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# Sex differences in the social behavior of juvenile spider monkeys (*Ateles geoffroyi*)

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Sex differences in the social behavior of juvenile spider monkeys (*Ateles geoffroyi*)

by

Michelle Amanda Rodrigues

A thesis submitted to the graduate faculty  
in partial fulfillment of the requirements for the degree of  
MASTER OF ARTS

Major: Anthropology

Program of Study Committee:  
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W. Sue Fairbanks  
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Iowa State University

Ames, Iowa

2007

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For Travis, Goldie, Clydette, and Udi

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## ABSTRACT

Previous studies indicate adult spider monkeys (*Ateles geoffroyi*) display marked sex differences, including some that may emerge early in life. However, the social behavior of juvenile spider monkeys and potential sex differences has not been adequately studied. Sex differences in the social behavior and proximity patterns of individually recognized juvenile black-handed spider monkeys (*A. geoffroyi ornatus*) were examined at El Zota Biological Field Station in Costa Rica. Both males and females exhibited sex-typical differences. Only females initiated grooming. Females centered interaction around their mothers and female peers, while males interacted more with adult and juvenile males. Juvenile males were also found in significantly larger parties than females, and were in parties containing adult males significantly more than females. The results of this study indicate that juvenile spider monkeys begin to exhibit sex-typical behaviors at an early age, and that these behavioral patterns prepare them for the social challenges of adulthood.

## CHAPTER 1 INTRODUCTION

### Introduction

Several studies have shown that adult spider monkeys (*Ateles* spp.) show marked sex differences in behavior. Males are generally more affiliative and social, ranging with other males, whereas females are more solitary, interact less, and range in smaller subgroups, alone, or with dependent offspring (Chapman, 1990; Eisenberg, 1976; Fedigan and Baxter, 1984). Research has shown that when aggression occurs, while rare, it is most often initiated by males and directed toward females (Campbell, 2003; Fedigan & Baxter, 1984). Certain studies have also demonstrated that, in the absence of normal behavioral development and adult conspecifics, ex-pet/confiscated animals often develop species-typical social structure (Milton, 2002; Milton, 2005; Anaya-Huertas & Mondragon-Ceballos, 1997). However, in a study that resocialized captive spider monkeys, not all animals exhibited equal social competence, and one individual with a poor rearing history was unable to form any affiliative relationships with conspecifics (Anaya-Huertas & Mondragon-Ceballos, 1997). Furthermore, Milton (2002, 2005) notes that although approximately 20 spider monkeys, ranging in age from young juveniles to adults, were released in a reintroduction project on Barro Colorado Island, Panama, only five individuals, aged about 18 months to 5 years of age, survived. Clearly, aspects of a normal social development confer survival benefits to individuals. However, the processes and events that characterize normal socialization are not well-known. There are no published accounts of studies investigating the behavioral development of wild immature spider monkeys and at what age immatures begin to exhibit sex differences in social interactions. Furthermore, the juvenile period is one that has often

been neglected in primate studies, despite the evolutionary significance of this developmental stage in primate life histories (Pereira & Fairbanks, 2002; Pereira & Leigh, 2003). This study addresses these subjects by examining patterns of sex differences and social behavior exhibited by wild juvenile black-handed spider monkeys at El Zota Biological Field Station in Costa Rica. These findings have significant implications in the realms of applied conservation projects as well as in addressing theoretical considerations.

### **Theoretical Background**

Long-term studies on spider monkey socioecology have indicated differences in how mothers and other conspecifics treat male and female immatures and suggest that each sex may face different pressures. Symington (1987) found a biased investment toward male infants in *A. paniscus* at Manu National Park, Peru; females had a longer interbirth interval after the birth of a son, carried male infants longer, and nursed male infants longer. She estimates that mothers invested 24% more in male infants, although investment appeared equal post-weaning. She also notes that mothers intervened in social situations on behalf of sons but not daughters. However, Symington's (1987) evidence is anecdotal rather than quantitative. She also hypothesizes that high-ranking females may be able to help their sons become integrated into the male hierarchy. Chapman et. al. (1989) report that immature males face almost twice as much aggression as immature females (Chapman, unpublished data, in Chapman et. al, 1989; Fedigan & Baxter, 1984). They note that male immatures were more than five times as likely to disappear (presumably die) as a result of such aggression. Chapman and Chapman (1987) suggest that male spider monkeys, both immatures and adults, are more likely to be injured in intraspecific conflict. This risk may reflect a male's higher level of participation in agonistic (including aggressive) behavior, as

males are more likely to initiate intraspecific aggression (Campbell, 2003; Fedigan & Baxter, 1984).

