
| Model: glm(# transfers to infants/total # samples~dry weight + %condensed tannins + %fiber + total difficulty level), family=quasibinomial | Intercept 0.31 | -1.18 | 1.70 | -0.70 | N/A |
| | Dry weight 1.47 | 0.39 | 0.11 | 3.58 | 0.003* |
Discussion

Results from this study support the hypotheses that capuchins engage in increased rates of food transfers 1) as a result of reliance on a difficult-to-acquire diet and 2) to help meet the needs of their proportionately large, metabolically demanding brains. In support of the food difficulty hypothesis, infants are the recipients of the majority of food transfers, which come from both sexes and all ages classes, not just the mother. Furthermore, infant and younger juvenile capuchins are more likely to use scrounge behaviors to obtain food items that are more difficult to acquire. Similar findings have been reported for chimpanzees (Silk, 1978; Nishida and Turner, 1996) and orangutans (Jaeggi et al., 2008), suggesting that the relationship between reliance on a difficult-to-acquire diet and increased rates of food transfer may extend across primates.

The main fuel for the brain under non-starvation conditions is glucose, and individuals with proportionately larger brains have higher glucose requirements (Holliday, 1986). In support of the brain nutrient hypothesis, NSC and free simple sugar content, both sources of glucose, were both positively associated with food transfer rates in infants while controlling for food size, fiber content, and difficulty level. On the other hand increased fiber and tannin content, which are likely to decrease nutrient absorption, exhibit a negative relationship with food transfer rates in infants. Protein and lipid content

| DQU Condensed Tannins | 0.80 | -0.23 | 0.11 | -2.16 | 0.047* |
| % Fiber | 0.88 | -0.13 | 0.08 | -1.70 | 0.108 |
| Total Difficulty Level | 0.86 | -0.15 | 0.16 | -0.90 | 0.384 |

Notes: Dry weight is for the edible portion of the food item in grams. Percent nutrient values refer to the percent of the dry weight. Odds ratios are the increased (>1) or decreased (<1) odds that a food item will be involved in a food transfer to an infant with one additional % (or gram) of the nutrient (or dry weight).
were not positively associated with food transfer rates. By definition, infants still acquire some nutrients through nursing. It is possible that infants acquire sufficient quantities of lipid and protein through nursing, but do not obtain sufficient quantities of glucose. Alternatively and/or simultaneously, it is possible that insects, which generally contain relatively high quantities of protein and lipids compared with fruit (McCabe, 2005), are not difficult for infants to obtain in sufficient quantities. The results of chapter 3 indicate that insects do not require a long learning phase in order to obtain at adult rates, whereas some fruits do. Together, the lower absolute requirements for protein and lipids and the likely higher efficiency of obtaining these nutrients from insects at young ages, suggest that nonstructural carbohydrates, including sugars and starches, rather than protein and lipids, are limiting nutrients for infants. The results of from this chapter, which indicate that the content of nonstructural carbohydrates, and to an even greater extent, the content of free simple sugars, are strong, positive predictors of whether a food is received by an infant through a food transfer, further support this notion.

Juveniles, who no longer receive nutrients through nursing, are likely to have at least slightly different nutritional requirements than infants. The proportion of daily energy requirements that must be in the form of glucose should still be higher in juveniles than in adults, but should not be as high as in infants. The results from this study indicate that juveniles do not obtain any significant quantity of nutrients through food transfers, however, it is still possible that juveniles employ different food acquisitions strategies than those used by adults.

Whereas food transfers appear to enable rapid growth rates in callitrichids, *Aotus*, and *Callicebus*, capuchins, along with chimpanzees, orangutans, and humans, may be
locked into slow growth as a consequence of their proportionally large brains. For the latter, food transfers may prevent starvation and/or help provide the necessary nutrients for their slow-paced growth. Given that large brains are metabolically demanding, yet highly vulnerable to energy shortages (Cunnane, 2005), they are likely to impose constraints on growth (Deaner et al., 2003). The results of this chapter indicate that they are also likely to select for behavioral adaptations that deliver relatively high quantities of glucose to infants, who are less capable of efficiently obtaining sufficient amounts of this nutrient, yet require that a higher daily proportion of their nutrients come in the form of glucose than any other age class.
Chapter 3: Feeding Strategies for Difficult-To-Acquire Foods in

Juvenile Capuchin Monkeys (*Cebus capucinus*)

Abstract

Capuchin monkeys are known to rely on a suite of difficult-to-acquire (DtA) dietary items. In this sense they are often compared to chimpanzees because both are known to engage in high levels of extractive foraging, hunt relatively large vertebrate prey, and use tools in the wild. Despite a potentially large impact on juvenile growth and survival, there are few studies that focus on the consequences of this type of diet on juveniles. Young juveniles are at a foraging disadvantage for two main reasons: first, they are smaller and noticeably weaker than adults; second, they have had less time to practice and learn foraging skills. In an attempt to more deeply understand the consequences of reliance on a DtA diet on juveniles, this study examines the strategies used by juveniles to obtain DtA food items, and the effect that these strategies have on nutrient acquisition. It was hypothesized that young juvenile capuchin monkeys use alternative foraging behaviors such as picking up food dropped by more proficient foragers, foraging in close proximity to older individuals, and a greater reliance on easy-to-acquire (EtA) foods, in order to overcome the challenges of their difficult-to-acquire diet. In support of this hypothesis, young juveniles used easier, alternative foraging strategies to harvest difficult-to-acquire oil palm fruits more frequently than adults, spent more of their time in proximity to other individuals when foraging for DtA fruits, but not when foraging for easy-to-acquire (EtA) fruits, and while in proximity of other individuals, achieved higher
bite rates. In addition, younger juveniles spent more time foraging for easy foods and less time foraging for hard foods than did adults. All of these findings were also true of subadults, but not for older juveniles. It is likely that older juveniles exhibit the benefits of several years of foraging experience, but do not yet experience the levels of aggression in feeding contexts that subadults face. A deeper understanding of the consequences that reliance on a DtA diet has on immature capuchins is likely to provide insight into many aspects of capuchin socioecology, including levels of social tolerance, growth rates, and life history.

Introduction

Among primates, capuchin monkeys are known to specialize in foraging for especially difficult-to-acquire (DtA) food items (Izawa, 1979; Frayaszy et al., 1990, 2004c; Janson and Boinski, 1992; Frayaszy and Boinski, 1995). Examples include prying open hard-shelled fruits (Izawa, 1979), catching and eating vertebrate prey including lizards, frogs, birds, squirrels, and coati pups (Izawa, 1978; Rose, 1997), and carrying heavy rocks to appropriate anvil stones in order to smash open palm nuts (Ottoni and Mannu, 2001). These foraging behaviors entail a high degree of skill, strength, or both, compared with more common primate foraging activities of plucking ripe fruits or young leaves and ingesting them as found. In the case of wild capuchins where direct food provisioning is rare (Rose, 1997), the challenges of inhabiting a dietary niche that is skill and/or strength-intensive should have the greatest impact on younger juveniles who lack both the strength and the experience of their older group mates. The mechanisms that enable juveniles to
overcome these challenges will help reveal which adaptations allowed for survival in their complex dietary niche.

Young juveniles do not obtain many food items through food transfers (Perry & Rose, 1994, This study Chapter 1) but may use other strategies, that are not strictly independent, to obtain DtA foods. One option is to pick up food items that were dropped by others (were pre-foraged) on a previous day. Another option is to forage near older individuals. In doing so, younger individuals may gain information about (a) which items are edible, (b) which fruits are of ideal ripeness, and (c) how to harvest and/or process foods. Close proximity to an experienced forager could also have a less intentional consequence of increasing the likelihood of acquiring food items by increasing the probability that a juvenile is in the vicinity of edible items.

A food type that provides a useful model to study whether younger individuals exploit dropped, DtA food items more frequently than older individuals, is oil palm fruits (Elaeis oleifera). Oil palm fruits, which were highly valued food items and very difficult to acquire when harvested from the tree, were often observed harvested from the ground after they had been dropped. The difficulty in foraging for these fruits from the tree was due mostly to the thick stem that held each fruit tightly in place within a densely spiked, though large, infructescence. While foraging on oil palm fruits, several group members were usually present at one time. Some individuals would attempt to free whole ripe fruits from the large cluster of fruits, while other individuals often scanned the ground for dropped, partially eaten fruits. Oil palm fruits are dropped either because they are not ripe enough and are voluntarily discarded, or because they are slippery. Harvesting these dropped fruits from the ground is a very easy way to acquire these highly desirable fruits.
Both social rank and an individual’s ability to harvest fruits from the tree are likely to influence whether he/she foraged for palm fruits on the ground or in the tree. In a study of foraging positions in groups of wild capuchin monkeys, Janson (1990 a; b) found that juveniles received low levels of aggression and were able to occupy the best feeding positions, while subadult and adult males received high levels of aggression from the dominant male and occupied peripheral positions where foraging was suboptimal. Thus, when younger juveniles forage for dropped fruits, it may be a strategy to obtain food items more efficiently than would be possible through independently harvesting the fruit from the tree, while for subadults, harvesting fruits from the ground may be a strategy to avoid aggression.

In general, immature primates are found to pay close attention to foraging activities of others more often when they involve difficult-to-acquire, difficult-to-process, or rare food items (Rapaport and Brown, 2008). These situations provide immature individuals the opportunity to gain valuable information about dietary breadth and foraging techniques. Thus a greater reliance on difficult-to-acquire foods may increase the likelihood of both increased social tolerance, and social learning (Rapaport and Brown, 2008). Several studies have already found evidence of social learning in capuchins. Perry and Ordoñez (2006) found that immature capuchins are more likely to show interest in foods that are rare, require more steps to process, and are large. Boinski et al. (2000) found that in foraging contexts that involved the use of substrates, one to several immature capuchins would frequently “closely and persistently monitor” the foragers’ actions. Similarly, O’Malley and Fedigan (2005) found that juvenile capuchins watch the food processing behaviors of adults more often than the other way around.
Thus, it seems very likely that juvenile capuchins learn information about more complex foraging techniques by watching older individuals.

A third strategy that juveniles may employ to obtain sufficient nutrients is to spend a greater proportion of time on easy-to-acquire foods. A detailed study of brown capuchins foraging in bamboo patches by Gunst et al. (2008) revealed that young capuchins also utilize this strategy. In their study site, bamboo patches were a source for both easy foods (surface insects, leaves, and pith) and difficult foods (embedded insects). While in bamboo patches, infants and young juveniles spent significantly more time foraging for easy foods and less time foraging for embedded insects than did older juveniles, sub adults, and adults (Gunst et al., 2008).

This study examines the foraging strategies of younger juveniles compared with older juveniles, subadults, and adults. To do this, the following hypotheses were tested:
**Hypotheses and Predictions**

Hypothesis 1: The capuchin diet poses challenges to juvenile capuchins who must find alternative methods to exploit DtA foods.

- Prediction 1a: Younger individuals will take advantage of dropped, DtA oil palm fruits more frequently than older individuals.
- Prediction 1b: Juvenile capuchins will achieve higher return rates by foraging for dropped oil palm fruits than from harvesting the fruits directly from the tree.

Hypothesis 2: Immature capuchins gain important information about foraging through social learning. In situations where immature capuchins stand to gain the most information they will be most likely to position themselves near older individuals.

- Prediction 2a: Younger individuals forage for DtA food items in close proximity to other individuals more frequently than older individuals.
- Prediction 2b: There will be little or no relationship between age class and foraging proximity for easy-to-acquire (EtA) foods, because in no age class are individuals in a position to acquire a substantial amount of valuable foraging information.

Hypothesis 3: Foraging in proximity to older individuals allows immature individuals better access to DtA food items.

- Prediction 3: Immature individuals will attain higher bite rates while in the proximity of other individuals when foraging for DtA foods.
Hypothesis 4: Due to lower foraging efficiency on DtA foods, to meet nutrient requirements, younger individuals must spend more time exploiting EtA foods.

- Prediction 4: Younger individuals spend a greater proportion of time foraging for EtA food items than do adults

Methods

Study site: Observations took place at the Pacuare Nature Reserve in the Limón Province of Costa Rica. The site is located 25 km north of the capital Puerto Limón, between the Tortuguero Canals and the Caribbean Sea (10°10’N, 83°14W). The reserve contains 800 ha of mixed primary and secondary, tropical, wet, lowland forest. The three study groups have territories in the southern portion of the reserve. Their habitat consists of secondary, primary, and swamp lowland forest habitats.

Study groups: The three study groups (“A”, “B” and “C”) had been studied intermittently by the author since 2005. Individuals were recognized by their body size, sex, and unique physical features such as cap line irregularities, head shape, and scars. Identities were well established by the author prior to the start of this study. Data were collected on 49 individuals within the three study groups. Subjects included 6 infants (age 0-1 year), 5 younger juveniles (ages 1-3 years), 5 older juveniles (ages 3-5 years), 6 subadults (ages 5-7 years) and 27 adults (older than 7 years). Age classes were defined as in similar studies involving foraging in juvenile capuchins (MacKinnon, 2006; Gunst et al., 2008, 2010) and are designed to reflect differences in tolerance, experience, size, and reproductive activity. Younger juveniles receive higher tolerance in feeding contexts (Janson, 1985, 1990 a), and in captivity are between 50 and 80% of an adult female body
weight (Fragaszy and Bard, 1997). Older juveniles receive an intermediate amount of aggression in foraging contexts and still have some growth left to do. Subadult females have reached or are close to adult size, but have generally not started to reproduce (Di Bitetti and Janson, 2001). Subadult and adult males receive the most aggression from the alpha male and are the least tolerated at preferred feeding sites (Janson, 1985). By 7 years most males have emigrated from their natal groups (Jack and Fedigan, 2004).

Data collection: Data were collected from October 2009 through August 2010. Along with a field assistant, I conducted scan samples (Altmann, 1974) every 30 minutes while in the presence of a study group. Scan samples lasted for 5 minutes during which time the first behavior observed for each individual positively identified over the interval was recorded. Between scan samples we conducted focal follows (Altmann, 1974) on individuals engaging in foraging activities. Focal follows lasted for the duration of a foraging event on one food type; if the focal individual stopped foraging or changed to a different food item the focal follow was ended. Subjects were chosen based on visibility and the food item being foraged, such that, each individual was not followed more than once per day for each food item. During focal follows, I narrated behaviors while my field assistant recorded them in real time on an HP iPaq using Noldus Observer 8.0 and Pocket Observer 3.1 behavioral data collection software (Noldus Information Technology, Wageningen, Netherlands).

Definitions: Return rates for this study are computed as bite count per forage time. Forage time consisted of three non-overlapping behaviors: search, harvest, and process. Search was defined as the visual, olfactory, and/or manual investigation of potential food sites. Harvest was the removal of a food item from a substrate. Process
was manipulation of a food item that an individual already had in his/her possession in order to improve ingestion or digestibility. *Total forage time* is the total duration of these three behaviors. Once a focal individual had a food item in his/her possession each bite was recorded. *Collect dropped* was foraging for a food that another individual had previously harvested and then dropped. An individual was considered in *Proximity* to another individual when he/she was estimated to be within one meter of the other individual.

*Food difficulty levels*: Food items were assigned a difficulty level for each of the different components of foraging: search, harvest, and process. In order to distinguish difficulty due to strength from difficulty due to skill these categories were assigned separately according to two sets of criteria. Strength levels were categorized by whether no (“1”), moderate (“2”), or intense (“3”) force was necessary to complete the behavior. Intense force was defined as force that required leveraging using body positions or use of an object by older juveniles, subadults, and/or adults. Examples of foraging behaviors that require intense force include tearing apart canes in search of embedded larvae or pounding open a hard-shelled fruit on a branch. A moderately forceful manipulation was defined as one that required solely manual pressure by older juveniles, subadults, and/or adults. Examples include removing a fruit from a thick stem or removal of a thin, hard shell. For skill, the difficulty classification was based on whether zero (“1”), one (“2”), or greater than one (“3”) skillful manipulation was necessary to complete the behavior. A skillful manipulation was defined as an action that requires one of the following: a dexterous manipulation, sequence-specific, condition-specific, or location-specific action. Examples include avoiding defense systems such as thorns or spikes, and locating larvae
within canes. The values for total strength and total skill levels were computed by taking
the sum of the difficulty levels for search, harvest, and process. All food items in this
dataset were successfully acquired by each age-sex category and, thus, strength levels are
designed to reflect the extra time it might take a weaker individual to acquire a food item,
rather than whether an individual is likely to obtain a particular food item at all. Total
difficulty is equal to the sum of total strength and total skill. Table 1.2 lists each food item and its difficulty levels.