Chapman and colleagues (Chapman et. al, 1989; Nunes & Chapman, 1997) pose the post-weaning resource competition hypothesis (Silk 1983; Chapman et. al, 1989) to explain female-biased sex ratios in spider monkey populations. This hypothesis holds that females will limit the number of individuals of the non-dispersing sex in order to reduce competition with their own offspring, by either restricting resources or directing aggression to unrelated immatures. In spider monkey communities, adult females are unlikely to be related to other females' offspring. Additionally, limiting other individuals' access to resources would be difficult in a fission-fusion society, where individuals break into subgroups of variable composition to avoid direct feeding competition. Thus, females would be most likely to reduce competition for their own offspring by directing aggression to other females' male offspring. However, Nunes and Chapman (1997) note that the mechanisms used in regulating sex ratios are different at various sites. At Santa Rosa, Costa Rica (Chapman et. al, 1989), a higher mortality rate for immature males (*A. Geoffroyi*) due to aggression directed toward them from adult females is interpreted to be the means used to produce the biased sex ratio, since the sex ratio at birth is fairly equivalent. However, in *A. paniscus*, at Manu National Park, the monkeys had a biased sex ratio at birth; post-birth, male and female immatures had equal rates of survivorship (Symington, 1987). At Maraca Island, Brazil, male immatures (*A. belzebuth belzebuth*) faced increased mortality, but there was no evidence that they received more aggression than female immatures (Nunes and Chapman, 1997). Nunes and Chapman (1997) suggest that the cause of mortality at this site may be related to poor health. It should be noted that different species were studied at each of these

sites. Whether the variability in sex ratio and the mechanisms that underlie it are related to environmental pressures or species differences remains unclear.

## **Theoretical Implications**

### **Evolution of the Juvenile Period**

One particularly unique aspect of primate evolution is the extension of immaturity, in which animals delay reproductive maturity (Pereira & Fairbanks, 2002; Pereira & Leigh, 2003). This occurs during the developmental periods of gestation, infancy, juvenility, and adolescence. While each of these stages contributes to the extension of immaturity, the juvenile period is particularly elongated amongst primates (Pereira & Fairbanks, 2002). Thus, the evolutionary advantages of extended juvenility and the social and developmental process that occur at this time are significant in furthering our understanding of primate evolution. Despite this significance, the juvenile period has been severely overlooked in primatological research (Pereira & Fairbanks, 2002; Pereira & Leigh, 2003). It has been hypothesized that social factors are one of the key evolutionary pressures that influenced both the extension of the juvenile period and the evolution of social and cognitive complexity amongst primates (Dunbar, 2003; Byrne, 1996; Godfrey et. al, 2001; Pagel & Harvey, 2002; Pereira & Fairbanks, 2002). Thus, examining the process of social development in a species such as *Ateles*, which is characterized by an extremely slow life history, even among primates, has important implications in understanding the social advantages of the long juvenile period.

### **Evolution of Relationships in Fission-Fusion Societies**

The fission-fusion social structure that characterizes spider monkeys bears a striking resemblance to the social structure of chimpanzees (Di Fiore & Campbell, 2007; Di Fiore &

Fleischer, 2005). Studies on *Ateles* sociality may elucidate differences between *Ateles* and chimpanzee species (*Pan* sp.) (Barrett, et. al, 2003), thus providing insight into the differences in the evolution of fission-fusion societies among these species. As fission-fusion social systems are uncommon among primates (Barrett et. al, 2003), the behavioral convergence between spider monkeys and chimpanzees provides an opportunity to identify key factors influencing social relationships and structure in these genera. Identification of the similarities and differences between these two genera can help tease out the differing contributions of ecological and phylogenetic factors influencing the evolution of such a social structure and may shed light on the evolution of social relationships and the social structure of humans. Pusey (1990) reports that immature chimpanzees at Gombe, Tanzania exhibit adult-like sex differences. She notes that male juveniles spent more time with their mothers than female juveniles did (male median=88.5%,; female median=100%), and that male juveniles groomed mothers and maternal siblings less than did female juveniles (male median=67%; female median=94%). Additionally, juvenile males displayed more and groomed adult males at higher rates than did juvenile females. Comparisons between data collected on juvenile spider monkeys and the behavioral patterns reported by Pusey (1990) can determine if these two species behavioral convergence begins early in life. Furthermore, this convergence is not limited to only the *Ateles* and *Pan* genera but is apparent in comparison of several species of African apes and members of the Ateline clade, such as between the muriquis (*Brachyteles* sp.) and bonobos (*Pan paniscus*), and gorillas (*Gorilla* sp.) and howler monkeys (*Alouatta* sp.) (Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005). An examination of the behavioral similarities of spider monkeys and chimpanzees must be set within the context of their similarities and differences to close phylogenetic



relatives and may yield further insights into the evolution of primate social behavior in general.

### **Objectives**

The purpose of this study was to investigate differences in social behavior between male and female juvenile black-handed spider monkeys. As rates of overt social behaviors are low among spider monkeys, and spatial patterns are indicative of the strength of affiliative relationships (Di Fiore & Fleischer, 2005; Strier, 1994; Strier, 2002; Symington, 1990), data was collected on social interactions as well as social spacing. The following questions were addressed:

**1) Is there a difference in the time engaged in social interactions between male and female juveniles?**

Ho: There is no difference in the time engaged in social interactions between male and female juveniles.

Ha: Male juveniles engage in social interactions more often than female juveniles.

**2) Do male and female juveniles engage in different types of social interactions?**

Ho: Males and females do not engage in different types of social behavior.

Ha: Males and females do engage in different types of social behavior.

**3) Do conspecifics initiate more interactions with juvenile males than juvenile females?**

Ho: Conspecifics initiate an equal amount of interactions with juvenile males and juvenile females.

Ha: Conspecifics initiate more interactions with juvenile males than juvenile females.

**4) Do juvenile males initiate interactions with conspecifics more frequently than juvenile females?**

Ho: Juvenile males and juvenile females initiate equal amounts of interactions with conspecifics.

Ha: Juvenile males initiate more interactions with conspecifics than juvenile females.

**5) Do male and female juveniles differ in the time they spend in proximity (within five meters) to other conspecifics (excluding mothers)?**

Ho: There is no difference in the time male and female juveniles spend in proximity to nonmother conspecifics.

Ha: Male juveniles spend more time in the proximity of nonmother conspecifics.

**6) Do male and female juveniles differ in the distances they maintain from other conspecifics (excluding mothers?)**

Ho: There is no difference in the distances maintained between male and female juveniles from nonmother conspecifics.

Ha: Male juveniles maintain closer distances from nonmother conspecifics than do female juveniles.

**7) Do male and female juveniles differ regarding the age/sex class with whom they spend the most time in proximity (excluding mothers)?**

Ho: There is no difference in the age/sex class that male and female juveniles spend the most time in proximity.

Ha: There is a difference in the age/sex class that male and female juveniles spend the most time in proximity.

### **Applied Significance of this Study**

#### **Conservation Applications**

A better understanding of spider monkey social development and the emergence of sex differences can aid several aspects of primate conservation and captive welfare. In particular, information on aspects of normal socialization can aid in evaluating captive environments, in the resocialization of confiscated pets, and in developing and evaluating reintroduction programs. Furthermore, information on how social factors influence juvenile mortality and survivorship can inform population models and wild management programs. As spider monkey species are endangered, hunted for bushmeat, kept as pets in various areas

throughout habitat countries, and overwhelmingly threatened by deforestation (Chapman & Peres, 2001; Cuarón, 2005; Estrada et. al, 2004; Kinzey, 1997; Mittermeier, 1987; Rylands, 1997; Sponsel, 1997; Lizzeralde, 2002), such information is extremely important.

### **Wild Population Management**

Sponsel (1997) notes that in Amazonia, spider monkeys are a preferred simian source of bushmeat due to their taste. Cuarón (2005) reports that spider monkeys were a preferred pet monkey species and have been hunted to extinction in some areas; as a result, the inclusion of howler monkeys (*Alouatta sp.*) have increased in the pet trade. Spider monkeys have also been hunted to derive oil from their fat, which is thought to have medicinal purposes (Mittermeier, 1987). Finally, like most other primates, spider monkeys are threatened by deforestation, which is occurring at alarming rates across their entire range (Chapman & Peres, 2001). As spider monkeys have low population densities and low reproductive rates, require large ranges, and have specific dietary preferences and habitat requirements, they are extremely sensitive to deforestation and habitat fragmentation (Chapman & Peres, 2001; Estrada et. al, 2004; Rylands, 1997). Once they are restricted by habitat destruction or decimated by human predation, spider monkey populations are particularly slow to recover from disturbance due to their long interbirth interval (Chapman & Chapman, 1990). While this interval averages around 36 months in wild populations, it ranges from 32 to 50 months and can be affected by differential costs of male and female offspring (Chapman & Chapman, 1990; Eisenberg, 1976; Symington, 1987). Furthermore, spider monkeys tend to have heavily female-biased sex ratios (Chapman et. al, 1989; Symington, 1987; Nunes and Chapman, 1997; Di Fiore and Campbell, 2007). Such biases limit the effective population size of the population and thus slow potential for population

growth and recovery (Caro, 1999; Nunney & Elam, 1994). Therefore, identification of factors that influence the sex ratios of both immatures and adults, as well as the rates of mortality for immatures have important implications for population models (Caro, 1999). Previous research suggests that social factors, such as dominance and aggression, may play a role in regulating sex ratios and mortality rates in spider monkeys (Chapman et. al, 1989; Nunes & Chapman, 1997; Symington, 1987). However, some of this research is conflicting and suggests that these factors may be mediated by environmental stresses. Specifically investigating how the social environment differentially affects male and female immatures and their survival can contribute to developing more effective models of population growth (Caro, 1999). Such models can assist in accurately assessing and managing wild populations. Thus, data on aspects of *Ateles* social behavior that can inform conservation questions is essential to effective management of wild populations.

### **Reintroduction, Resocialization, and Captive Welfare**

Data on the social development of free-ranging spider monkeys is necessary to inform captive rehabilitation and reintroduction programs. The popularity of spider monkeys as pets has contributed to their threatened status in the wild (Cuarón, 2005; Duarte-Quiroga & Estrada 2003). Furthermore, it has created a dilemma for zoos and rescue centers that are inundated with more confiscated animals than they can handle (Cuarón, 2005). Such animals may be kept in captivity for the duration of their lives or rehabilitated with the possibility of future reintroduction to the wild (Cuarón, 2005). Animals with a variety of rearing histories can be integrated in social groups with varying levels of success (Milton, 2002; Anaya-Huertas & Mondragon-Ceballos, 1997; personal observation). However, rearing history and age at resocialization are important factors in mediating such outcomes. An understanding of

what social processes and interactions occur at different developmental stages may assist in developing and evaluating resocialization programs.