Statistics: I carried out all statistical analyses in R v. 2.11.1 (R Development Team
2010). To examine the effect of age on the likelihood that an individual collects dropped
oil palm fruits from the ground versus new fruits from the tree, the proportion of scan
observations during which an individual was observed to harvest oil palm fruits from the
ground (PGO) was regressed against age class. The proportions were not normally
distributed and did not exhibit homogeneity of variances (as can be expected with
proportion data). To analyze these data, I used generalized linear models (GLMs) with a
quasi-binomial distribution. The quasi-binomial distribution was used to correct for over-
dispersion (Crawley 2007). For this analysis there were 105 ground harvest observations
out of 470 total oil palm harvest observations across twenty-eight individuals in each of
the five age classes. An analysis of deviance was conducted on this model to test whether
there were significant differences in PGO for different age classes. Unfortunately, the
number of dominant/submissive behaviors recorded for this project was too few to enable
a reliable calculation of social rank, so this was not added to the analysis.

Similar analyses were used to test whether younger individuals spend a greater
proportion of their foraging time on EtA foods. The proportion of scan samples devoted
to EtA, MtA (medium difficulty-to-acquire), and DtA fruits, and to surface and embedded insects were counted for each individual and a GLM with a quasibinomial distribution was used to test for differences across age classes. Surface insects are collected from the surface of leaves, branches, or the ground and are easier to acquire than are embedded insects. Embedded insects included larvae hidden within canes or branches, and termites within nests.

To examine the return rates achieved from the different oil palm harvest strategies I used a generalized linear mixed model (GLMM) to examine the effect of harvest location on foraging return rates, while controlling for the correlated structure of the data that results from different individuals contributing multiple and unequal numbers of foraging samples to the dataset. Return rates were computed from bite counts per foragetime, the response variable is in counts, and therefore a Poisson distribution was used. GLMMs were carried out in R with the lme4 package (Bates and Maechler 2009). Overdispersion occurs for many Poisson count models and if ignored can lead to an inappropriate model (Gelman and Hill, 2007). To determine whether dispersion had occurred in a model, I calculated the level of dispersion with the dispersion equation presented by Gelman and Hill (2007). When overdispersion is present for a Poisson model, observation number can be added as a random effect (Browne et al. 2005) to account for the additional variation. This is the technique I employed here.

Another GLMM was used to examine the effect of age on proximity during foraging. For this model the response variable was the amount of time spent within one meter of another individual out of the total time for the focal follow. The fixed effect was age class and the random effects were subject ID and food ID. Observation number was
added as a random effect to account for overdispersion. This model was run separately for DtA and EtA foods. The focal follow dataset was used here in order to examine the effect of age class on the amount of time spent in proximity. There were a total of 1133 focal follows: 582 for adults; 183 for subadults; 174 for older juveniles; and 193 for younger juveniles.

A final GLMM was used to examine the effects of proximity and food difficulty level on bite rates. For this model the response variable was bite rate, the fixed effect was a binary factor for proximity indicating whether or not the focal individual spent any time within one meter of another individual during the focal follow. The random effects were subject ID, food ID, and observation number. The focal follow dataset was also used here in order to examine bite rate. There were a total of 354 focal follows where the focal individual focused on DtA food items: 199 for adults; 47 for subadults; 47 for older juveniles; and 61 for younger juveniles. There were 578 focal follows where the focal individual focused on EtA food items: 286 for adults; 100 for subadults; 89 for older juveniles; and 103 for younger juveniles.

**Results**

**Alternative Forage Methods for DtA Foods**

In support of hypothesis 1, younger capuchins did take advantage of dropped oil palm fruits significantly more frequently than older individuals (see Figure 3.1, Table 3.1). Compared with adults, infants, younger juveniles, older juveniles, and subadults harvested oil palm fruits from the ground significantly more frequently. The statistical model predicted that the proportion of fruits that adults harvested from the ground was
6.6%, while younger age classes harvest a predicted 18-48% of their fruits from the ground. Although there were no significant differences between ground harvest rates of infants, younger juveniles, and older juveniles, there appears to be a trend where ground harvesting decreases with age. Subadults do not fit this pattern and harvested the second highest proportion of their oil palm fruits from the ground after infants.

Figure 3.1: Proportion of Oil Palm Fruits Harvested from the Ground

Figure 3.1: Proportion of oil palm fruits harvested from the ground (PGO) versus from the tree for each age class. PGO data combined from scan samples and focal follows. Bars indicated 95% confidence intervals.
Table 3.1: Proportion of Oil Palm Fruits Harvested From the Ground (PGS) for Each Age Class

| Age Class       | PGO | Estimate | Std. Error | z value | Pr(>|z|) |
|-----------------|-----|----------|------------|---------|---------|
| Adults          | 0.066 | -2.653  | 0.316      | -8.404  | <0.001  |
| Subadults       | 0.365 | -0.555  | 0.308      | 4.761   | <0.001* |
| Older Juveniles | 0.186 | -1.478  | 0.419      | 2.238   | 0.035*  |
| Younger Juveniles | 0.323 | -0.742  | 0.303      | 4.370   | <0.001* |
| Infants         | 0.478 | -0.087  | 0.570      | 3.940   | 0.001*  |

Model Output interpretation: Estimates are equal to the log of the predicted proportion of ground harvest observations. PGO=1/(1+1/e^Estimate). P-values for adults indicate the probability that the adult PGO is significantly different from e^0 (=1) and is thus not meaningful for this study. P-values for the other age classes indicate the probability that the PGO for the respective age class is the same as the PGO for adults. Model: GLM, quasi-binomial. *indicates significance at an α=0.05 level.

Also in support of hypothesis 1, juvenile capuchins achieved significantly higher return rates when harvesting oil palm fruits from the ground rather than from the tree (see figure 3.2, Table 3.2). (Due to small sample sizes, return rates for younger juveniles, older juveniles and subadults were combined for this analysis). Adults also exhibited a trend of higher return rates for dropped oil palm fruits, although this difference was not significant. Adults achieved a bite rate of 0.06 bites/forage time for tree fruits and 0.10 bites/forage time for dropped fruits (p=0.366). Juveniles achieved a bite rate of 0.04 for tree fruits and 0.09 for dropped fruits (p=0.008). It is not surprising that both adults and juveniles achieve higher return rates from dropped fruits which, when available, are much easier to harvest because they can simply be picked up. However, fruits are only available on the ground after they have been harvested from the tree and dropped. When an oil palm tree contained ripe fruits there were many more ripe fruits in the tree than on the ground, thus the tree could be considered a more reliable source of food. These results indicate that taking advantage of pre-foraged foods is one strategy that young juveniles
employ to obtain DtA foods, a strategy that subadults are likely to employ in order to avoid aggression.

**Figure 3.2: Bite Rates from Tree Compared to Ground Harvesting**

Figure 3.2: Oil palm return rates when foraged from the ground or the tree for adults versus juveniles (younger juveniles, older juveniles, subadults combined). Bars indicate 95% confidence intervals.
Table 3.2: Oil Palm Bite Rates for Tree Compared to Ground Foraging

| Age Class | Harvest Location | Bite Rate | Estimate | Std. Error | z value | Pr(>|z|) |
|-----------|------------------|-----------|----------|------------|---------|----------|
| Adults    | Tree             | 0.064     | -2.745   | 0.212      | N/A     | N/A      |
| Adults    | Ground           | 0.103     | -2.277   | 0.510      | -0.903  | 0.366    |
| Juveniles | Tree             | 0.038     | -3.274   | 0.244      | N/A     | N/A      |
| Juveniles | Ground           | 0.088     | -2.430   | 0.260      | -2.641  | 0.008*   |

Model an output interpretation: model<-lmer(bite count~tree_or_ground+(1|subject ID)+(1|observation number)+ offset(log(total forage time)), family = Poisson). Estimates are equal to the log of the predicted bite rate. Bite rates=e^Estimate). P-values indicate the probability that the bite rate for ground foraging is the same as for tree foraging. The model was run separately for adults and juveniles. *indicates significance at an α=0.05 level. N for Adults=100, N for Juveniles=91

Social Learning

In support of hypothesis 2, younger juveniles spent significantly more time in the proximity of other individuals than did adults when foraging for DtA foods (see Figure 3.3a, Table 3.3). Older juveniles and adults spent a similar amount of time in proximity to other individuals when foraging for DtA foods. Subadults, like younger juveniles, spent significantly more time in proximity to other individuals, compared with adults, when foraging for DtA foods. It is likely that younger juveniles spent the most time in proximity of other individuals while foraging for DtA foods because they stand to gain the most by watching others forage. It is interesting that subadults, but not older juveniles, spent a greater amount of time in the proximity of other individuals compared with adults.
Figure 3.3a: Proximity for DtA Foods

![Bar chart showing the proportion of time spent within 1 meter proximity of another individual during focal follows, where the focal individual was foraging for DtA food items, for each age class.]

Figure 3.3b: Proximity for EtA Foods

![Bar chart showing the proportion of time spent within 1 meter proximity of another individual during focal follows, where the focal individual was foraging for EtA food items, for each age class.]

60
Table 3.3: Proportion of Focal Follows Spent Within 1 Meter of Another Individual by Age Class And Food Difficulty Level

| Age Class         | Proximity | Estimate | Std. Error | Z-value | Pr(>|z|) |
|-------------------|-----------|----------|------------|---------|---------|
| **DtA Foods**     |           |          |            |         |         |
| Adults            | 0.000045  | -10.01   | 1.24       | N/A     | N/A     |
| Subadults         | 0.000424  | -7.77    | 1.48       | 1.99    | 0.047*  |
| Older Juveniles   | 0.000059  | -9.74    | 1.53       | 0.23    | 0.818   |
| Younger Juveniles | 0.000590  | -7.43    | 1.44       | 2.50    | 0.013*  |
| **EtA Foods**     |           |          |            |         |         |
| Adults            | 0.000001  | -13.53   | 1.45       | N/A     | N/A     |
| Subadults         | 0.000003  | -12.90   | 2.09       | 0.25    | 0.804   |
| Older Juveniles   | 0.000002  | -13.38   | 2.30       | 0.06    | 0.956   |
| Younger Juveniles | 0.000002  | -12.99   | 2.09       | 0.21    | 0.834   |

Model and output interpretation: model<-lmer(time_in_1m_proximity~age class + (1|subject ID)+(1|Food ID)+(1|observation number)+ offset(log(duration of focal follow)), family = Poisson). Estimates are equal to the log of the predicted proportion of forage focals spent in proximity to another individual. Proximity=e^(Estimate)). P-values for adults indicate the probability that the proportion of adult focal follows spent in proximity to another individual is significantly different from e^0 (=1) and is thus not meaningful for this study. P-values for the other age classes indicate the probability that the proportion of focal follows spent in proximity to another individual for the respective age class is the same as the proportion for adults. *indicates significance at an α=0.05 level.

In further support of hypothesis 2, when foraging for EtA foods, there were no significant differences in the time that younger juveniles, older juveniles, or subadults spent in the proximity to other individuals compared with the time that adults spent in the proximity of others (see Figure 3.3b, Table 3.3). All age classes spent much more time in proximity of other individuals when foraging for DtA compared with EtA foods: the predicted average proximity for DtA foods was between 0.0045-0.059% versus 0.0001-0.0003% for EtA (see Table 3.3). These results support the hypothesis that immature
capuchins situate themselves in positions that offer opportunities for social learning when social learning would be most beneficial.

**Nutrient acquisition of DtA foods**

In support of hypothesis 3, younger juveniles had higher return rates in focal follows where they were in proximity of another individual for some proportion of the time, when they were foraging for DtA foods (see Figure 3.4a and Table 3.4). However, this difference was not significant (p=0.081). When foraging for EtA foods, younger juveniles had slightly higher average return rates in focal follows where they were never in proximity of another individual (see Figure 3.4b, Table 3.4, p=0.377). Therefore, there appears to be a trend whereby younger juveniles achieve higher return rates when foraging in proximity to others for DtA foods, but future studies with larger sample sizes will be necessary to confirm this.
Figure 3.4a: Bite Rate for DtA Foods When In or Not In 1m Proximity of Other Individuals

Figure 3.4a: Number of bites per forage time (search time + harvest time + process time) in focal follows where the subject ate DtA food items and spent either some (“<1m”) or no (“>1m”) time within 1 meter proximity of another individual.

Figure 3.4b: Bite Rate for EtA Foods When In or Not In 1m Proximity of Other Individuals

Figure 3.4b: Number of bites per forage time (search time + harvest time + process time) in focal follows where the subject ate EtA food items and spent either some (“<1m”) or no (“>1m”) time within 1 meter proximity of another individual.
Table 3.4: Comparison of Bite Rates For DtA and Eta Foods When In or Not In 1m Proximity of Other Individuals

| Age Class       | Proximity | Bite Rate | Estimate | Std. Error | Z-value | Pr(>|z|) |
|-----------------|-----------|-----------|----------|------------|---------|---------|
|                 | DtA Foods |           |          |            |         |         |
| Adults          | No        | 0.059     | -2.836   | 0.339      | N/A     | N/A     |
| Adults          | Yes       | 0.057     | -2.872   | 0.393      | -0.130  | 0.897   |
| Subadults       | No        | 0.035     | -3.344   | 0.251      | N/A     | N/A     |
| Subadults       | Yes       | 0.012     | -4.414   | 0.492      | -1.938  | 0.053   |
| Older Juveniles | No        | 0.015     | -4.201   | 0.300      | N/A     | N/A     |
| Older Juveniles | Yes       | 0.045     | -3.108   | 0.293      | 2.607   | 0.009*  |
| Younger Juveniles | No    | 0.034     | -3.388   | 0.277      | N/A     | N/A     |
| Younger Juveniles | Yes  | 0.017     | -4.095   | 0.338      | -1.746  | 0.081   |
|                 | Eta Foods |           |          |            |         |         |
| Adults          | No        | 0.105     | -2.253   | 0.320      | N/A     | N/A     |
| Adults          | Yes       | 0.072     | -2.625   | 0.367      | -1.809  | 0.070   |
| Subadults       | No        | 0.138     | -1.982   | 0.312      | N/A     | N/A     |
| Subadults       | Yes       | 0.145     | -1.931   | 0.412      | 0.161   | 0.872   |
| Older Juveniles | No        | 0.159     | -1.841   | 0.425      | N/A     | N/A     |
| Older Juveniles | Yes       | 0.082     | -2.502   | 0.481      | -2.040  | 0.041*  |
| Younger Juveniles | No    | 0.144     | -1.938   | 0.344      | N/A     | N/A     |
| Younger Juveniles | Yes  | 0.185     | -1.686   | 0.406      | 0.884   | 0.377   |

Model and output interpretation: Model<-lmer(bite count~proximity_0_1+(1|focal_individual)+(1|food ID)+(1|observation number)+offset(log(total_forage_time)), Family=Poisson. Estimates are equal to the log of the predicted bite rate. Proximity indicates whether the focal individual was ever within 1 meter of another individual during the follow (yes) or spent no time in 1m proximity (no). Bite rate=e^(Estimate)). P-values indicate the probability that the bite rate for proximity yes was the same as for proximity no. *indicates significance at an α=0.05 level.

Older juveniles exhibit the opposite trends of younger juveniles with higher return rates for DtA foods when not in proximity of another individual, and higher return rates for Eta foods when they were at some point in proximity of another individual. These differences were both significant (see Table 3.4). Thus, older juveniles do not gain a foraging advantage from the proximity of other individuals while foraging for DtA foods.
as is likely for younger juveniles, but instead face a cost. This may help explain the pattern of time that older juveniles spend in proximity to other individuals shown in Table 3.3a.

Similar to younger juveniles, but presumably for different reasons, subadults achieve higher average return rates for DtA foods when in the proximity of other individuals. This difference approached significance (p=0.053, Table 3.4). When foraging for EtA foods, subadults achieve nearly identical return rates in and out of proximity of other individuals (Figure 3.4b).