Space in captivity is limited, and captive animals cannot contribute to the propagation of their species in the wild. Thus, reintroduction programs are considered a viable option for contributing to primate conservation as well as welfare (Baker, 1992; Cuarón, 2005; IUCN, in review). While there are many potential problems with reintroduction programs, information from wild populations is essential in guiding and evaluating such programs (B. Beck, pers. comm.; Cuarón, 2005; Stoinski, et. al, 1997). An understanding of the normal development of a species is essential to developing captive management protocols that promote the development of species-typical behavior (Thompson, 1996). Furthermore, data on species-typical behavior at different developmental stages can be informative in evaluating which animals may make suitable reintroduction candidates. Thus, baseline data on the social development of spider monkeys can help in both informing captive husbandry and in evaluating the suitability of captive animals for reintroduction (Kleiman, 1996, Thompson, 1996).

### **Conclusion**

More data from free-ranging populations of spider monkeys is necessary to determine what similarities and differences are present in the behavior of male and female immature spider monkeys. Furthermore, if such differences emerge, understanding whether they are a product of immature initiative, differential treatment from mothers and conspecifics, or both, can help to illuminate questions regarding the causes and implications of such differences. On an applied level, this information can help inform conservation and captive management programs. On a theoretical level, a better understanding of the development of social

behavior amongst wild spider monkeys can provide the foundations for understanding the patterns of social relationships prevalent in adult spider monkey societies.

How primate juveniles develop and become integrated in adult society is an area of research that has often been overlooked (Pereira & Fairbanks, 2002; Pereira & Leigh, 2003). However, one of the most unique aspects of primate life histories is the long period of immaturity and maternal dependence. Pereira and Leigh (2003:150) go so far as to state that the “immatures’ struggle may constitute *the single most important factor* structuring primate societies (emphasis added).” Thus, understanding the social experiences that occur during this period is essential to understanding the evolution of primate sociality.

Furthermore, the unique convergence of social structure in the African apes and the Atelines provides opportunity to investigate the effects of ecological differences in shaping social structure and relationships (Chapman, Wrangham, & Chapman, 1995; Di Fiore & Fleischer, 2005). The phylogenetic distance between these two taxa may be beneficial in teasing out the effects of ecological factors from the confound of phylogenetic relatedness (Chapman, Wrangham, & Chapman, 1995). As Barrett and colleagues (2003) note, how spider monkeys negotiate the cognitive challenges of monitoring and maintaining social relationships in a fission-fusion society is still unclear. A comparative study of social relationships in both the Atelines and the African apes may yield insight into the evolution of social relationships in dispersed societies. Since humans (*Homo sapiens*) also live in dispersed societies (Barrett et. al, 2003; Dunbar, 1993), such research may illuminate the evolutionary pressures that shaped our own social relationships. As Strier (2004: 192) notes, “further investigations into the dynamic properties of nonhuman primate sociality can provide new insights into the conditions under which the unique features of human sociality

emerged.” While identifying these factors requires the comparison and synthesis of a large amount of data on a variety of species, each study on aspects of primate social structure and behavior contributes to these goals. Thus, the investigation of the developmental sex differences in spider monkey social behavior and spatial relations is a step toward understanding the evolutionary pressures that shaped the emergence of primate sociality as a whole.

### References

- Anaya-Huertas, C, Mondragon-Ceballos, R. 1998. Social Behavior of Black-Handed Spider Monkeys (*Ateles Geoffroyi*) Reared as Home Pets. *International Journal of Primatology*. 19(4):767-784.
- Baker, LR. 2002. *IUCN/SSC Re-introduction Specialist Group: Guidelines for Nonhuman Primate Re-introductions*. Prepared by the Re-introduction Specialist Group of The World Conservation Union (IUCN) Species Survival Commission (SSC).
- Barrett, L, Henzi, P, Dunbar, R. 2003. Primate Cognition: from ‘What Now?’ to ‘What if?’ *TRENDS in Cognitive Sciences*. 7(11): 494-497.
- Byrne, R.W. 1996. Machiavellian Intelligence. *Evolutionary Anthropology*. 5(5):172-180.
- Carpenter, C.R. 1935. Behavior of Red Spider Monkeys in Panama. *Journal of Mammalogy*. 16(3):171-180.
- Campbell, CJ. 2003. Female-directed Aggression in Free-ranging *Ateles geoffroyi*. *International Journal of Primatology*. 24(2): 223-237.
- Caro, T. 1999. The Behavior-Conservation Interface. *TREE*. 14: 366-369.
- Chapman, CA. 1990. Association Patterns of Spider Monkeys: The Influence of Ecology and Sex on Social Organization. *Behavioral Ecology and Sociobiology*. 26: 409-414
- Chapman, CA, Chapman, LJ. 1987. Social Response to the Traumatic Injury of a Juvenile Spider Monkey (*Ateles geoffroyi*). *Primates*. 28(2): 271-275.
- Chapman, CA, Chapman, LJ. 1990. Reproductive Biology of Captive and Free-Ranging Spider Monkeys. *Zoo Biology*. 9(1): 1-9.

Chapman, CA, Peres, CA. 2001. Primate Conservation in the New Millennium: The Role of Scientists. *Evolutionary Anthropology*. 10: 16-33.

Chapman, CA., Fedigan, LM, Fedigan, L, Chapman, LJ. 1989. Post-weaning Resource Competition and Sex Ratios in Spider Monkeys. *OIKOS*. 54: 315-319.

Cuañon, AD. 2005. Further Role of Zoos in Conservation: Monitoring Wildlife Use and the Dilemma of Receiving Donated and Confiscated Animals. *Zoo Biology*. 24: 115-124.

Di Fiore, A, Campbell, CJ. 2007. The Atelines: Variations in Ecology, Behavior, and Social Organization. In *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, K, Panger, M, Bearder, SK. Oxford: Oxford University Press. 155-185.

Di Fiore, A, Fleischer, RC. 2005. Social Behavior, Reproductive Strategies, and Population Structure of *Lagothrix poeppigii*. *International Journal of Primatology*. 26(5): 1137-1173.

Duarte-Quiroga, A, and Estrada, A. 2003. Primates as Pets in Mexico City: An Assessment of the Species Involved, Source of Origin, and General Aspects of Treatment. *American Journal of Primatology*. 61: 53-60.

Dunbar, RIM. 1993. Coevolution of Neocortical Size, Group Size, and Language in Humans. *Behavioral and Brain Sciences*. 16(4): 681-735.

Dunbar, R.I.M. 2003. The Social Brain: Mind, Language, and Society in Evolutionary Perspective. *Annual Reviews of Anthropology*. 32: 163-181.

Eisenberg, JF. 1976. Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contribution to Zoology*. 213: 1-108.

Estrada, A, Luecke, L, Van Belle, S, Barrueta, E, Meda, MR. 2004. Survey of Black Howler (*Alouatta pigra*) and spider (*Ateles geoffroyi*) monkeys in the Mayan sites of Calakmul and Yaxchilán, Mexico and Tikal, Guatemala. *Primates*. 45: 33-39.

Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.

Godfrey, L.R., Samonds, K.E., Jungers, W.L., Sutherland, M.R. 2001. Teeth, Brains, and Primate Life Histories. *American Journal of Physical Anthropology*. 114: 192-214.

IUCN (in review). IUCN/SSC Primate Specialist Group Section on Great Apes: Guidelines for Ape Re-introductions. Ed. Beck, B, Walkup, K, Rodrigues, M, Unwin, S, Travis, D, Stoinski, T.

Kinzey, 1997. *Ateles*. *New World Primates: Ecology, Evolution, Behavior*. Ed. Kinzey, WG. New York: Aldine de Gruyter. 192-199.



- Kleiman DG. 1996. Reintroduction Programs. *Wild Mammals in Captivity: Principles and Techniques*. Chicago: University of Chicago Press. 297-305.
- Lizzeralde, M. 2002. Ethnoecology of Monkey Among the Bari of Venezuela: Perception, Use, and Conservation. *Primates Face to Face: Conservation Implications of Human-Nonhuman Primate Interconnections*. Ed. Fuentes, A, Wolfe, D. New York: Cambridge University Press. 85-100.
- Milton, K. 2002. Diet and Social Organization of a Free-Ranging Spider Monkey Population: The Development of Species-Typical Behavior in the Absence of Adults. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 173-181.
- Milton, K, Hopkins, ME. 2005. Growth of a Reintroduced Spider Monkey (*Ateles geoffroyi*) Population on Barro Colorado Island, Panama. In *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*. Ed. Estrada, A, Garber, PA, Pavelka, MSM, Luecke, L. 417-435.
- Mittermeier, RA. 1987. Effects of Hunting on Rain Forest Primates. *Primate Conservation in the Tropical Rain Forest*. Ed. Marsh, CW, and Mittermeier, RA. New York: Alan R. Liss, Inc. 109-146.
- Nunes, A, Chapman, CA. 1997. A Re-evaluation of Factors Influencing the Sex Ratio of Spider Monkey Populations with New Data from Maraca Island, Brazil. *Folia Primatologica*. 68: 31-33.
- Nunney, L, Elam, DR. 1994. Estimating the Effective Population Size of Conserved Populations. *Conservation Biology*. 8(1): 175-185.
- Pagel, M.D., Harvey, P.D. 2002. Evolution of the Juvenile Period in Mammals. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 28-37.
- Pereira, ME, Fairbanks, LA. 2002. Foreword 2002: Family, Friends, and the Evolution of Childhood. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. vii-xxiii.
- Pereira, M.E., Leigh, S.R. 2003. Modes of Primate Development. In *Primate Life Histories and Socioecology*. Ed. Kappeler, P.M., Pereira, M.E. Chicago: University of Chicago Press. 149-176.
- Pusey, AE. 1990. Behavioural Changes at Adolescence in Chimpanzees. *Behaviour*. 115: 203-246.

Rylands, AB, Mittermeier, RA, Rodriguez-Luna, E. 1997. Conservation of Neotropical Primates: Threatened Species and an Analysis of Primate Diversity by Country and Region. *Folia Primatologica*. 68: 134-160.

Silk, JB. 1983. Local Resource Competition and Facultative Adjustment of Sex Ratios in Relation to Competitive Abilities. *The American Naturalist*. 121(1): 56-66.