Time Allocation

The proportion of forage-related scan samples that each age class spent on five different food types: EtA fruits, MtA, fruits, DtA fruits, surface insects, and embedded insects, are shown in Figures 3.5a-e. In support of hypothesis 4, younger juveniles spent a significantly lower proportion of their foraging scans on DtA fruits and significantly higher proportion of their foraging scans on surface insects compared with adults (see Figure 3.5c, 3.5d, Table 3.5). There were no significant differences in the proportion of forage scans spent on EtA, MtA, or embedded insects between adults and other age classes. There was a trend whereby adults spent a higher proportion of forage scans on hard fruits and embedded insects, and a lower proportion of forage scans on easy fruits, medium fruits, and surface insects compared with each of the younger age classes (see Table 3.5). There were no significant differences between the sexes for any food type, for any age class.
Figure 3.5a: Proportion of Forage Scans Devoted to Easy Fruits by Sex and Age Class

Figure 3.5b: Proportion of Forage Scans Devoted to Medium Fruits by Sex and Age Class

Figure 3.5c: Proportion of Forage Scans Devoted to Hard Fruits by Sex and Age Class
Figure 3.5d: Proportion of Forage Scans Devoted to Surface Insects by Sex and Age Class

Figure 3.5e: Proportion of Forage Scans Devoted to Embedded Insects by Sex and Age Class

Figure 3.5: Predicted proportion of forage scans spent on each food type by sex and age class for easy fruits (3.5a), medium fruits (3.5b), hard fruits (3.5c), surface insects (3.5d) embedded insects. Model: <-glm(number of scans for one of the food types/number of forage scans ~ age class*sex, quasi-binomial)
### Table 3.5: Proportion of Scan Samples Spent on Each Food Type by Age Class

| Age Class          | Proportion | Estimate | Std. Error | t value | Pr(>|t|) |
|--------------------|------------|----------|------------|---------|---------|
| **EtA Fruits**     |            |          |            |         |         |
| Adults             | 0.14       | -1.776   | 0.103      |         |         |
| Subadults          | 0.17       | -1.576   | 0.189      | 0.929   | 0.358   |
| Older Juveniles    | 0.15       | -1.702   | 0.201      | 0.327   | 0.746   |
| Younger Juveniles  | 0.15       | -1.760   | 0.176      | 0.079   | 0.937   |
| **MtA Fruits**     |            |          |            |         |         |
| Adults             | 0.10       | -2.164   | 0.164      |         |         |
| Subadults          | 0.13       | -1.872   | 0.287      | 0.885   | 0.381   |
| Older Juveniles    | 0.12       | -1.981   | 0.304      | 0.530   | 0.599   |
| Younger Juveniles  | 0.12       | -1.968   | 0.258      | 0.643   | 0.524   |
| **DtA Fruits**     |            |          |            |         |         |
| Adults             | 0.25       | -1.087   | 0.087      |         |         |
| Subadults          | 0.18       | -1.531   | 0.207      | -1.974  | 0.055   |
| Older Juveniles    | 0.23       | -1.219   | 0.185      | -0.645  | 0.522   |
| Younger Juveniles  | 0.18       | -1.537   | 0.180      | -2.255  | 0.029*  |
| **Surface Insects**|            |          |            |         |         |
| Adults             | 0.24       | -1.127   | 0.061      |         |         |
| Subadults          | 0.29       | -0.907   | 0.112      | 1.721   | 0.093   |
| Older Juveniles    | 0.26       | -1.051   | 0.120      | 0.567   | 0.574   |
| Younger Juveniles  | 0.30       | -0.861   | 0.095      | 2.350   | 0.024*  |
| **Embedded Insects**|          |          |            |         |         |
| Adults             | 0.05       | -2.911   | 0.170      |         |         |
| Subadults          | 0.02       | -3.951   | 0.561      | -1.774  | 0.083   |
| Older Juveniles    | 0.02       | -3.704   | 0.503      | -1.493  | 0.143   |
| Younger Juveniles  | 0.05       | -2.992   | 0.304      | -0.232  | 0.817   |

Model and output interpretation: `model<-glm( # hard forage scans/total # forage scans~age class, family = quasi-binomial).` Estimates are equal to the log of the predicted odds of forage scans devoted to hard (top) or easy (bottom) foods. Proportions= \( \frac{1}{1+e^{\text{Estimate}}} \). P-values for adults indicate the probability that the proportion of adult forage scans spent on hard or easy foods is significantly different from \( \frac{1}{1+e^{0}} \), (=1) and is thus not meaningful for this study. P-values for the other age classes indicate the probability that the proportion of forage scans spent on hard or easy foods for the respective age class is the same as the proportion for adults. *indicates significance at an \( \alpha=0.05 \) level. MtA are fruits that require a medium amount of difficulty to acquire.
Discussion

Capuchins inhabit a complex foraging niche and exploit many difficult-to-acquire food items (Izawa, 1978, 1979; Fragaszy et al., 1990, 2004 a; Janson and Boinski, 1992; Fragaszy and Boinski, 1995). They also have proportionally large brains (Jerison, 1973; Martin, 1984; Fragaszy et al., 1990; Hakeem et al., 1996; Hartwig, 1996; Rilling and Insel, 1999) which coincide with high daily metabolic requirements (Milton and May, 1976; Leonard and Robertson, 1992). A complex foraging niche may pose the greatest challenges to young juveniles who have less experience and strength compared with older group members. This study examined juvenile foraging strategies within this dietary niche, and tests whether juvenile capuchins use alternative foraging behaviors to learn about and obtain DtA food items.

Strategies utilized by younger juveniles included: taking advantage of pre-foraged DtA fruits, foraging for DtA fruits in close proximity to others, and spending a greater proportion of time foraging for EtA foods. Older juveniles and subadults also take advantage of pre-foraged oil palm fruits more frequently than adults but, older juveniles do not forage for DtA fruits in close proximity to others or spend a greater proportion of time foraging for EtA foods. Subadults, similar to younger juveniles, do forage for DtA fruits in close proximity to others but, do not spend a greater proportion of their time foraging for EtA foods.

If the patterns in juvenile foraging behavior were only in response to differences in skill and strength levels, we would expect to see a gradient of each behavior where younger juveniles would exhibit the most extreme differences compared with adults, and subadults would exhibit the smallest differences. However, this does not appear to be the
case for any of the alternative foraging strategies. It is likely that lower levels of tolerance by adults towards subadults in feeding contexts (Janson, 1990 a; b). For oil palm fruits, which are highly desirable and tightly packed, subadults likely harvest fruit from the ground due to higher rates of aggression from dominant individuals, while younger juveniles probably lack the skill and strength to efficiently harvest these fruits from the tree.

The patterns of proximity are difficult to explain by tolerance patterns because subadults, who Janson (1990 a; b) found were less tolerated in preferred feeding locations, spend greater time in proximity to other individuals than did older juveniles. That subadults, but not older juveniles, achieved higher return rates for DtA foods while in proximity of other individuals suggests that individuals in each of these age classes spaces themselves in accordance with achieving the highest return rates. One explanation for this pattern could be that older juveniles go through a phase of individual exploration where improvements in foraging efficiency are made mainly through trial and error as opposed to social learning. It is then possible that subadults enter a new phase of social learning where they learn to perfect their foraging techniques. If this is accurate, it may be the case that younger juveniles gain information mostly about dietary breadth through social learning while subadults learn specific foraging techniques. More detailed studies on the information gained by immature capuchins at different stages of development will be necessary to confirm or refute this theory. Another possibility, given the small number of individuals in each age class, is that one or more unusually independent older juveniles, dependent subadults, or both, were present in this study population, which may not accurately reflect the patterns of the average capuchin population.
Results from this study indicate that capuchin monkeys exhibit a prolonged period of development for foraging behaviors. If an individual has a prolonged development with respect to foraging skills, he/she is likely to benefit from high social tolerance in order to take advantage of social learning opportunities. Reliance on a DtA diet and a high level of social tolerance are both hypothesized to increase rates of social learning (Coussi-Korbel and Fragaszy, 1995; van Schaik et al., 1999; Rapaport and Brown, 2008; Reader et al., 2011). Results of this study support this hypothesis. Younger juveniles, who have the least experience and therefore the most to gain from social learning, spend more time in proximity to other individuals than any other age class, when foraging for DtA foods, but not when foraging for EtA foods. Furthermore, as a result of foraging in proximity of other individuals, presumably more experienced foragers, when foraging for DtA foods, young juveniles increase their foraging efficiency which suggests that nutritional benefits are accrued along with information.

While the results from this study indicate that foraging for DtA foods leads to greater rates of proximity, it is still not clear why this is the case. More detailed studies on the behaviors of individuals while in proximity to others will be necessary to determine what information is transferred. Studies that record which behavior and/or object is the target of an individual’s attention while in proximity to another, will be especially useful. While juveniles are found to spend more time in proximity to other individuals while foraging for DtA foods, this does not necessarily reflect social learning. An indication that social learning may not be occurring would be if the juveniles are found to not pay special attention to any particular object or behavior associated with the proximate individuals. In this case, an alternative explanation is that proximity is serving
to protect juveniles from predation at a time when greater concentration is necessary,
rather than providing them with information about what to eat or how to obtain or process
a food item.
Chapter 4: A Test of the Ecological Complexity Model for Long Juvenile Periods in White-faced Capuchin Monkeys (Cebus capucinus)

Abstract

The ecological complexity hypothesis proposes that long juvenile periods evolve in response to reliance on a complex dietary niche. The premise is that juveniles require an extended developmental period to learn complex foraging skills, and that these skills are necessary for efficient acquisition of foods that are difficult to extract. Capuchin monkeys in the wild provide an ideal opportunity to test this model because they have long juvenile periods relative to other primates with a similar body size, and they are known to rely on a diet that is notably more difficult-to-acquire than the diets of closely related and sympatric primate species. In this study I test two predictions from the ecological complexity hypothesis on wild capuchins in Costa Rica: that capuchin monkeys achieve adult foraging return rates for difficult-to-acquire food items late in the juvenile period; and that variance in return rates is at least partially associated with differences in foraging skill. In support of these predictions, I found that adults had significantly higher foraging return rates for difficult-to-acquire food items than any other age class. In addition, food items that were difficult to acquire were foraged at nearly identical rates by adult males and significantly smaller adult females, suggesting that strength does not explain all variation in return rates. Together these results imply that capuchin foraging skills do require a long learning phase, and that the ecological
complexity hypothesis should not be ruled out as an explanation for the adaptation of long juvenile periods in capuchin monkeys.

**Introduction**

Compared with mammals of similar body size, primates have long juvenile periods (Wootton, 1987; Charnov and Berrigan, 1993). Despite substantial research on this topic, the reasons for this long delay in onset of reproduction remain unclear (Pereira and Fairbanks, 2002). Capuchin monkeys exhibit an extraordinarily long juvenile period for a primate of their size (Harvey and Clutton-Brock, 1985; Ross, 1991), with an age at first birth that is similar to that of monkeys several times their size (Ross, 1991). Thus, whatever factors led to the adaptation of long juvenile periods in primates may be especially pronounced in capuchins.

Several theories have been proposed to explain the evolution of long juvenile periods in primates and other mammals. It should be noted that the factors outlined in these theories are not mutually exclusive but instead have likely acted in concert. The ecological and social complexity hypotheses (ECH and SCH) maintain that organisms occupying more complex ecological or social niches accrue greater rewards from skill and knowledge, and that this acts as a selective pressure for longer juvenile periods. These hypotheses are also referred to as the “needing-to-learn” hypotheses (Ross and Jones E., 1999) and differ from each other in that the ECH posits that reliance on a difficult-to-acquire diet requires additional time spent learning various food acquisition skills (Clutton-Brock and Harvey, 1980; Gibson, 1986; Kaplan et al., 2000), while the SCH proposes that a complex social environment selects for long juvenile periods.
(Dunbar, 1992, 1998; Barton, 1996; Joffe, 1997). A third model, the developmental constraints model hypothesizes that brains require a long time to fully develop even after they reach adult size and, thus, long juvenile periods are a result of the time it takes larger brains to mature (Sacher and Staffeldt, 1974; van Schaik et al., 2006). A fourth model is the ecological risk avoidance hypothesis which posits that by growing slowly, juveniles decrease their daily nutrient requirements and thus are better able to avoid risk of starvation from too little food. This hypothesis is thought to be particularly relevant when predation is a high risk because juveniles rely on protection from other group members but suffer disproportionately from costs of feeding competition in large groups (Janson and van Schaik, 1993). A final model that explains variation in timing at first reproduction is the demographic model, which posits a relationship between mortality and the length of the juvenile period. A long juvenescence can only be adaptive when mortality rates are low because if mortality rates are high, the chance of dying before the onset of reproduction is greater, and thus will result in selection for earlier reproduction (Reznick and Bryga, 1987; Charnov and Berrigan, 1993). Low mortality rates are therefore a necessary precondition for long juvenile periods. Primates apparently have lowered mortality rates because they have long juvenile periods relative to other mammals of comparable size (Charnov and Berrigan, 1993). A cause or consequence of this long juvenile period is that primates grow more slowly (Charnov and Berrigan, 1993). A question that remains from this model is why primates exhibit these traits. The above models offer potential explanations that so far have some theoretical support, but largely lack empirical support (Pereira and Leigh, 2003).
Among primates, capuchin monkeys grow slowly (Leigh, 2001). In addition, capuchins have big brains relative to their body size (Hakeem et al., 1996; Hartwig, 1996; Rilling and Insel, 1999; Hartwig et al., 2011), are known for their complex dietary niche (Fragaszy et al., 2004 c), which in certain species regularly involves tool use (Ottoni and Izar, 2008), seem to exhibit triadic awareness in social contexts (Perry et al., 2004) and have relatively complex social conventions (Perry, 2011). Therefore, each of the above models could explain the long juvenile period of capuchin monkeys.

In this study I test whether the ECH is a viable model to explain the adaptation of long juvenile periods in white-faced capuchin monkeys. The logic behind the ECH is grounded in Life History Theory (Ross and Jones E., 1999; Kaplan et al., 2000). Based on the premise that organisms have a finite amount of energy to spend on three basic investments throughout life (growth, reproduction, and maintenance), Life History Theory describes how organisms maximize their fitness by adjusting the amount of energy put toward each of these three investments according to age and condition (Gadgil and Bossert, 1970). The Embodied Capital Theory of Evolution expands on the three categories on which energy can be spent to include skill and knowledge as components of an organism’s “embodied capital” (Kaplan et al., 2001). In turn, skill and knowledge can be used to increase energy capture rates, survival, and reproduction. According to the ECH, organisms that rely on a more complex diet should benefit from spending more time and energy on skill acquisition. During the juvenile period, when individuals are acquiring much of the skills and knowledge necessary to survive and eventually reproduce, this is energy not spent on growth or maintenance. Thus, if individuals are spending more energy on skill acquisition, they should exhibit slow growth rates. Slow
growth is associated with long juvenile periods (Charnov and Berrigan, 1993). To support the ECH it must be demonstrated that foraging skill levels continue to improve throughout the majority of the juvenile phase and approach those of adults only near the end of juvenility. That is, foraging skills require a long time to master and thus could feasibly lead to a delay in reproduction.

If increased energy spent on skill acquisition is leading to longer juvenile periods in capuchins, in order for inhabitation of this complex dietary niche to be adaptive, the skills that require a long time to learn must lead to higher fitness, presumably through higher return rates. Higher adult foraging return rates could increase fitness in at least two different ways. First, faster foraging rates could lead to greater energy intake, which could then lead to more energy available for reproduction. Second, it could decrease the amount of time that is necessarily spent foraging, thereby freeing time for other fitness increasing activities such as predator avoidance, social networking, or territory defense. Given that capuchins spend a significant proportion of their daylight hours foraging, (at least 30%; Fragaszy and Boinski, 1995; McCabe, 2005; Melin et al., 2009), either of these benefits are likely to have an impact on fitness even if the differences in forage rates are small.

In order to support the ECH, it is not enough to demonstrate that return rates are not maximized until near the end of the juvenile period. Foraging advantages due to larger body size and a higher social status are likely to affect measurements of efficiency that may have little to do with underlying skill, and thus need to be controlled for. It is possible that foraging return rates are not maximized until near the end or after the juvenile period, but that the differences in return rates could be explained entirely by
differences in strength and access to resources. If this were the case, the ecological risk avoidance model would be a more appropriate model to explain long juvenile periods in capuchins than the ECH. Beyond this, data from this study will not provide implications for any of the other models described above.

Among nonhuman primates, the capuchin diet is remarkable in that (a) it contains a large amount of animal protein for a monkey of its size (Janson and Boinski, 1992), (b) capuchins hunt for relatively large vertebrates such as squirrels and nestling coatis (Rose, 1997), and (c) when foraging on plant matter they rely almost exclusively on the nutrient-dense, often protected storage and reproductive organs of plants (Gibson, 1986; Fragaszy et al., 2004 c). For example, capuchin monkeys are known to frequently exploit foods with elaborate defense mechanisms such as items with spines or thorns, biting or stinging insects, or food encased in hard shells (Fragaszy et al., 2004 c). Given this dietary niche, it seems likely that capuchins would take a long time to acquire the skills necessary to forage at an adult level.

Previous studies that have looked at foraging efficiency across age classes in capuchin monkeys have found increasing efficiency with age, but have yet to find significant differences between older juveniles and adults (Janson and van Schaik, 1993; Fragaszy and Boinski, 1995; Gunst et al., 2008, 2010). Three out of four of these studies found a general trend (not statistically significant) where older juveniles were less efficient than adults. Thus, if real differences in efficiency exist between these age classes, they are likely to be small. However, in the past, return rates have been calculated as the frequency of intervals where foraging and/or feeding either did or did not happen (Fragaszy and Boinski, 1995; Gunst et al., 2008) rather than as the exact
amount of time spent foraging. In an attempt to achieve a higher level of precision I measured actual time spent on each forage behavior and the total number of bites taken. Precise measurements of foraging behaviors and bites have the potential to reveal small differences in foraging times with smaller sample sizes.