Sponsel. LE. 1997. The Human Niche in Amazonia: Explorations in Ethnoprimateology. *New World Primates: Ecology, Evolution, Behavior*. Ed. Kinzey, WG. New York: Aldine de Gruyter. 143-165.

Stoinski, T, Beck, B, Bowman, M, Lehnhardt, J. 1997. The Gateway Zoo Program: Recent Initiative in Golden Lion Tamarin Reintroductions. *Primate Conservation: The Role of Zoological Parks*. Ed. Wallis, J. American Society of Primatologists. 113-129.

Strier, KB. 1994. Brotherhood Among Atelins: Kinship, Affiliation, and Competition. *Behaviour*. 130: 151-167.

Strier, KB, 2002. Growing Up in a Patrifocal Society: Sex Differences in the Spatial Relations of Immature Muriquis. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 138-147.

Symington, MM. 1987. Sex Ratio and Maternal Rank in Wild Spider Monkeys: When Daughters Disperse. *Behavioral Ecology and Sociobiology*. 20: 421-425

Symington, MM. 1990. Fission-fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology*. 11(1): 47-61.

Thompson, KV. 1996. Behavioral Development and Play. *Wild Mammals in Captivity: Principles and Techniques*. Chicago: University of Chicago Press. 352-271.

## CHAPTER 2 LITERATURE REVIEW: LIFE HISTORY AND THE JUVENILE PERIOD

### Introduction

Amongst mammals, primates tend to be characterized by relatively ‘slow’ life history patterns (Leigh & Blomquist, 2007). However, within the primate order, there is variation in the speed and timing of life history events. The life history pattern of spider monkeys, (*Ateles*) is on the slow end of the continuum, as it extends beyond what would be expected for primates of this size (Chapman & Chapman 1990; Di Fiore & Campbell, 2007). In particular, spider monkeys are characterized by very long periods of growth. Such a long growth period puts immature individuals in a situation in which they risk mortality for years before they can contribute to their own reproductive success and, thus, could only have evolved if this period conferred considerable benefits. The specific patterns of spider monkey socioecology and development must be considered in a broad theoretical context in order to determine what selection pressures contributed to the evolution of the long immature period, and what benefits this period may confer.

### *Ateles* Patterns

#### Socioecology

Species in the genus *Ateles* are arboreal New World monkeys of the Atelinae subfamily (Di Fiore & Campbell, 2007). These primates are unique in that they live in fission-fusion social communities, in which individuals break into subgroups of various size and composition (Carpenter, 1935; Chapman, 1990; Fedigan & Baxter, 1984; Di Fiore & Campbell, 2007; Ramos-Fernandez, 2005; van Roosmalen & Klein, 1988; Schaffner & Aureli, 2005; Symington, 1990). They have a patrilineal social system, which is

characterized by male residence and female dispersal (Chapman et. al, 1989; Di Fiore & Campbell, 2007; Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1987). Spider monkeys are frugivores that exploit ripe fruit resources, and their fission-fusion social system is considered an adaptation to finding patchy food items over large ranges (Robinson & Janson, 1987; van Roosmalen and Klein, 1988). This type of social system is uncommon amongst primates, but is an example of a remarkable ecological convergence with the social structure of apes of the genus *Pan*, particularly *Pan troglodytes* (Aureli et. al, 2006; Barrett et. al, 2003; Chapman, Wrangham, & Chapman 1995; Di Fiore & Campbell, 2006; Fedigan & Baxter, 1984; Goodall 1986; Robinson & Janson, 1987; Symington, 1990). Spider monkeys exhibit marked sex differences in social behavior (Fedigan & Baxter, 1984) but very little sexual dimorphism (Chapman & Chapman, 1990; Corner & Richtsmeier, 1993; Di Fiore & Campbell, 2006; Schultz, 1926). Within spider monkey communities, subgroup composition is variable, and the only constant association is between mothers and offspring (Chapman, 1990; Eisenberg, 1976; Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988). While males are generally affiliative towards immatures, they do not make any major contributions to infant care in the wild (Eisenberg, 1976; van Roosmalen & Klein, 1988; Watt, 1994).

### **Life History (Tables 1 & 2)**

While life history data for *Ateles* is still somewhat sparse (Di Fiore & Campbell, 2007), the general life history parameters indicate that spider monkeys have a slower life history than would be expected for their size (Carpenter, 1935; Chapman & Chapman, 1990; Eisenberg, 1976). Gestation is from seven to seven and a half months, while weaning occurs between 24-36 months (Eisenberg, 1976; Nunes & Chapman, 1997; van Roosmalen & Klein,

*Table 1: Spider Monkey Life History*

<b>Life History Event</b>	<b>Age/Duration</b>	<b>Source</b>
Gestation	7-7.5 months	Eisenberg, 1976; Nunes and Chapman, 1997
Age of independent locomotion	12-15 months	van Roosmalen and Klein, 1988
Weaning age	24-36 months	Symington, 1987, van Roosmalen and Klein, 1988
Age at first birth	7-8 years	Chapman and Chapman, 1990
Interbirth interval (IBI)	32-50 months	Eisenberg, 1976, Chapman and Chapman 1990
Maximum lifespan	44 years	Chapman and Chapman, 1990

1988; Symington, 1987). Young infants rely solely on mother's milk and are carried on the ventrum of the mother for the first several months of life (Eisenberg, 1976; van Roosmalen & Klein, 1988). Infants begin to ride on the mother's back at around six months of age and begin to eat solid food around eight months. Immature spider monkeys begin traveling independently between 12-15 months of age, about a year before they are fully weaned (van Roosmalen & Klein, 1988). These independently locomoting individuals are considered juveniles, as weaning age is extremely variable. Weaning is a very gradual process, and variability in age of weaning is likely to be related to differential levels of maternal investment (Symington, 1987; van Roosmalen & Klein, 1988). From approximately age 36 months to 50 months, juveniles are weaned but continue to range with their mothers. Animals are generally considered subadults at 50-65 months, at which point they are close to adult size but remain more gracile than adults (van Roosmalen & Klein, 1988). Females' age at first birth is at seven to eight years, and the interbirth interval ranges from 32-50 months, with an average of about three years (Chapman & Chapman, 1990). The maximum lifespan in captivity has been recorded at 44 years (Chapman & Chapman, 1990). However, typical longevity in both captivity and the wild is reported to be in the 20s (Chapman & Chapman, 1990; Di Fiore & Campbell, 2007). Spider monkeys have relatively large brains for their

*Table 2: Spider Monkey Brain/Body Weights*

<b>Measure</b>	<b>Weight (g)</b>	<b>Source</b>
Neonatal brain weight	64	Schultz, 1941, Sacher and Schaffeldt, 1974
Neontal body weight	512	Schultz, 1941, Sacher and Schaffeldt, 1974
Adult brain weight	109	Sacher and Schaffeldt,1974
Adult body weight	7640	Sacher and Schaffeldt,1974

body size, with a brain/body ratio of 0.15 as neonates, and 0.015 as adults (Fedigan & Rose, 1995).

These extended life history parameters and large brain/body size ratio are best illustrated in comparison to *Alouatta*, a genus that is a member of the same subfamily that is often sympatric with *Ateles*. Although *Ateles* is only about a kilogram larger on average, spider monkeys have a gestation period of about a month and half longer, an interbirth interval of approximately 15 months longer, and a weaning age that is one and a half to two years later (Fedigan & Rose, 1995). Additionally, despite similar body size, spider monkeys have a brain size that is approximately twice that of *Alouatta* (Fedigan & Rose, 1995). Larger brain sizes are likely to be related to slower life history patterns.

### **Development in a Life History Context**

#### **‘Slow’ versus ‘Fast’ Life Histories**

Theories regarding life history evolution focus on examining how different stages of the life cycle are under selection to maximize reproductive success (Pereira, 2002). These various life history variables include ages at different life stages (gestation, weaning, age of reproductive maturity, senescence, mortality) and morphological variables (adult brain size, adult body size, neonatal brain size, neonatal body size, metabolic rate [Leigh & Blomquist, 2007]). General theories of life history evolution focus on patterns of r-selection versus K-

selection (MacArthur & Wilson, 1967; Rubenstein, 2002). These terms refer to the maximization of opposing variables:  $r$  refers to the growth rate of a population, while  $K$  refers to the carrying capacity of a population. In environments with low population density and many resources, the ability to produce many offspring quickly is more advantageous. However, in environments where the population is near carrying capacity and resources are scarce, heavy investment in few offspring is more advantageous. Thus,  $r$ -selected species are those that tend to have fast life histories, with short growth periods, early ages of reproduction, large litter sizes, short life-spans, and little offspring investment; conversely,  $K$ -selected species tend to have slow life histories, with long periods of growth and development, late ages of reproduction, small litter sizes, and slow lifespans. These strategies are also related to body size, as larger species tend to exhibit longer, slower life history patterns (Purvis et. al, 2003).

Among the two generalities, primates follow a pattern of  $K$ -selection (Janson & van Schaik, 2002; Lee, 1996; Leigh & Blomquist, 2007). However, as Leigh and Blomquist (2007) point out, the dichotomy of  $r$ -strategist versus  $K$ -strategist, or ‘slow life history’ versus ‘fast life history’ may be a limited paradigm. Different life history stages may be under different selection pressures. Furthermore, since different structures grow at different times, growth spurts render the pace of growth uneven (Leigh & Blomquist, 2007, Pereira & Leigh, 2003). Thus, while the concepts of  $r$ -selected, ‘fast’ life history patterns versus  $K$ -selected, ‘slow’ life history patterns may be valuable as general descriptors, they may be overly simplistic categories.

## **Developmental Stages**

In evaluating how selective pressures have affected growth and development, it is necessary to separate the growth period into several stages. The major periods of growth in mammals include gestation, infancy, and juvenility. Gestation refers to the period of fetal growth, infancy refers to the period of growth whilst dependent on the mother's milk, and juvenility refers to the period between weaning and reproductive maturity (Lee, 1999).