Another major difference in this study was an assessment of how skill and strength influence foraging return rates. Ideally, one could control for variation due to strength and access to resources and then could determine whether any of the remaining variation in return rates could be explained by skill. Unfortunately, strength and access to resources are difficult to control for, both are likely to interact with skill, and several additional confounding factors should be considered. The first factor is time allocation. According to optimal foraging theory, time allocation should be expected to reflect return rates (Pyke et al., 1977); if an individual is more likely to achieve high return rates for a particular foraging behavior, he/she should spend more time engaging in that behavior.

Strength is likely to affect time allocation which, in turn, is likely to affect skill. Stronger individuals should be able to achieve higher return rates for foods that require a greater amount of strength, and thus, would be predicted to allocate more time to these foods than weaker individuals. It is likely that this greater time allocation would then lead to increased skill. However, it is also possible that higher return rates could lead to less time allocated to foraging for items because an individual would be able to acquire an optimal quantity of the food item more quickly. Thus, strength and skill difference probably affect time allocation but more studies are needed to determine the nature of these relationships. For food items that require both strength and skill to obtain, it may be informative to consider the time allocated to foraging for that item.
Another factor that is likely to affect return rates is dominance. Even without an overt display of aggression or submission, it is likely that more dominant individuals are able to occupy preferred foraging positions when such positions exist (Janson, 1990 a). These positions then may allow for higher return rates that do not reflect skill or strength. Thus, when dominance could lead to a better forage position, it needs to be controlled for.

A final factor that has been demonstrated to affect return rates is dichromatic versus trichromatic vision (Melin et al., 2010). Capuchin males are dichromatic (red-green color blind) while on average two-thirds of females are trichromatic and the remaining one-third are dichromatic (Melin et al., 2010). In one study, trichromatic individuals had higher return rates on the types of fruit that turn reddish when ripe (Melin et al., 2009), while in another study dichromatic individuals had higher return rates on color-camouflaged prey items such as cryptic insects (Melin et al., 2010). However, a separate study did not find a significant relationship between color vision phenotype and energy return rates for reddish fruits (Vogel et al., 2006). Ideally, color vision phenotype would be controlled for along with strength, dominance, and time allocation. Unfortunately, the data on which females are dichromatic versus trichromatic is currently unavailable for this study population.

With each of these potentially confounding factors in mind, I employed several approaches to help distinguish the effects of skill versus strength. First, I assigned difficulty ranks to each food item and examined the partial correlations between strength and skill level with return rates. Next, I compared the foraging efficiencies of adult males and adult females who exhibit a substantial degree of sexual dimorphism. For this comparison, significantly higher return rates by males would suggest that either, a)
strength has a large effect on foraging efficiency, or b) males are able to monopolize access to better (relatively easier-to-acquire) food items within each food species. Similar return rates for males and females could be the result of at least three different scenarios: 1) strength does not have a large effect on foraging efficiency, 2) strength does have a large effect on foraging efficiency but only up until a certain threshold which adult females have already attained, or 3) females and males achieve similar return rates through different methods with males taking advantage of strength and females taking advantage of skills.

In a final attempt to determine whether skill acquisition is still incomplete toward the end of juvenescence, I compared foraging return rates between adult females and subadult females. Subadult females are near the size of adult females; Fragaszy and Adams-Curtis (1998) found that a captive group of tufted capuchins had achieved 88% of their adult weight by five years of age. This is likely to be slightly lower in wild conditions where food is generally more limited. Given that adult and subadult females are of similar size, if strength correlates closely with size, adults and subadult females should have similar strength. Therefore it is likely that higher return rates in adult females, compared with those of subadult females, would be, at least partly, due to differences in skill.

Predictions

The ecological complexity model would be supported if 1) older juveniles have significantly lower foraging return rates for difficult-to-acquire food items than adults,
and 2) these differences in foraging return rates are partly associated with differences in skill.

Methods

Study site: This study was conducted at the Pacuare Nature Reserve in the Limón Province of Costa Rica. The reserve is located 25 km north of the capital Puerto Limón, between the Tortuguero Canals and the Caribbean Sea (10°10’N, 83°14’W). It contains 800 ha of mixed primary and secondary, tropical, wet, lowland forest. The three study groups have territories in the southern portion of the reserve. Their habitat consists of secondary, primary, and swamp lowland forest habitats.

Study groups: I began habituating the three study groups, “A”, “B” and “C”, intermittently in 2005. I used body size, sex, and unique physical features such as cap line irregularities, head shape, and scars to identify each individual. Prior to the start of this study I could reliably identify each study individual. For this study, my field assistants and I collected data on 49 individuals within the three study groups. Subjects included 6 infants (age 0-1 year), 5 younger juveniles (ages 1-3 years), 5 older juveniles (ages 3-5 years), 6 subadults (ages 5-7 years) and 27 adults (older than 7 years). When I had observed subjects at an early phase of infancy (while still riding on the mother’s neck) I designated my earliest sighting as his/her birth month. I took many photos of each individual throughout this study and during the previous pilot studies and habituation periods that began in 2006. For juvenile and subadult subjects who I had not observed in early infancy, I estimated their ages by comparing my earliest pictures of them with the chronological pictures of individuals of known ages. Age classes were defined in a
similar way as other studies that examine foraging in juvenile capuchins (MacKinnon, 2006; Gunst et al., 2008) and were designed to reflect differences in experience, size, reproductive activity, and tolerance. Females were classified as adults if they were estimated to be greater than 7 years old or if they had given birth. In the wild, the average age at first birth for *Cebus capucinus* is seven years at Santa Rosa National Park (Fedigan and Jack, 2001), and 6.22 years at Lomas Barbudal (Perry et al., 2012). Males were also classified as adults if they were estimated to be greater than 7 years old, to maintain a similar level of experience for the adult age class, although males grow for several more years (Fedigan et al., 1996). Younger juveniles are more highly tolerated in feeding contexts (Janson, 1985, 1990 a), and in captivity are between 50 and 80% of an adult female body weight (Fragaszy and Bard, 1997). Older juveniles receive an intermediate amount of aggression in foraging contexts and still have some growth left to do. Subadult females have reached or are close to adult size, but have generally not started to reproduce (Di Bitetti and Janson, 2001). Subadult and adult males receive the most aggression from the alpha male and are the least tolerated at preferred feeding sites (Janson, 1985). To look at changes in return rates into adulthood, adults were also assigned an estimated age of either 10, 15, 20, or 25 based on whether they looked young, middle-aged, mature, or older respectively. The head shape, number of scars, amount of facial fur, and number of age spots were used to estimate the ages of adult males. The length of eyebrows, color of eyebrows, and number of age spots were used to estimate ages of adult females.

*Data collection*: Data for this study was collected from October 2009 through August 2010. I spent a total of seven and a half months prior to this, identifying and
habituating individuals in each of the three study groups. Along with a field assistant, I conducted continuous focal follows (Altmann, 1974) on individuals engaging in foraging activities. Focal follows lasted for the duration of a foraging event on one food type; if the focal individual stopped foraging or changed to a different food item the focal follow was ended. Subjects were chosen based on visibility and the food item being foraged, such that, each individual was not followed more than once per day for each food item. During focal follows, I narrated behaviors while my field assistant recorded them in real time on an HP iPaq using Noldus Observer 8.0 and Pocket Observer 3.1 behavioral data collection software (Noldus Information Technology, Wageningen, Netherlands). Inter- and Intra- observer reliability were measured by comparing focal follow entries created from digital voice recordings of sample focal follows. Data were kept after a ≤1 second discrepancy in foraging behavior timing was achieved per minute test follow (duration: three-five minutes). Because this study was specifically focused on skill acquisition rather than other social factors that might compromise foraging efficiency, focal follows were only included in the dataset if aggression and displacements did not occur (i.e. subject access to food items was not obviously inhibited by social interactions). In addition to focal follows, every thirty minutes, my assistant and I carried out a scan sample. Data from scan samples were used to calculate time allocation. Scan samples (Altmann, 1974) were conducted every 30 minutes while in the presence of a study group. Scan samples lasted for 5 minutes during which time the first behavior observed for each individual positively identified over the interval was recorded.

Return rates: Return rates for this study are computed as bite count per forage time. Forage time consisted of three non-overlapping behaviors: search, harvest, and
process. Search was defined as the visual, olfactory, and/or manual investigation of potential food sites. Harvest was the removal of a food item from a substrate. Process was manipulation of a food item that an individual already had in his/her possession in order to improve ingestion or digestibility. Total forage time is the total duration of these three behaviors. Once a focal individual had a food item in his/her possession each bite was recorded. Ingestion time is not included as forage time because the factor of interest is not how fast an individual can put food into his/her mouth once it is ready to ingest, but rather, how efficient he/she is at obtaining and preparing food items for ingestion.

Food difficulty levels: Food items were assigned a difficulty level for each of the different components of foraging: search, harvest, and process. In order to distinguish difficulty due to strength from difficulty due to skill these categories were assigned separately according to two sets of criteria. Strength levels were categorized by whether no (“1”), moderate (“2”), or intense (“3”) force was necessary to complete the behavior. Intense force was defined as force that required leveraging using body positions or use of an object by older juveniles, subadults, and/or adults. Examples of foraging behaviors that require intense force include tearing apart canes in search of embedded larvae or pounding open a hard-shelled fruit on a branch. A moderately forceful manipulation was defined as one that required solely manual pressure by older juveniles, subadults, and/or adults. Examples include removing a fruit from a thick stem or removal of a thin, hard shell. For skill, the difficulty classification was based on whether zero (“1”), one (“2”), or greater than one (“3”) skillful manipulation was necessary to complete the behavior. A skillful manipulation was defined as an action that requires one of the following: a dexterous manipulation, sequence-specific, condition-specific, or location-specific action.
Examples include avoiding defense systems such as thorns or spikes, and locating larvae within canes. The values for total strength and total skill levels were computed by taking the sum of the difficulty levels for search, harvest, and process. All food items in this dataset were successfully acquired by each age-sex category and, thus, strength levels are designed to reflect the extra time it might take a weaker individual to acquire a food item, rather than whether an individual is likely to obtain a particular food item at all. Total difficulty is equal to the sum of total strength and total skill (see Appendix A for a description of search, harvest, and process requirements for the top ten most commonly eaten food items, and their associated strength and skill, and total difficulty level assignments). Finally, in order to compare foods that were relatively difficult to acquire with foods that were relatively easy to acquire, foods were split into three categories (roughly thirds) based on their total difficulty score. Foods that had scores in the highest range were categorized as difficult to acquire (DtA), while foods that had scores in the lowest range were categorized as easy to acquire (EtA). Although this method of level assignment was ordinal and thus less specific and more subjective than strictly quantitative measurements, it provides an easy and practical system for separation of foraging behaviors into strength and skill levels.

Statistics: I carried out all statistics in R v. 2.11.1 (R Development Team 2010). I used generalized linear mixed models (GLMMs) to examine the effect of age class on foraging return rates while controlling for the correlated structure of the data that results from different individuals contributing multiple and unequal numbers of foraging samples to the dataset. To carry out GLMMs in R, I used the lme4 package (Bates and Maechler, 2009). Subject identification and food item were random effects in all models.
presented here. Mixed effect models work well with longitudinal studies where there are repeated measures of the same subject (Crawley, 2007). Given that foraging return rates were computed from bite counts per forage time, the response variable is in counts, (is not normally distributed). Bolker et al. (2009) argue convincingly that using GLMMs is the best way to analyze non-normal data with random effects.

I used the following GLMM to model the effect of age class on return rates:

\[
\text{bite number} \sim \text{age class} + (1|\text{subject ID}) + (1|\text{food ID}) + (1|\text{observation number}) + \text{offset}(\log(\text{forage time})),
\]

\[
\text{family}=\text{poisson}
\]

In this model age class is the fixed effect, subject ID and food ID are random effects. Overdispersion occurs for many Poisson count models and if ignored can lead to an inappropriate model (Gelman and Hill, 2007). To determine whether dispersion had occurred in a model, I calculated the level of dispersion with the dispersion equation presented by Gelman and Hill (2007). When overdispersion is present for a Poisson model, observation number can be added as a random effect (Browne et al., 2005) to account for the additional variation. This is the technique I employed here. To examine the overall trend of change in return rates throughout the lifespan, I used estimated ages, including the estimated ages for adults, instead of age classes.

In order to examine the effect of strength vs. skill on foraging rates, first, I included both skill level and strength level into a GLMM to determine whether their respective partial correlations were significant when both of these difficulty levels were
included in the model. Next, I compared return rates of adult males and adult females for samples where they had foraged for DtA fruits. To do this, sex was added to a model with food item and subject identity as random effects. Given that adult white-faced capuchin males (average 3.68 kg) are significantly larger than females (average 2.54 kg) (Smith and Jungers, 1997), if strength is an important factor affecting variance in bite rates, adult males should have significantly higher bite rates than adults females. Last, I compared return rates for adult females and subadult females foraging on DtA fruits. Subadult females (ages 5-7 years) have completed most of their growth (Fragaszy and Bard, 1997) and are therefore likely to be nearly as strong as adult females, but still do not begin to reproduce until age 7 (Fedigan and Jack, 2001). If adult females have higher return rates for DtA fruits than do subadult females, it is likely that these differences stem largely from differences in skill rather than from differences in strength.

Results

Activity Budgets: Each age class spent roughly equal amounts of time foraging for fruit (roughly 25%), foraging for insects (≈15%), travelling (10-15%), socializing (≈25%), and resting (≈5%) (see Figure 4.1). When forage time is broken down by categories of fruits (easy, medium, and difficult) and insects (embedded and surface), each age class spend roughly the same proportion of time foraging for easy and medium fruits, and embedded insects (see figure 4.2). However, as age class increases from younger juveniles to adults, (but omitting subadult females), there is a trend whereby time spent foraging on surface insects decreases while time spent foraging on DtA fruits increases. Differences in time allocation could reflect differences in return
rates and corresponding optimal foraging strategies, different nutritional requirements, or both. Subadult females exhibit a foraging time allocation pattern that is more similar to younger juveniles than to older juveniles or adults.

Figure 4.1: Activity Budgets by Age Class

![Activity Budget Graph](image)

**Activity Budget**

- **Percent of Time**:
  - Forage Fruit
  - Forage Insects
  - Forage Unknown
  - Resting
  - Travelling
  - Other Solitary
  - Social

**Activity**

- Adults
- Subadults
- Older Juveniles
- Younger Juveniles
- Infants
Return rates for DtA fruits: For DtA fruits, there were no significant differences between male and female return rates for any age class. Therefore, for this analysis, sexes were combined. There were significant differences ($p<0.05$) between adults and all other age classes with adults achieving significantly higher return rates (see Table 4.1, Figure 4.3a). One unexpected result for return rates of DtA fruits is the low foraging efficiency exhibited by subadults. If return rates are the result of differences in strength and skill, we should expect subadults to do better than the older and younger juveniles given that they are both older and larger. This finding indicates that there are one or more additional factors influencing return rates. The sharp difference in return rates between adults and all other age classes is not present when adults are divided into age classes rather than lumped together (figure 4.3b and Table 4.2). Instead return rates appear to remain relatively constant throughout the juvenile period and then start to increase throughout
young- and mid-adulthood, reaching a maximum in mature adults. There is then a sharp
decrease between mature adults and older adults. Mature adults have a significantly
higher return rate for DtA fruits, than all other age classes except for middle-aged adults
(see Table 4.2).

Table 4.1: Bite Rate versus Age Class for DtA (top) and EtA (bottom) Fruits

| Age Class       | Bite Rate | Estimate | Std. Error | z value | Pr(>|z|) |
|-----------------|-----------|----------|------------|---------|---------|
| DtA Fruits      |           |          |            |         |         |
| Adults          | 0.07      | -2.71    | 0.29       | -9.28   | <0.001  |
| Subadults       | 0.02      | -3.91    | 0.49       | -2.67   | 0.008*  |
| Older Juveniles | 0.03      | -3.61    | 0.43       | -2.41   | 0.016*  |
| Younger Juveniles | 0.03    | -3.66    | 0.43       | -2.52   | 0.012*  |
| EtA Fruits      |           |          |            |         |         |
| Adults          | 0.15      | -1.90    | 0.22       | -8.81   | <0.001  |
| Subadults       | 0.21      | -1.55    | 0.25       | 1.72    | 0.086   |
| Older Juveniles | 0.15      | -1.93    | 0.27       | -0.13   | 0.896   |
| Younger Juveniles | 0.18    | -1.70    | 0.26       | 0.97    | 0.332   |

Model Output interpretation: Estimates are equal to the log of the predicted bite rate. Bite rates
equal $e^{\text{Estimate}}$. P-values for adults indicate the probability that the adult bite rate is significantly
different from $e^0 (=1)$ and are thus not meaningful for this study. P-values for the other age classes
indicate the probability that the respective age class has an average bite rate that is the same as the average
bite rate of adults. *indicates significance at an $\alpha=0.05$ level.
Figure 4.3a: Return Rates for DtA vs. EtA Fruits

Return Rates for DtA vs. EtA Fruits

Figure 4.3b: Hard Fruit Return Rates with Adult Age Classes

Hard Fruit Return Rates with Adult Age Classes
Table 4.2: Bite Rate versus Age Classes with Adults Divided by Estimated Age For DtA (Top) And EtA (Bottom) Fruits

| Age Class        | Ages | Bite Rate | Estimate | Std. Error | z value | Pr(>|z|) |
|------------------|------|-----------|----------|------------|---------|---------|
| **DtA Fruits**   |      |           |          |            |         |         |
| Mature Adults    | 20   | 0.09      | -2.37    | 0.35       | -6.73   | <0.001  |
| Younger Juveniles| 2-3  | 0.02      | -3.72    | 0.45       | -3.44   | 0.001*  |
| Older Juveniles  | >3-5 | 0.03      | -3.64    | 0.45       | -3.29   | 0.001*  |
| Subadults        | >5-7 | 0.02      | -3.95    | 0.51       | -3.48   | 0.001*  |
| Young Adults     | >7-10| 0.04      | -3.31    | 0.43       | -2.59   | 0.010*  |
| Middle-aged Adults| 15  | 0.07      | -2.64    | 0.46       | -0.70   | 0.482   |
| Older Adults     | 25   | 0.01      | -4.59    | 0.70       | -3.27   | 0.001*  |
| **EtA Fruits**   |      |           |          |            |         |         |
| Mature Adults    | 20   | 0.19      | -1.67    | 0.25       | -6.74   | <0.001  |
| Younger Juveniles| 2-3  | 0.19      | -1.64    | 0.26       | 0.12    | 0.909   |
| Older Juveniles  | >3-5 | 0.15      | -1.87    | 0.24       | -0.78   | 0.437   |
| Subadults        | >5-7 | 0.23      | -1.49    | 0.30       | 0.76    | 0.446   |
| Young Adults     | >7-10| 0.17      | -1.80    | 0.28       | -0.46   | 0.646   |
| Middle-aged Adults| 15  | 0.17      | -1.80    | 0.25       | -0.49   | 0.622   |
| Older Adults     | 25   | 0.06      | -2.78    | 0.38       | -2.86   | 0.004*  |

Model Output interpretation: Estimates are equal to the log of the predicted bite rate. Bite rates equal \( e^{\text{Estimate}} \). Mature adults had the highest predicted return rates and were used for the reference group. P-values for mature adults indicate the probability that the mature adult bite rate is significantly different from \( e^{0} (=1) \) and are thus not meaningful for this study. P-values for the other age classes indicate the probability that the respective age class has an average bite rate that is the same as the average bite rate of mature adults. *indicates significance at an \( \alpha=0.05 \) level.
**Return rates for EtA fruits:** For EtA fruits, there was a significant difference between males and females for younger juveniles only: young juvenile males had a bite rate that was 57% that of young juvenile females, p=0.034. When foraging for EtA fruits, there were no significant differences between adults and any other age class. However, the comparison between adults and subadults approached significance with subadults having slightly higher return rates (p=0.086 Poisson model, p=0.075 negative binomial model) (see Table 4.1, Figure 4.4a). The same pattern is evident when adults are divided into separate age classes (see Figure 4.4b and Table 4.2). There are no significant differences between mature adults and any other age class except older adults, for EtA fruit. Older Adults forage significantly slower for both DtA and EtA fruits.

**Figure 4.4a: Return Rates for EtA Fruits**

![Return Rates for EtA Fruits](image_url)
Return rates for DtA vs. EtA insects: Insects fell into two categories: embedded insects which were DtA, and surface insects which were EtA. There were no significant differences between adults and any other age class for EtA or DtA insects (see Figures 4.5a, 4.5b). However, there was a significant difference between adult male and adult females when foraging for embedded insects: males foraged at an estimated rate 299.8% that of females (p=0.002). It is likely that this is due to the different types of embedded insects that males foraged for compared with females. Males generally preferred termite mounds which produced many, relatively small bites, while females generally preferred to extract larva from canes which produced larger, but fewer bites. There were no significant sex differences in return rates for surface insects.
Figure 4.5a: Return Rates for Embedded Insects

Return Rates for Embedded Insects

- Adults
- Subadults
- Younger Juveniles

Age Class

Figure 4.5b: Return Rates for Surface Insects

Return Rates for Surface Insects

- Adults
- Subadults
- Older Juveniles
- Younger Juveniles

Age Class

- Females
- Males
Skill vs. strength: The purpose of the next set of analyses was to examine whether the increases in return rates with age, that were observed for hard fruits, were partly the result of increases in skill, or if they can be explained entirely by strength. Within hard fruits there was variation in harvest skill and strength levels, and also in process skill and strength levels. However, there was almost no variation in the search strength, search skill, or total strength levels (see Figure 4.6). Therefore, in order to determine how skill and strength levels may account for variation in the return rates of hard fruits, the GLMM statistical models included skill and strength levels for harvest or process to predict return rates (see Table 4.3). With harvest strength and skill levels as predictors of bite rates, both were significant, but the association of strength with bite rate was positive while the association of skill with bite rate was negative. That is, increases in strength requirements lead to higher bite rates while increases in skill requirements leads to lower bite rates. For process strength and skill levels, the same pattern is seen, but here, strength level is not a significant predictor of bite rate. Thus both younger ages and higher skill requirements are associated with decreases in return rates (slower foraging rates) in DtA fruits. However, higher strength requirements are associated with increases in return rates. These results indicate that increased skill, not strength, may allow adults to forage more efficiently.
Figure 4.6: Correlation between Skill and Strength Levels for Fruits

Table 4.3: Hard Fruit Bite Rate Predicted by Harvest (above) and Process (below) Strength and Skill Levels

|                | Bite Rate | Estimate | Std. Error | z value | Pr(>|z|) |
|----------------|-----------|----------|------------|---------|---------|
| Intercept      | 0.04      | -3.32    | 0.65       | -5.09   | 0.000   |
| Harvest strength level | 2.59      | 0.95     | 0.43       | 2.22    | 0.027*  |
| Harvest skill level   | 0.42      | -0.86    | 0.32       | -2.73   | 0.006*  |

Model: lmer(bite count ~ harvest strength + harvest skill + (1|focal_individual) + (1|food_dificulty_id) + (1|observation#) + offset(log(forage_time)), family=poisson)

|                | Bite Rate | Estimate | Std. Error | z value | Pr(>|z|) |
|----------------|-----------|----------|------------|---------|---------|
| Intercept      | 0.50      | -0.70    | 0.97       | -0.72   | 0.470   |
| Process strength level | 1.43      | 0.36     | 0.29       | 1.24    | 0.217   |
| Process skill level   | 0.26      | -1.35    | 0.56       | -2.40   | 0.016*  |

Model Output interpretation: Estimates are equal to the log of the predicted bite rates. The bite rate for strength levels indicate the factor increases in bite rate for each one unit increase in strength level, while skill level is held constant. The bite rates for skill levels indicate the factor decreases in bite rate for each one unit increase in harvest skill, while strength level is held constant. *indicates significance at an α=0.05 level.
Another tactic to examine the effect of strength vs. skill is to look at bite rates for adult males versus adult females. Given that adult males are significantly larger than adult females and presumably considerably stronger, if strength differences are responsible for a significant amount of the variation in bite rate, adult males should have higher bite rates than adult females for DtA fruits. In fact, adult males were found to have very similar (not significantly different) return rates compared to adult females for these foods: males took 1.01 bites for every bite that a female took, p=0.978 (see Figure 4.7). As mentioned in the introduction, however, this could mean one of several things: a) strength does not have a large effect on return rates, b) once individuals have reached the size of an adult female strength does not have a large effect on return rates, or c) strength does have a large effect on return rates but females are able to overcome their lack of strength with a heavier reliance on skill.

**Figure 4.7: Return Rates for DtA Fruits: Adult Males, Adult Females, and Subadult Females**

![Return Rate for DtA Fruits](chart.png)

- Adult Male
- Adult Female
- Subadult Female

*Age-Sex Category*
One last comparison should help to reveal whether individuals are still acquiring skill throughout the juvenile period. Subadult females are approximately the same size as adult females but have not begun to reproduce. If these subadult females are delaying reproduction in order to acquire more foraging skills, then return rates should still be lower than those of adult females. Return rates for DtA fruits for subadult females were on average only 32.8% that of adult females (see Figure 4.7). This difference approached significance (p=0.052) and further suggests that skill acquisition is still underway late in the juvenile period.

Discussion

While it has long been noted that certain species including humans, are characterized by long juvenile periods (Harvey and Clutton-Brock, 1987; Ross, 1998; Robson et al., 2006), the socio-ecological factors that select for an extended juvenescence remain unclear (Ross and Jones 1999; Pereira and Leigh 2003). The foraging ecology of both humans and capuchins is likely to require more investment into learning and skill acquisition than that of other, closely-related species. Each is known to exploit a wide variety of dietary items that are difficult to obtain and that other, closely-related species do not eat (Kaplan et al., 2000; Fragaszy et al., 2004 c). According to the ECH, species living in a complex dietary niche delay the onset of reproduction in order to develop skills for efficient exploitation of difficult-to-acquire food items.

Results of this study provide support for the ECH for capuchin monkeys. In order to support the ECH, two conditions needed to be met. The first was that juveniles do not
achieve adult return rates until near the end of the juvenile period. This would indicate that learning to forage could take a long time and thus feasibly select for a delay in the onset of reproduction. The second condition was: if older individuals are in fact more efficient foragers for difficult-to-acquire food items, this variance must be partially due to differences in skill.

In support of the first condition, mature adult capuchins had significantly higher return rates than any other age class except for middle-aged adults, for DtA, but not for EtA fruits. This implies that reliance on difficult-to-acquire food items poses challenges to juveniles and may indeed lead to a long period of learning. In support of the second condition, three lines of evidence imply that variation in skill explains some of the observed variance in return rates for DtA fruits. First, the partial correlation of skill was a significant predictor of bite rates for DtA fruits with strength in the model: holding strength constant, each increase in skill requirement results in a predicted decrease in bite rate. Thus it is likely that a significant portion of the variation in return rates, that was observed across age classes for DtA fruits, can be explained by adults’ greater skill in harvesting and processing DtA fruits. On the other hand, with skill held constant, an increase in harvest strength requirement is associated with a higher bite rate. It is surprising that increases in strength requirements would lead to higher returns in bite rates. Perhaps higher strength requirements do not greatly hinder the foraging rate of capuchin monkeys but generally lead to larger food resources, and thus higher return rates.

Two comparisons further imply that the observed variation in return rates, for DtA fruits, was at least partially due to differences in foraging skills and not solely due to
differences in strength. The very similar return rates for DtA fruits by adult females and significantly larger adult males imply that strength does not explain a significant amount of the variation in return rates, at least for individuals who have achieved the strength level of an adult female. It is not unlikely that males and females achieve these similar return rates through different means, where, males may take advantage of their strength while females may rely more on skills. If this were the case, it would not change the general conclusion that skill level is an important factor influencing return rates, however, it could mean that the acquisition of skill is less important for males.

The second comparison sought to examine whether skill acquisition remains incomplete toward the end of the juvenile period in females specifically. Subadult females, who are nearly equal in size to adult females, had lower return rates for DtA fruits compared with adults. Female subadults are likely to have similar strength to adult females, thus, this difference in return rates is likely to be the results of differences in skill. Similarly, the pattern whereby return rates are not maximized until well into adulthood well after the completion of growth, when strength levels have presumably remained stable for quite some time, further suggests that skill acquisition is an important factor in determining return rates for DtA fruits.

Thus, results from this study support two key predictions of the ECH which proposes that reliance on a difficult-to-acquire diet requires additional time spent learning and selects for a long juvenile period: 1) capuchins do not achieve adult-level return rates on DtA foods until the end of the juvenile period, (and even then continue to improve their return rates for quite some time), and 2) the reason for this delay seems to stem at least in part from differences in skill. There are at least two possible inconsistencies
however. First, if capuchins require a long time to mature in order to learn foraging skills, why do subadults not demonstrate higher return rates than juveniles for DtA fruits? One potential explanation is that, due to their low return rates, younger and older juveniles only forage for DtA fruit items in the most favorable conditions. On the other hand, subadults, who should be more skilled at foraging, might take on DtA fruits in less favorable conditions (such as when they are rarer or fewer are ripe). This would result in apparently low return rates for subadults, despite greater skill and strength. Subadults are less tolerated at preferred food sites (Janson, 1990 a), which may be because they are more skilled at foraging and therefore viewed more as competition, by adults. Thus, less favorable foraging conditions might be all that is available to subadults. More data are necessary to confirm or refute this theory.

A second possible inconsistency is that adults did not have significantly higher return rates when foraging for either class of insect (surface or embedded). One possible explanation for this result is that juveniles are able to learn the skills necessary to forage for all insects, but not all fruits, at adult efficiency levels, by a young age. Another possible explanation is that the solitary nature of insect foraging is more reflective of foraging skills than is fruit foraging due to less scramble competition. Although this second possibility should not be ruled out, there are several reasons why it seems improbable here. First, no foraging events with displacements or aggression were included in the dataset, making it less likely that dominance was allowing some individuals better access to fruit resources. Second, DtA foods are not necessarily foods that are closely spaced (easily monopolized). Palm fruits are an exception. They are both difficult to forage and tightly packed. When palm fruits were removed from the analysis
the same trend with similar return rates was observed for DtA fruits as when palm fruits were not excluded. Therefore, it appears plausible that difficult-to-acquire fruits pose relatively tricky challenges for juvenile foragers, and that these challenges may require a long learning period. Foraging for insect foods, on the other hand, appears to be mastered by individuals in this population at a young age.

A limitation to this study stems from the difficulty in controlling for differences in access to resources due to dominance rank. Although it was easy to avoid using samples with overt displays of dominance such as aggression or displacements, it is very likely that predetermined social rank affects access to food resources without the need for an overt display of status, as was found by Vogel (2005). For example, low ranking individuals are likely to remain in less preferred feeding positions if past interactions at a particular forage site resulted in aggression. To fully control for differential access to resources, individuals would have to be separated from other group members, such as in a laboratory setting. Another possibility would be to verify the results of this study after the dominance hierarchy is fully known. There were too few interactions involving overt displays of dominance and submission in this dataset to confidently determine or control for social rank.

A final limitation is the cross-sectional as opposed to longitudinal nature of this study. Although the results presented here imply that juveniles continue to increase foraging efficiency throughout the juvenile period and beyond, measurements of foraging efficiency on the same individual throughout the juvenile period would provide more concrete evidence.
Chapter 5: The Nutritional Value of Difficult-to-Acquire Foods in
White-Faced Capuchin Monkeys: Implications for Tool Use, Brain Size,
and Long Juvenile Periods

Abstract

Exploitation of difficult-to-acquire (DtA) foods has been linked to several other
traits including tool use, a large brain relative to body size, and slow life histories.
Capuchin monkeys take advantage of many DtA items. Reliance on a DtA diet is likely to
pose significant energetic costs to all individuals and additional costs to juveniles who
lack the strength and experience of older group members. To investigate the advantages
of this dietary niche, this study examines four potential benefits of obtaining DtA
compared with easy-to-acquire (EtA) foods. The hypotheses tested in this study examined
whether DtA foods provide higher return rates in terms of food quantity, the quantity of
any macronutrient, or increased digestibility, or if DtA foods serve as an important source
of fallback nutrients. Return rates were measured in bites and grams of each
macronutrient (proteins, lipids, and nonstructural carbohydrates) ingested per forage time.
Concentrations of fiber and tannins, both of which inhibit the digestion of nutrients in
capuchins, were used to compare digestibility of DtA and EtA fruits. Finally, the
proportion of the diet devoted to DtA and EtA foods during each sample interval was
compared with the availability of these foods during the same time interval. Capuchins
did not achieve higher return rates for DtA foods as measured by number of bites or by
number of grams of any class of macronutrient. However, DtA foods did have lower
concentrations of some types of fiber, lower concentrations of tannins, and were more heavily exploited when EtA foods were less available. Results from this study imply that the most plausible benefit from acquisition of DtA food items for capuchin monkeys is as a source of fallback nutrients.

Introduction

The capuchin diet consists mainly of ripe fruits and insects (Chapman and Fedigan, 1990; Fragaszy and Boinski, 1995; Perry and Ordoñez, 2006). For a primate of their body size, capuchins are atypical in that a high proportion of their dietary protein comes from insects (Janson and Boinski, 1992), and that overall their diet is exceptionally high quality (Sailer et al., 1985; Leonard and Robertson, 1997; Fish and Lockwood, 2003). Diet quality can be viewed as the measurement of net energy and/or nutrients obtained from the diet. High quality diets consist of foods that are nutrient-dense and require little energy to digest. As body size increases within primates and within mammals, dietary quality generally decreases (Clutton-Brock and Harvey, 1977; Gaulin, 1979; Sailer et al., 1985). This is because high quality foods are less abundant in time and space (Milton, 1980) and larger body sizes require more food. An alternative strategy, which is comparatively rare, is to maintain a high quality diet but spend more time and/or effort foraging. Examples of primate taxa that maintained a high quality diet while increasing body size include chimpanzees, humans, and capuchins (Gaulin, 1979; Janson and Boinski, 1992; Milton, 1999, 2003). Curiosity and ingenuity are hallmark personality traits of these three taxa, which is emphasized by their propensity for tool use and behavioral diversity in foraging and social practices (Fragaszy et al., 1990; Panger et
al., 2002; Perry, 2011). These characteristics can be useful for exploitation of high quality foods that are difficult to acquire. Bigger brains could also be advantageous if they increase efficiency in the exploitation of high quality foods, but only if the foods acquired provide enough energy to offset the high metabolic costs of the larger brain.

Capuchin monkeys display a substantial number of ape-like characteristics that suggest convergent evolution. These include: tool use (Ottoni and Mannu, 2001; Fragaszy et al., 2004 b), slow life histories (Ross, 1991; Fedigan and Rose, 1995), a large brain to body mass ratio (Hakeem et al., 1996; Hartwig, 1996; Rilling and Insel, 1999), and reliance on a difficult-to-acquire (DtA) diet (Rose, 1997; Fragaszy et al., 2004 c). This last characteristic, reliance on a DtA diet, is often linked to each of the former traits: tool use (Parker and Gibson, 1977; van Schaik et al., 1999; Boinski et al., 2000), slow life histories (Janson and van Schaik, 1993; Kaplan et al., 2000), and a proportionately large brain (Clutton-Brock and Harvey, 1980; Barton, 1996; Kaplan et al., 2000). This necessarily requires that the nutritional benefits of exploiting DtA foods outweigh the cost of increased foraging effort.

Capuchins exploit a large number of DtA food resources that other closely-related species do not eat or do not eat efficiently (Izawa, 1979; Fragaszy et al., 1990, 2004 c; Janson and Boinski, 1992; Fragaszy and Boinski, 1995). Some of these food items seem to serve an important function as fallback foods during seasons when other more easily acquired foods are less available (Janson and Boinski, 1992; Peres, 1994; Wright et al., 2009). Other DtA foods are eaten throughout the year (MacKinnon, 2006; Gunst et al., 2008) and thus seem to serve as a regular source of nutrients. Specialization in DtA food items is likely to have a large impact on juveniles who lack the strength and skills utilized
by adults to obtain these foods. Reliance on difficult food items may select for a longer juvenile period, which may be required to learn skills necessary to forage for these items efficiently (Clutton-Brock and Harvey, 1980; Gibson, 1986; Kaplan et al., 2000). Therefore reliance on DtA food items appears to be associated with significant costs. In order for these costs to be worthwhile, DtA foods must somehow provide nutritional benefits.

The primary goal of this paper is to investigate why capuchins exploit DtA food items by examining the nutritional benefits gained from these food items. In doing so, we are likely to learn about which ecological factors select for exploitation of DtA foods. Simultaneously we are likely to gain insight into the ecological factors that select for tool use, slow life histories, and larger brains.

There are several ways that DtA foods could be beneficial despite the greater energetic and time requirements needed to obtain them. First, DtA foods might provide higher return rates for proficient foragers. This would be possible if a greater quantity of nutrients are obtained from DtA items, as long as the difference in size is large enough to offset the longer time required to obtain DtA items. Second, DtA foods may contain higher quantities of certain types of nutrients, such as protein or fat, which may be rare in easy foods. Third, they may provide higher return rates indirectly if they contain lower concentrations of anti-nutrients: secondary plant chemicals and fiber which can inhibit absorption of certain nutrients. Fourth, they may simply serve as alternative food sources which can be exploited when the quantity of available easy foods are insufficient to meet energy requirements. The following hypotheses stem from these four potential benefits:
**Hypotheses**

1. If higher return rates are possible with DtA foods, then individuals should achieve higher return rates for difficult food items than for easy food items.

2. If DtA food items contain classes of nutrients that are less available in easy-to-acquire (EtA) foods, return rates for DtA foods should provide significantly more of these classes of nutrients than EtA foods.

3. If DtA food items provide higher return rates indirectly because they contain lower concentrations of fiber and/or secondary plant chemicals, there will be significantly higher quantities of these anti-nutrients in EtA food items.

4. If DtA foods act as fallback or supplemental foods, they should be eaten more frequently when EtA foods are less available.

These hypotheses were tested using return rates from individuals in three groups of wild capuchin monkeys. Food items eaten by study subjects were each assigned one of three difficulty levels and a subset of these food items were analyzed for macronutrient and anti-nutrient content. The macronutrients discussed include protein, lipids, simple sugars, nonstructural carbohydrates (NSCs), and total kilocalories (KCAL). The anti-nutrients include tannins and fiber. Five fiber fractions were compared for DtA and EtA foods: Neutral detergent fiber (NDF), Acid detergent fiber (ADF), hemicellulose, cellulose, and lignins. NDF is composed of hemicellulose, cellulose, and lignins, while ADF is composed of cellulose and lignins but not hemicellulose. The degree to which capuchins can obtain energy from fiber is unclear. However, the small colon (Milton, 1987; Hartwig et al., 2011) and short retention times of capuchins (Lambert, 1998)
suggest that capuchins obtain little energy from fiber. Instead, fiber is likely to increase passage times and decrease nutrient absorption in capuchins, thereby acting as an anti-nutrient. Tannins are secondary plant compounds that can inhibit the digestion of protein (Robbins et al., 1987). Two tannin measures were compared in DtA and EtA foods: condensed tannins, and total tannins (condensed and hydrolysable). Food availability was measured biweekly for seven months along with the proportions of food eaten from each difficulty level.

Methods

Study site: Observations took place at the Pacuare Nature Reserve in the Limón Province of Costa Rica. The reserve is located 25 km north of the capital Puerto Limón, between the Tortuguero Canals and the Caribbean Sea (10°10’N, 83°14W). It contains 800 ha of mixed primary and secondary, tropical, wet, lowland forest. The three study groups have territories in the southern portion of the reserve. Their habitat consists of secondary, primary, and swamp lowland forest habitats.

Study groups: I began habituating the three study groups, “A,” “B” and “C,” intermittently in 2005. I used body size, sex, and unique physical features such as cap line irregularities, head shape, and scars to identify each individual. Prior to the start of this study I could reliably identify each of 49 study individual. My field assistants and I collected data on these 49 individuals within the three study groups between October of 2009 and August of 2010. Subjects included 6 infants (age 0-1 year), 5 younger juveniles (ages 1-3 years), 5 older juveniles (ages 3-5 years), 6 subadults (ages 5-7 years) and 27 adults (older than 7 years). Ages are estimated in the following way: when I had observed
subjects at an early phase of infancy (while still riding on the mother’s neck) I designated my earliest sighting as his/her birth month. I took many photos of each individual throughout this study and during the previous pilot studies and habituation periods that began in 2006. For juvenile and subadult subjects who I had not observed in early infancy, I estimated their ages by comparing my earliest pictures of them with the chronological pictures of individuals of known ages. Females were considered adults if they were estimated to be greater than 7 years old or if they had given birth. Males were considered adults if they were estimated to be greater than 7 years old or if they had reached full size which occurs around age 7 in captivity (Fragaszy and Adams-Curtis, 1998). Age classes were defined as in similar studies involving foraging in juvenile capuchins (Gunst et al. 2008; Gunst et al. 2010; MacKinnon 2006) and are designed to reflect differences in experience, size, reproductive activity, and tolerance. Younger juveniles are more highly tolerated in feeding contexts (Janson 1985; Janson 1990), and in captivity are between 50 and 80% of an adult female body weight (Fragaszy and Bard 1997). Older juveniles receive an intermediate amount of aggression in foraging contexts and still have some growth left to do. Subadult females have reached or are close to adult size, but have generally not started to reproduce (Di Bitetti and Janson 2001). Subadult and adult males receive the most aggression from the alpha male and are the least tolerated at preferred feeding sites (Janson 1985). By 7 years, most males have emigrated from their natal groups (Jack and Fedigan 2004).

**Behavioral data collection:** Data were collected from October 2009 through August 2010. I spent a total of seven and a half months prior to this, identifying and habituating individuals in each of the three study groups. Along with a field assistant, I
conducted continuous focal follows (Altmann 1974) on individuals engaging in foraging activities. Focal follows lasted for the duration of a foraging event on one food type; if the focal individual stopped foraging or changed to a different food item the focal follow was ended. Subjects were chosen based on visibility and the food item being foraged, such that, each individual was not followed more than once per day for each food item. During focal follows, I narrated behaviors while my field assistant recorded them in real time on an HP iPaq using Noldus Observer 8.0 and Pocket Observer 3.1 behavioral data collection software (Noldus Information Technology, Wageningen, Netherlands). Inter- and Intra-observer reliability were measured by comparing focal follow entries created from digital voice recordings of sample focal follows. Data were kept after a $\leq$1 second variance in foraging behavior timing was achieved per test follow. Because this study was specifically focused on skill acquisition rather than other social factors that might compromise foraging efficiency, focal follows were only included in the dataset if aggression and displacements did not occur (i.e. subject access to food items was not obviously inhibited by social interactions). In addition to focal follows, every thirty minutes, my assistant and I carried out a scan sample. Data from scan samples were used to calculate the forage time allocated to each food type. Scan samples (Altmann 1974) were conducted every 30 minutes while in the presence of a study group. Scan samples lasted for 5 minutes during which time the first behavior observed for each individual positively identified over the interval was recorded.

**Food Availability:** To measure food availability throughout the study period, a total of eleven transects, each 50 meters long, were monitored approximately every two weeks. Transects were set up along trails that were frequently traveled by one or more of
the study groups and were chosen in an attempt to maximize the diversity of fruit trees monitored. Along each transect, all plant food sources including trees, shrubs, epiphytes, and small herbaceous plants, within three meters of either side of the trail were listed, measured, and monitored. The things that were monitored for trees and shrubs included: the percent of the canopy/shrub that contained ripe fruit, unripe fruit, and flowers, and an estimate of the number of fruits on the ground. For epiphytes and small herbaceous plants the number of stalks that contained flowers, unripe, and ripe fruits were counted.

*Return rates:* Return rates were either computed as bite counts or as grams of the particular macronutrient of interest (lipids, protein, free simple sugars, or nonstructural carbohydrates), per forage time. Grams of each nutrient were calculated by dividing the average dry weight of each food item by the average number of bites needed to complete each food item, and multiplying this quotient by the proportion of the dry weight that was made up of the respective nutrient. Forage time consisted of three non-overlapping behaviors: search, harvest, and process. Search was defined as the investigation of potential food sites. Harvest was the removal of a food item from a substrate. Process was manipulation of a food item that an individual already had in his/her possession in order to improve ingestion or digestibility. Total forage time is the total duration of these three behaviors. Once a focal individual had a food item in his/her possession each bite was recorded.

*Food difficulty levels:* Food items were assigned a difficulty level for each of the different components of foraging: search, harvest, and process. In order to distinguish difficulty due to strength from difficulty due to skill these categories were assigned separately according to two sets of criteria. Strength levels were categorized by whether
no ("1"), moderate ("2"), or intense ("3") force was necessary to complete the behavior. Intense force was defined as force that required leveraging using body positions or use of an object by older juveniles, subadults, and/or adults. Examples of foraging behaviors that require intense force include tearing apart canes in search of embedded larvae or pounding open a hard-shelled fruit on a branch. A moderately forceful manipulation was defined as one that required solely manual pressure by older juveniles, subadults, and/or adults. Examples include removing a fruit from a thick stem or removal of a thin, hard shell. For skill, the difficulty classification was based on whether zero ("1"), one ("2"), or greater than one ("3") skillful manipulation was necessary to complete the behavior. A skillful manipulation was defined as an action that requires one of the following: a dexterous manipulation, sequence-specific, condition-specific, or location-specific action. Examples include avoiding defense systems such as thorns or spikes, and locating larvae within canes. The values for total strength and total skill levels were computed by taking the sum of the difficulty levels for search, harvest, and process. All food items in this dataset were successfully acquired by each age-sex category and, thus, strength levels are designed to reflect the extra time it might take a weaker individual to acquire a food item, rather than whether an individual is likely to obtain a particular food item at all. Total difficulty is equal to the sum of total strength and total skill (see Appendix A for a description of search, harvest, and process requirements for the top ten most commonly eaten food items, and their associated strength and skill, and total difficulty level assignments). Finally, in order to compare foods that were relatively difficult to acquire with foods that were relatively easy to acquire, foods were split into three categories (roughly thirds) based on their total difficulty score. Foods that had scores in the highest
range were categorized as difficult-to-acquire (DtA), foods that had scores in the lowest range were categorized as easy-to-acquire (EtA), and foods with in the middle range were categorized as medium-to-acquire (MtA).

Nutritional Analysis: Samples of 23 plant food items were collected in the field and processed for future nutritional analysis. Following the protocols used by Conklin-Brittain et al. (2006), processing consisted of weighing each food item to determine the wet weight, dividing items into the parts that were eaten versus the parts that were not eaten, reweighing each part, drying samples in an electronic food dehydrator, weighing the dried samples, and lastly, packing the samples into zip-lock bags with silica packs. Dried samples were transported to the Primate Nutritional Ecology Laboratory at Harvard University where they were analyzed for the following macronutrients: protein, lipids, free simple sugars (water-soluble sugars), total nonstructural carbohydrates (i.e. simple sugars and starch), and total fiber (equal to the sum of: cellulose, hemicellulose, and lignins). The methods used to analyze food items for this project followed the methods described in Conklin and Wrangham (1994). Water content was calculated as the difference between wet field weight and dry weight. “Dry weight” as discussed in the analysis refers to the dry weight of only the edible portion of the food item.

Statistics: All statistics were carried out in R v. 2.11.1 (R Development Team 2010). For Hypothesis 1 generalized linear mixed models (GLMMs) were used to examine the difference in return rates for easy and hard foods, within each age class. For these models, return rates were computed in terms of the number of bites per forage time, food difficulty level was the fixed effect, and focal subject was the random effect. A
Poisson distribution was used to fit these data because foraging return rates were calculated from the number of bites per forage time, and thus, the response variable was in counts, and not normally distributed. Observation number was added as an additional random effect to account for overdispersion (Browne et al., 2005) which was present in this dataset. Separate models were run for each age class. GLMMs were carried out in R using the lme4 package (Bates and Maechler, 2009).

For Hypothesis 2 GLMMs were also used to determine whether capuchins are able to achieve higher return rates for any class of macronutrient. The response variable in these models was grams of one of the classes of macronutrients, and the predictor variable was again difficulty level. One model was run for each class of macronutrient and this process was done twice: once for adults, and once for juveniles, which combined the samples of younger juveniles, older juveniles and subadults, who all had similar return rates.

For Hypothesis 3 Kruskal-Wallis rank sum tests were used to compare the concentrations of fiber and tannin in EtA, MtA, and DtA fruits. Five measures of fiber and two measures of tannins were used. Neutral detergent fiber (NDF) is a measure of total fiber and includes the fiber subfractions hemicellulose, cellulose, and lignins. Acid detergent fiber (ADF) includes the fiber subfractions cellulose and lignins. The three individual components of total fiber were also examined: hemicellulose (HC), cellulose (Cs), and lignins (Ls). The two measures for tannin concentrations were condensed tannins (CT), and total tannins: condensed plus hydrolysable, estimated by radial diffusion (RD). All fiber fractions are measured as percent of dry weight. Quebracho was the standard for CT and RD assays.
For Hypothesis 4 to examine whether DtA fruits were eaten more frequently when easier fruits were not available, the Spearman’s rank correlation was calculated for the availability of either EtA or MtA fruits with the proportion of DtA fruits eaten. A total of 25 different species of plants were monitored for fruit availability. Of these, ten were classified as EtA, nine were classified as MtA, and the remaining six were classified as DtA. The relative availability of fruits by difficulty level was estimated as follows: First the fruit availability for individual trees/plants of one species was combined. Next the amount of fruit on all trees/plants of a species out of the total amount observed in any of the survey dates was calculated for each survey date. Finally, the average proportions for all trees/plants within each difficulty level were calculated for each survey date. The proportions of food types eaten were calculated from scan samples that involved a forage-related behavior. There were six categories of foods: EtA, MtA, and DtA fruits, surface insects, embedded insects, and unidentified. The number of observations involving each food type for each half-month period were counted and summed in order to compute the proportion of forage observation for each food class.

**Results**

**Hypothesis 1:** If higher return rates, as measured by number of bites/forage time, are possible with difficult foods, then individuals should achieve higher return rates for difficult food items than for easy food items, if not in all age classes, at least in older age classes
Although the average dry weight for DtA fruits was significantly higher than the dry weight for EtA and MtA fruits (see figure 5.0, table 5.0), this did not translate into higher return rates for DtA fruits, thus, Hypothesis 1 was not supported for fruits. In no age class did difficult fruits provide higher return rates than easy fruits (see Figure 5.1 and Table 5.1). In contrast, return rates for hard fruits were lower than for easy and medium fruits in each age class. For adults the rate of bites/forage time was 0.14 for EtA fruits but only 0.09 for DtA fruits (p-value=0.11). Bite rates for subadults, older juveniles and younger juveniles for DtA fruits were less than half the rate achieved for EtA fruits (p-values≤0.001).

Figure 5.0: Dry Weight by Difficulty Level

![Dry Weight by Difficulty Level](image)

Dry Weight by Difficulty Level

- EtA fruits
- MtA fruits
- DtA fruits

Dry Weight in Grams

Difficulty Level
Table 5.0: Fruit Dry Weight by Difficulty Level

<table>
<thead>
<tr>
<th>Dry Weight</th>
<th>Mean for EtA fruits</th>
<th>Mean for MtA fruits</th>
<th>Mean for DtA fruits</th>
<th>Kruskal-Wallis rank sum statistic</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Weight</td>
<td>1.11</td>
<td>1.09</td>
<td>3.59</td>
<td>6.0439</td>
<td>2</td>
<td>0.049*</td>
</tr>
</tbody>
</table>

Figure 5.1: Fruit Return Rates by Age Class and Difficulty Level

Bars indicate 95% confidence intervals
Table 5.1: Fruit Bite Rate by Age Class and Difficulty Level

| Age Class       | Difficulty Level | Bite Rate Estimate | Std. Error z-value | Pr(>|z|) |
|-----------------|------------------|--------------------|--------------------|---------|
| Adults          | Easy             | 0.142 -1.952       | 0.188 N/A          | N/A     |
| Subadults       | Easy             | 0.196 -1.631       | 0.202 N/A          | N/A     |
| Older Juveniles | Easy             | 0.161 -1.824       | 0.367 N/A          | N/A     |
| Younger Juveniles | Easy       | 0.164 -1.805       | 0.232 N/A          | N/A     |
| Adults          | Medium           | 0.191 -1.654       | 0.201 1.082        | 0.279   |
| Subadults       | Medium           | 0.231 -1.464       | 0.239 0.535        | 0.593   |
| Older Juveniles | Medium           | 0.162 -1.820       | 0.387 0.009        | 0.993   |
| Younger Juveniles | Medium       | 0.172 -1.760       | 0.314 0.116        | 0.908   |
| Adults          | Difficult        | 0.088 -2.429       | 0.229 -1.612       | 0.107   |
| Subadults       | Difficult        | 0.031 -3.462       | 0.355 -4.480       | <0.001* |
| Older Juveniles | Difficult        | 0.015 -4.218       | 0.586 -3.470       | 0.001*  |
| Younger Juveniles | Difficult   | 0.031 -3.469       | 0.318 -4.232       | <0.001* |

Model Output interpretation: Estimates are equal to the log of the predicted bite rate. Bite rates equal \(e^{(\text{Estimate})}\). P-values indicate the probability that the bite rate for the respective age class and difficulty level is the same as the bite rate for that age class for easy fruits. * indicates significance at an \(\alpha=0.05\) level. Model: \(-\text{mer}(\text{Bite count} | \text{difficulty level} + (1 | \text{focal individual}) + (1 | \text{food difficulty id}) + (1 | \text{observation number}) + \text{offset(log(forage time)),family=Poisson})\). This model was run separately for each age class. N=608 Observations, 323 for adults, 99 for subadults, 93 for older juveniles, and 93 for younger juveniles.

Similarly, Hypothesis 1 was also not supported for insects. Bite rates for insects, as for fruits, were higher for easy (surface) insects than for difficult (embedded) insects (see Figure 5.2 and Table 5.2). However, differences between DtA and EtA insects were much smaller than for fruits. The biggest difference is seen in younger juveniles who had a bite rate of 0.032 for surface insects but only 0.025 for embedded insects (p=0.17). In no age class was the difference between surface and embedded insects significant.
Table 5.2: Insect Return Rates by Type

| Age Class       | Type    | Bite Rate | Estimate | Std. Error | z-value | Pr(>|z|) |
|-----------------|---------|-----------|----------|------------|---------|----------|
| Adults          | Surface | 0.022     | -3.828   | 0.103      | N/A     | N/A      |
| Subadults       | Surface | 0.031     | -3.482   | 0.153      | N/A     | N/A      |
| Older Juveniles | Surface | 0.022     | -3.834   | 0.190      | N/A     | N/A      |
| Younger Juveniles | Surface | 0.032     | -3.432   | 0.133      | N/A     | N/A      |
| Adults          | Embedded| 0.021     | -3.858   | 0.154      | -0.160  | 0.875    |
| Subadults       | Embedded| 0.029     | -3.549   | 0.208      | -0.262  | 0.793    |
| Older Juveniles | Embedded| 0.018     | -4.013   | 0.288      | -0.576  | 0.565    |
| Younger Juveniles | Embedded | 0.025    | -3.698   | 0.156      | -1.359  | 0.174    |

Model Output interpretation: Estimates are equal to the log of the predicted bite rate. Bite rates equal \(e^{\text{Estimate}}\). P-values indicate the probability that the bite rate for the respective age class for embedded insects is the same as the bite rate for that age class for surface insects. Model: `lmer(Bites~Insect type+(1| focal individual) + (1|food difficulty id)+(1|observation number)+offset(log(forage time)),family=poisson)`. This model was run separately for each age class. N=496 observations: 245 for adults, 81 for subadults, 76 for older juveniles, 94 for younger juveniles.
Hypothesis 2: If difficult-to-acquire food items contain classes of nutrients that are less available in easy-to_acquire foods, return rates for difficult foods should provide significantly more of these classes of nutrients than easy foods.

This hypothesis was not supported either. In both juveniles and adults return rates for EtA fruits were higher than for DtA fruits for nearly every class of macronutrient. For adults this difference was not significant for any class of macronutrient (See Figure 5.3a, Table 5.3). The one macronutrient that adults achieved higher return rates for DtA fruits compared with EtA fruits was lipids: 0.00024 versus 0.00017 grams/second of forage time (p=0.85). Interestingly, the higher return rate for lipids led to nearly identical return rates for KCAL for DtA and EtA fruits in adults. Juveniles had higher return rates for EtA fruits compared with DtA fruits for all classes of macronutrients (see Figure 5.3b). These differences were significant for NSCs, KCALs, and for dry weight (see Table 5.4). Neither age class achieved significantly higher return rates for hard fruits, which implies that capuchins do not specialize in DtA food items in order to maximize return rates for any class of macronutrient.
Figure 5.3a: Adult Return Rates by Difficulty Level

Figure 5.3b: Juvenile Return Rates by Difficulty Level
## Table 5.3: Adult Nutrient Return Rates by Difficulty Level

| Nutrient               | Difficulty Level | Return Rate | Estimate | Std. Error | z-value | Pr(>|z|) |
|------------------------|------------------|-------------|----------|------------|---------|----------|
| Free Simple Sugar (g)  | Easy             | 0.002       | -6.046   | 0.533      | N/A     | N/A      |
| NSC (g)                | Easy             | 0.004       | -5.514   | 0.525      | N/A     | N/A      |
| Lipid (g)              | Easy             | <0.001      | -8.707   | 1.399      | N/A     | N/A      |
| Protein (g)            | Easy             | <0.001      | -8.851   | 1.233      | N/A     | N/A      |
| KCAL (number)          | Easy             | 0.027       | -3.621   | 0.344      | N/A     | N/A      |
| Dry weight (g)         | Easy             | 0.011       | -4.513   | 0.317      | N/A     | N/A      |
| Free Simple Sugar (g)  | Medium           | 0.003       | -5.930   | 0.537      | 0.154   | 0.877    |
| NSC (g)                | Medium           | 0.005       | -5.403   | 0.538      | 0.147   | 0.883    |
| Lipid (g)              | Medium           | <0.001      | -8.716   | 1.453      | -0.004  | 0.997    |
| Protein (g)            | Medium           | <0.001      | -8.823   | 1.261      | 0.016   | 0.987    |
| KCAL (number)          | Medium           | 0.041       | -3.185   | 0.354      | 0.885   | 0.376    |
| Dry weight (g)         | Medium           | 0.012       | -4.449   | 0.327      | 0.141   | 0.888    |
| Free Simple Sugar (g)  | Difficult        | 0.001       | -6.732   | 0.610      | -0.846  | 0.397    |
| NSC (g)                | Difficult        | 0.002       | -6.072   | 0.591      | -0.706  | 0.480    |
| Lipid (g)              | Difficult        | <0.001      | -8.324   | 1.464      | 0.190   | 0.850    |
| Protein (g)            | Difficult        | <0.001      | -9.575   | 1.420      | -0.385  | 0.700    |
| KCAL (number)          | Difficult        | 0.028       | -3.577   | 0.378      | 0.086   | 0.932    |
| Dry weight (g)         | Difficult        | 0.009       | -4.750   | 0.350      | -0.504  | 0.614    |

Model Output interpretation: Estimates are equal to the log of the predicted return rate. Return rates equal $e^{(\text{Estimate})}$. P-values indicate the probability that the return rate for the respective nutrient and difficulty level is the same as the return rate for that nutrient at the easy difficulty level. Model: `lmer(grams of nutrient ~ difficulty level + (1| focal individual) + (1| food difficulty id) + (1| observation number) + offset(log(forage time)), family=Poisson)`. This model was run separately for each nutrient. N=288.
### Table 4.4: Juvenile Nutrient Return Rates by Difficulty Level

| Nutrient                | Difficulty | Return Rate | Estimate | Std. Error | z-value | Pr(>|z|) |
|-------------------------|------------|-------------|----------|------------|---------|----------|
| Free Simple Sugar (g)   | Easy       | 0.004       | -5.578   | 0.478      | N/A     | N/A      |
| NSC (g)                 | Easy       | 0.008       | -4.873   | 0.490      | N/A     | N/A      |
| Lipid (g)               | Easy       | 0.001       | -7.092   | 0.735      | N/A     | N/A      |
| Protein (g)             | Easy       | <0.001      | -7.799   | 0.820      | N/A     | N/A      |
| KCAL (number)           | Easy       | 0.048       | -3.035   | 0.266      | N/A     | N/A      |
| Dry weight (g)          | Easy       | 0.019       | -3.940   | 0.307      | N/A     | N/A      |
| Free Simple Sugar (g)   | Medium     | 0.002       | -5.996   | 0.522      | -0.590  | 0.555    |
| NSC (g)                 | Medium     | 0.004       | -5.493   | 0.537      | -0.853  | 0.393    |
| Lipid (g)               | Medium     | 0.001       | -7.073   | 0.731      | 0.019   | 0.985    |
| Protein (g)             | Medium     | 0.000       | -8.361   | 0.993      | -0.436  | 0.663    |
| KCAL (number)           | Medium     | 0.042       | -3.171   | 0.292      | -0.343  | 0.732    |
| Dry weight (g)          | Medium     | 0.011       | -4.503   | 0.338      | -1.235  | 0.217    |
| Free Simple Sugar (g)   | Difficult  | 0.001       | -7.352   | 0.802      | -1.901  | 0.057    |
| NSC (g)                 | Difficult  | 0.001       | -6.831   | 0.789      | -2.109  | 0.035*   |
| Lipid (g)               | Difficult  | <0.001      | -8.043   | 1.105      | -0.717  | 0.473    |
| Protein (g)             | Difficult  | <0.001      | -11.171  | 3.094      | -1.053  | 0.292    |
| KCAL (number)           | Difficult  | 0.010       | -4.652   | 0.386      | -3.447  | 0.001*   |
| Dry weight (g)          | Difficult  | 0.003       | -5.707   | 0.478      | -3.112  | 0.002*   |

Model Output interpretation: Estimates are equal to the log of the predicted return rate. Return rates equal e^\(\text{Estimate}\). P-values indicate the probability that the return rate for the respective nutrient and difficulty level is the same as the return rate for that nutrient at the easy difficulty level. Model: lmer(grams of nutrient ~ difficulty level+(1| focal individual) + (1|food difficulty id)+(1|observation number)+offset(log(forage time)),family=Poisson). This model was run separately for each nutrient. N=248. * Indicates significance at an α=0.05 level.

**Hypothesis 3:** If DtA food items provide higher return rates indirectly because they contain lower concentrations of fiber and/or secondary plant chemicals, there will be significantly higher quantities of these anti-nutrients in EtA food items.

EtA fruits tended to have higher concentrations of anti-nutrients: fiber and tannins, than DtA fruits, but this difference was only significant for one sub-fraction of fiber: ADF (see figure 5.4 and Table 5.5). The average total fiber (NDF) for EtA fruits was 31.4% compared with 19.3% for DtA fruits (p=0.27). ADF is NDF minus...
hemicellulose. Hemicellulose was the only fiber sub-fraction that had a lower concentration in EtA fruits which explains why ADF but not NDF concentrations were significantly different. The average concentration of ADF in EtA fruits was 24.66% compared with 11.53% for DtA fruits (p=0.018). Both subfractions of ADF: cellulose and lignins had higher concentrations in EtA fruits, but these differences were not significant alone. EtA fruits had higher levels of both total tannins (measured through radial diffusion), and condensed tannins, but these differences were not significant. For many of these comparisons the statistical power was well below 0.80 for the amount of variation observed between EtA and DtA fruits, thus greater sample sizes will be necessary to more conclusively determine whether EtA fruits have significantly more fiber and higher concentrations of tannins. These results provide a preliminary indication that EtA fruits may have higher quantities of anti-nutrients. Therefore, it is possible that capuchins exploit DtA food items in order to minimize intake of anti-nutrients. It is also possible that capuchins could achieve higher return rates from DtA foods that are easier to digest.
Table 5.5: Anti-Nutrient Concentrations for EtA, MtA, and DtA Fruits

<table>
<thead>
<tr>
<th>Anti-nutrient</th>
<th>Mean for EtA fruits</th>
<th>Mean for MtA fruits</th>
<th>Mean for DtA fruits</th>
<th>Kruskal-Wallis rank sum statistic</th>
<th>df</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>NDF</td>
<td>31.36</td>
<td>24.70</td>
<td>19.33</td>
<td>2.59</td>
<td>2</td>
<td>0.274</td>
</tr>
<tr>
<td>ADF</td>
<td>24.66</td>
<td>10.96</td>
<td>11.53</td>
<td>8.08</td>
<td>2</td>
<td>0.018*</td>
</tr>
<tr>
<td>HC</td>
<td>6.72</td>
<td>13.77</td>
<td>7.80</td>
<td>1.26</td>
<td>2</td>
<td>0.532</td>
</tr>
<tr>
<td>Cs</td>
<td>12.93</td>
<td>7.63</td>
<td>7.53</td>
<td>3.16</td>
<td>2</td>
<td>0.206</td>
</tr>
<tr>
<td>Ls</td>
<td>11.70</td>
<td>3.33</td>
<td>4.00</td>
<td>6.69</td>
<td>2</td>
<td>0.035*</td>
</tr>
<tr>
<td>CT</td>
<td>6.68</td>
<td>2.26</td>
<td>1.60</td>
<td>2.13</td>
<td>2</td>
<td>0.345</td>
</tr>
<tr>
<td>RD</td>
<td>3.83</td>
<td>3.67</td>
<td>1.45</td>
<td>2.56</td>
<td>2</td>
<td>0.279</td>
</tr>
</tbody>
</table>

NDF=neutral detergent fiber, ADF=acid detergent fiber, HC=hemicellulose, Cs=cellulose, Ls=lignins, CT=condensed tannins, and RD=radial diffusion—a measure of total tannins. All fiber fractions are measured as % of dry weight. Tannins are reported as a percentage of Quebracho units. Total N=22: 9 EtA, 7 MtA, 6 DtA.
**Hypothesis 4:** If difficult-to-acquire foods act as fallback or supplemental foods, they should be eaten more frequently when easy-to-acquire foods are less available.

On average, EtA and MtA fruits had the highest availability from May through July of the study period, and the least availability between January and April (see Figure 5.5a). On the other hand, the availability of DtA fruits did not vary as much as either EtA or MtA fruits, and instead remained relatively stable from January through July. The proportion of each food type eaten, calculated from scan samples, including: EtA, MtA, and DtA fruits, surface insects, and embedded insects, varied considerably across the study period for all food types except embedded insects, which made up only a small proportion of forage observations in any given month (see Figure 5.5b). There appears to be a general pattern whereby the proportion of forage observations dedicated to DtA fruits decreases from February through August, while the proportion of forage observations dedicated to easy fruits and surface insects increased during this same period. The correlation between the availability of EtA fruit and the proportion of forage observations dedicated to DtA fruits was -0.40 (p=0.088). The correlation between the availability of MtA fruit and the proportion of forage observations dedicated to DtA fruits was -0.43 (p=0.073) (see Table 5.5). The low sample size here (N=13) results in low power (approximately 0.36), thus, a longer study with more survey periods would help to verify this correlation. These results provide a preliminary indication that capuchins are more likely to forage on DtA fruits when the EtA and MtA fruits are less available. However a larger sample size will be necessary to confirm this trend.
Figure 5.5a: Fruit Availability

![Graph of Fruit Availability]

Figure 5.5b: Proportion of Forage Observations on Different Food Types by Month

![Graph of Proportion of Forage Observations on Different Food Types by Month]
Table 5.6: Correlations between Food Availability and Foods Eaten

<table>
<thead>
<tr>
<th>Availability</th>
<th>Proportion Eaten</th>
<th>Rho</th>
<th>S</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average proportion of EtA fruits available</td>
<td>DtA Fruits</td>
<td>-0.40</td>
<td>510</td>
<td>0.088</td>
</tr>
<tr>
<td>Average proportion of MtA fruits available</td>
<td>DtA Fruits</td>
<td>-0.43</td>
<td>520</td>
<td>0.073</td>
</tr>
</tbody>
</table>

Test details: Spearman’s rank correlation rho, alternative hypothesis: true rho is less than 0, N=13

Discussion

Reliance on a DtA diet has been linked to many of the traits that distinguish humans, great apes, and capuchins from other primates. These traits include: tool use (Parker and Gibson, 1977; van Schaik et al., 1999), slow life histories (Janson and van Schaik, 1993; Kaplan et al., 2000), and proportionately large brains (Clutton-Brock and Harvey, 1980; Barton, 1996; Kaplan et al., 2000). Therefore, reliance on a DtA diet is a particularly interesting trait. An understanding of the benefits garnered from the acquisition of DtA food items should help us understand the ecological factors that select for this trait. However, few studies have investigated the specific nutritional benefits associated with the exploitation of DtA foods.

This study tested four hypotheses regarding the potential nutritional benefits to capuchins provided by foraging for DtA food items. The results indicate that 1) capuchins do not achieve higher return rates in terms of bites per forage time when foraging for DtA foods. Conversely, individuals in all ages achieved higher return rates for EtA foods than for DtA foods, although adults exhibited less variation in return rates between foods of different difficulty levels. 2) Capuchins do not obtain higher return rates for any class of macronutrient when foraging for DtA fruits. Again, both adults and juveniles generally
achieved higher macronutrient return rates for EtA and MtA fruits, although this difference was only significant for total kilocalories and grams of nonstructural carbohydrates in juveniles. 3) DtA fruits do seem to have lower concentrations of fiber and tannins, both of which can inhibit the absorption of nutrients. However, with the exception of the ADF sub-fraction of fiber and lignin concentration, these differences were not significant. Future tests with a larger sample of food items will be necessary to verify this trend. Therefore there is a possibility that DtA foods provide higher return rates as a result of easier or more complete digestion of nutrients. However, the effect of the anti-nutrients would have to be considerable in order to counter the higher rates of nutrient intake in EtA foods. Finally, 4) capuchins do appear to spend a greater proportion of foraging time on DtA fruits when EtA and MtA fruits are less available. This trend was nearly significant but further tests with slightly larger samples sizes will be necessary to verify it.

Given that capuchins have proportionately large brains (Hakeem et al., 1996; Hartwig, 1996; Rilling and Insel, 1999), quick passage rates (Lambert, 1998), and an active lifestyle (Fragaszy et al., 2004 c), they have relatively high and constant requirements for carbohydrate energy sources. If, as these results imply, EtA and MtA foods provide higher return rates, the most likely benefit of foraging on DtA foods is as an important supply of fallback nutrients. However, it would be premature to rule out the possibility of higher return rates from DtA foods in adults when anti-nutrients are taken into consideration. In addition there may be differences in micronutrient content between DtA and EtA foods that could influence foraging decisions.
A weakness of this study is a failure to control for rank when estimating return rates. There were too few agonistic and submissive interactions to reliably compute rank relationships for the subjects in this study, but it is very likely that rank influences return rates. Future studies with rank estimates for subjects, larger samples of food items and food availability measures, will help confirm or refute the trends observed here.

In conclusion, I would like to propose a possible scenario to explain the observed links between tool use, large brains, and long juvenile periods with DtA diets that is consistent with results from this study:

Background: As mentioned in the introduction, reliance on insects for a primary source of protein requires capuchins, who are large compared with other insectivorous primates, to spend a large proportion of each day actively foraging (Janson and Boinski, 1992). Capuchins must exploit new sources to obtain sufficient quantities of insects, and rely more heavily on embedded pupae and the protected nests of social insects (Janson and Boinski, 1992). Long days of active foraging, require relatively high quantities of energy. The capuchin reliance on high-quality protein sources therefore necessitates ingestion of either, greater quantities of the foods that provide energy, or foods that provide greater quantities of energy.

Scenario A: It seems plausible that low quality-foods (foods that are low in nutrients and/or require a lot of energy to digest) would not provide capuchin with enough energy to sustain their metabolic requirements. Results of this study imply that when EtA food sources are rare, capuchins are likely to rely on more DtA foods. If DtA foods provide the best way to sustain capuchin’s high metabolic requirements during these times, their benefits could easily outweigh the costs involved in their acquisition. In
contrast, primates who can get by with relatively low quantities of carbohydrates may benefit more by conserving energy, thereby decreasing their risk of predation or antagonistic intergroup encounters. A reliance on DtA foods could have selected for traits such as a curious and inventive personality, tool use, proportionately large brains, and a tolerant social structure (Ottoni and Izar, 2008). These traits would likely increase the efficiency at which capuchins could exploit DtA foods.

After capuchins evolved a large brain relative to their body size, they would require that a greater proportion of their nutrients were in the form of glucose (Hollliday, 1986). It is likely that capuchins already had relatively long day ranges that were necessary to obtain sufficient quantities of insects. Primates that exploit insects for a significant proportion of their diet tend to have larger home ranges (Clutton-Brock and Harvey, 1977) and presumably longer day ranges compared with primates who have similar diets but incorporate fewer insects. These long day ranges require high quantities of energy but, prior to large brains, this energy did not necessarily have to come from glucose. Therefore, it may or may not have required a significant shift in diet to assure high enough quantities of glucose to support the metabolic requirements or a larger brain. The combination of reliance on insects for protein at a relatively large body size and a large brain relative to body size, both factors that increase energy requirements, could have locked capuchins into an especially high-quality diet.

In this scenario the enhanced cognitive abilities that enable more efficient acquisition of DtA foods would select for proportionately larger brains. Consequently, the metabolic requirements of larger brains would reinforce the need for those same foods. These elevated nutritional requirements could have then intensified selection for
curious, inventive personalities and tool use. Simultaneously, higher energetic requirements may have selected for slow growth, which would have been beneficial to prevent starvation in small, inexperienced juveniles who have proportionately higher metabolic requirements than adults (Leonard and Robertson, 1992). One consequence of slow growth would have been long juvenile periods.

It should be noted that a high-quality diet is equivalent to a low-fiber diet and an easily digestible diet. Easily digestible diets only require small digestive systems (i.e. small digestive systems could be viewed as a side-effect of high-quality diets). The expensive tissue hypothesis highlighted the correlation between large brains with small guts, relative to body size (Aiello and Wheeler, 1995), and proposed that a high-quality diet was essential for the evolution of proportionately larger brains. According to the scenario proposed here, a high-quality diet would not just allow for a greater proportion of energy to go towards larger brains, but would select for larger brains.

The scenario of reliance on a high-quality diet at larger body sizes has parallels for chimpanzees and humans. Great apes have larger body sizes than their Old World monkey relatives (Smith and Jungers, 1997). Whereas gorillas have adapted the strategy of acquiring larger quantities of lower quality food, chimpanzees appear to have increased their diet quality while still maintaining a larger body size (Conklin-Brittain et al., 1998; Milton, 2003). Compared with gorillas, chimpanzees have proportionately larger brains (Rilling and Insel, 1999), engage in tool use more frequently in the wild (Parker and Gibson, 1977), and grow more slowly (Leigh, 1994; Leigh and Shea, 1995). Humans have even higher quality diets than our chimpanzee cousins (Milton, 2003), and maintain a similar or slightly larger body size (Smith and Jungers, 1997). Compared with
chimpanzees, humans have proportionally larger brains (Rilling and Insel, 1999), engage in tool use more frequently, and grow more slowly (Leigh, 2001).

Recent studies have found weaker correlations between relative brain size and gut size than Aiello and Wheeler (1995) found in their original study, suggesting that energy necessary for fueling large brains can come from alternative sources (Hladik et al., 1999; Isler and Van Schaik, 2006; Hartwig et al., 2011). For example, Isler and van Schaik (2006) found a negative correlation between relative brain size and pectoral size in birds, indicating that energetic costs of locomotion may constrain brain size in birds. It is also very likely that a metabolic need for exploitation of large quantities of high-quality foods is not the only type of selection pressure for large brains. Hartwig et al. (2011) found a variety of diet and gut types in New World monkeys with larger relative brain sizes, and suggested that large group size may be a better explanatory factor for the variation in brain size exhibited in this group. Therefore, while the scenario proposed here may explain some of the variation in these traits between capuchins, chimpanzees, and humans and closely related species, other factors are also involved in selection of brain size and juvenile periods across animal taxa.

**Future Research:** Results from this study indicate that reliance on a DtA diet in capuchin monkeys is likely the consequence of reliance on a high-quality diet. Larger body sizes make reliance on a high-quality diet more difficult. Reliance on a DtA diet then may select for tool use (Parker and Gibson, 1977; van Schaik et al., 1999), large brains (Clutton-Brock and Harvey, 1980; Barton, 1996; Kaplan et al., 2000), and long juvenile periods (Janson and van Schaik, 1993; Kaplan et al., 2000). Several lines of
research would help support or refute the theory that the combination of reliance on a high quality diet with a large body size selects for tool use, large brains, and long juveniles periods. First, if larger brains help with exploitation of DtA foods, capuchins and chimpanzees should be more efficient at obtaining and processing DtA food items than closely related and/or sympatric species. Second, if tool use helps with extraction of high-quality, DtA foods, there should be a correlation between reliance on DtA foods and frequencies of tool use. Finally, the combination of reliance on DtA foods, and possession of a proportionately large brain, should be predictive of a long juvenile period.
Chapter 6: Conclusions

Capuchins are often noted for their suite of human-like morphological, behavioral, and life history traits (e.g. Fragaszy et al., 1990; Boinski et al., 2000). Reliance on a difficult-to-acquire (DtA) diet is hypothesized to select for many of the traits that distinguish humans from other primates (Kaplan et al., 2000). Similar hypotheses have been put forward for capuchins (Parker and Gibson, 1977; Janson and Boinski, 1992; Boinski et al., 2000). This study is one of the first to quantify the effects of reliance on DtA foods, in capuchins. The results presented here provide evidence on whether several capuchin traits could be adaptations for reliance on DtA foods. These traits include increased rates of food transfers, a greater role for social learning, and a long juvenile period. This research sheds light on the coevolution of diet, life history traits, morphology, and behavior, and is informative in the context of many hallmark human traits.

Chapter 1 of this dissertation looked at whether infants used food transfers to obtain DtA foods, and whether foods that were acquired through transfers had a nutritional profile that would serve to satisfy the large metabolic requirements of an immature individual with a proportionately large brain. Main findings from this chapter included:

- Infants, but not individuals in any other age class, obtained food through transfers significantly more frequently than adults.
- The difficulty level associated with obtaining a food item was a significant predictor of the likelihood that an infant would obtain that food through a transfer rather than independently. This finding supports the food
difficulty hypothesis which proposes that species with a greater reliance on DtA foods will engage in food transfers more frequently.

- The best nutrient predictors of food transfers were free simple sugar and nonstructural carbohydrate content. These are both sources of glucose which is the nutrient required in the highest quantity by the brain.

Together, these three findings imply that infant capuchins use food transfers to obtain DtA foods that have high glucose content. Capuchins’ large brains put an especially large tax on infants and young juveniles because brain energy requirements are proportionately greater in younger (smaller) individuals. It is possible that capuchin infants have a preference for sweet foods to help ensure they meet their high brain-glucose requirements.

Chapter 2 examined foraging differences between juvenile and adults foraging for DtA foods. These included: 1) the strategies used to obtain DtA foods; 2) the likelihood of being in proximity to other individuals; 3) how proximity affects return rates in each age class; and 4) the proportion of time that each age class spends on various types of food. The main findings of this chapter included:

- Juveniles utilize pre-foraged, DtA oil palm fruits (fruits dropped by other individuals) significantly more frequently than do adults. Juveniles obtain higher return rates when foraging on dropped fruits than when they have to harvest the fruit from the tree.

- Younger juveniles and subadults, but not older juveniles, spend more time in proximity to other individuals when foraging for DtA foods. Younger juveniles and subadults achieved higher return rates when foraging for
DtA foods while in proximity to other individuals, although this difference was not significant.

- All juveniles spent a higher proportion of their time foraging for surface insects and a lower proportion of their time foraging for DtA fruits than did adults, but this difference was only significant for younger juveniles.

The pattern whereby younger juveniles and subadults, but not older juveniles, obtain higher return rates while in the proximity of other individuals when foraging for DtA fruits, presents interesting opportunities for further inquiry. One possibility is that these patterns reflect different learning phases whereby proximity to other individuals plays a varying role. Another possibility is that age-dependent rank relationships alone may explain variation in return rates and proximity patterns. Regardless, this pattern highlights the complex nature of foraging ontogeny and a need to examine this topic more thoroughly.

Chapter 3 presented foraging rates for DtA and easy-to-acquire (EtA) foods across age classes to determine when in the lifespan capuchins achieve maximum foraging efficiency. These data provide a test of the ecological complexity hypothesis which posits that species living in a complex dietary niche delay the onset of reproduction in order to develop skills for efficient exploitation of difficult-to-acquire food items. The main findings of this chapter included:

- Adults had higher foraging return rates for DtA fruits than any other age class. When adults were divided into age classes, it became apparent that foraging return rates continue to increase through early adulthood.
• There were no significant differences across age classes for EtA fruits, embedded insects, or surface insects. These findings imply that 1) fruit difficulty level does have an impact on return rates, and 2) insect foraging, involving either surface or embedded insects, may not take very long to master.

• Variance in return rates across ages appears to be at least partially, if not mostly, a result of differences in skill, and not due solely to differences in strength.

The results of this chapter support the ecological complexity hypothesis but do not rule out the possibility that additional factors simultaneously select for long juvenile periods. For example, slow growth, which would be predicted by the ecological risk avoidance hypothesis, may decrease the risk of starvation while juvenile learn foraging skills.

Chapter 4 examines the more fundamental question of why capuchins forage for DtA foods in the first place and then speculates on the relationships between reliance on DtA foods, long juvenile periods, tool use, and relatively large brains, given the results. To do this, four potential benefits that could be associated with the acquisition of DtA foods are explored. The main findings of this chapter included:

• Return rates for DtA foods were not significantly higher than for EtA foods in terms of bites or for any class of nutrient. Instead, individuals in all age classes, but especially juveniles, obtained higher return rates for EtA foods.
• DtA foods had lower concentrations of fiber and tannins, both of which can inhibit digestion. However, sample sizes were small, power low, and only one class of fibers exhibited significant differences: ADFs.

• There was a negative correlation between the availability of EtA fruits and the proportion of time that capuchins spent foraging for DtA fruits.

The results of this chapter imply that the most likely reason why capuchins forage for DtA foods is as a source of fallback nutrients. That is, when high-quality foods that are EtA are not available, capuchins begin to exploit high-quality foods that are more DtA. However, it is possible that adult capuchins achieve higher return rates from DtA foods if the higher concentrations of anti-nutrients such as fiber and tannins in EtA foods, have a large enough effect. Capuchins have large brains, active lifestyles, and quick passage rates. These characteristics require high-quality foods; foods that are easy to digest and provide a large quantity of nutrients. As body size increases, high-quality foods are more difficult to obtain in the necessary quantities. Although capuchins are not particularly large monkeys, they appear to inhabit a dietary niche that consists of exceptionally high-quality foods, for a primate of their body size. This interaction between body size and diet quality is a plausible selection factor for reliance on a DtA diet, increased rates of food transfer and social learning, long juvenile periods, and large brains. A similar scenario may apply to humans.
References


Bates D, and Maechler M. 2009. lme4: Linear mixed-effects models using {S4} classes. {R} package version 0.999375-32.


McCabe G. 2005. Diet and nutrition in white-faced capuchins: effects of group, sex and reproductive state. Bioanthropology MA.


Robinson JG. 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkey, Cebus olivaceus: implications for foraging theory. Smithsonian 431:1-60.