Gestation occurs over a discrete time period from conception until birth and, during this time, all the fetus' energetic needs are supplied by the mother. Infancy is demarcated as the period between birth and weaning and, during this time, the immature's energetic needs are still met by the mother. The juvenile period, by contrast, is a growth period during which the immature individual could survive the death of the mother and must meet its own energetic needs (Pereira, 2002). Thus, due to the different demands each of these periods place on mother and offspring, each of these periods may be affected differently by various factors and selection pressures. In conjunction with these three developmental periods, a key variable considered in life history theory is the interbirth interval (IBI), which refers to the time between births of successive offspring. This interval corresponds to the periods of infancy, reproductive cycling, and gestation that occurs between infants and is often the limiting factor on females' reproductive success (Charnov, 1991; Fedigan & Rose, 1995; Lee, 1996).

While the demarcation between gestation and infancy is clear, the demarcation between infancy and juvenility is not. Lee (1996) stresses that weaning is not a discrete event but a gradual process. Particularly in primates, weaning age is mediated by factors beyond those that are generally considered by life history theory. Variability in weaning age



may be mediated by social factors, ecology, and maternal nutrition (Lee, 1996). In particular, social factors play a considerable role in determining levels of maternal investment and weaning age. Research has indicated that dominance rank, the dispersal patterns of the species, and the sex of the offspring play an important role in determining weaning age within a species (Altmann, 1980; Bercovitch, 2002; Lee, 1996; Symington, 1987). Furthermore, even at the later end of the juvenile period, social factors such as dominance rank may accelerate or slow juveniles' rate of growth in comparison to peers (Pereira & Leigh, 2003). Thus, while biological factors such as body size, brain size, and energetic needs may be predominant factors in determining gestation, social factors increasingly contribute to determining the lengths of infancy and the juvenile period.

### **Bodies, Brains, and Energy**

Most variation in the pace of life history patterns is related to body size (Fedigan & Rose, 1995; Godfrey et. al, 2001; Harvey et. al, 1987; Pagel & Harvey, 2002). It is therefore the primary factor to consider in accounting for long periods of immaturity. Factors such as neonatal body weight, age at weaning, and interbirth interval all strongly correlate with body weight (Harvey et. al, 1987). The design constraint, or allometric hypothesis (Godfrey et. al, 2001; Pereira & Fairbanks, 2002b,) considers this variable the key limiting factor for development. While this hypothesis posits that it is body size that is directly responsible for determining growth periods, mediating factors must be considered as well. Pagel and Harvey (2002) consider the length of the reproductive life span the key determinant of delayed maturity. However, since lifespan is strongly associated with body size, this theory ultimately considers body size as the determining factor. However, while body size would

predict longer periods of immaturity for species with long lifespans, it cannot account for periods of delayed maturity *beyond* what would be expected for body size.

Once body size is accounted for, brain size is considered the next key factor in explaining long growth periods. Most theoretical discussions regarding the long period of immaturity in primates consider brain size as the key mediating factor (Fedigan & Rose, 1995; Pereira & Fairbanks, 2002a). This theory makes intuitive and empirical sense, as primates have larger brains than would be expected for their body size and metabolic needs and allocate a higher percentage of their metabolic activity to their brains. Harvey and Bennett (1983) explain that while most mammals allocate 5% of their total metabolism to sustaining the brain, primates allocate 9-20%. Brains are costly organs to maintain, and sustaining brain growth is even more costly. In a study encompassing a wide cross-section of placental mammals, Sacher and Schaffeldt (1974) determined that the length of gestation was determined primarily by brain growth. They concluded that the brain served as a 'pacemaker,' the limiting factor that set the pace of growth for all other tissues. Thus, the larger the brain needs to grow, the longer the animal will need to achieve that growth. While the relationship between large brains and long growth periods is generally accepted and is supported by empirical evidence (Fedigan & Rose, 1995; Godfrey et. al, 2001), the conclusion that the brain sets the pace of growth is debated. Leigh and Blomquist (2007) note that the intensity and timing of maternal investment in brain growth mediates the pace. As Lee (1999) explains, there are two possible strategies: intensive investment to sustain rapid brain growth and produce a young, low-weight weanling, or invest slowly over a longer period of time, to produce a larger weanling that has a slow rate of brain growth. Squirrel

monkeys (*Saimiri sciureus*) provide an example of the former strategy, while tamarins (*Saguinus fuscicollis*) exemplify the latter strategy (Leigh and Blomquist, 2007). Leigh and Blomquist (2007) explain that in the latter strategy, offspring bear more of the costs of brain growth themselves. These alternate strategies indicate that rate of brain growth is variable and thus cannot be considered an absolute pace-setter for somatic growth.

The variability seen in the pace of brain growth is related to the metabolic needs of the mother and offspring. Thus, theories relating to energetic needs may be valuable in explaining these variations. The maternal energy hypothesis (Martin, 1996) considers the basal metabolic rate of the mother as the key factor in determining the brain size of the offspring. Other hypotheses, such as the protein richness hypothesis (Froehlich et. al, 1981; Godfrey et. al, 2001) suggest that the amount of protein in the diet mediates the rate of growth. These two ideas may be related, as Martin (1996) suggests that relationships that are observed between brain size and social and ecological variables may be a byproduct of energetic relationships.

### **Big Brain, Small Gut**

One of most prevalent patterns that emerges in an examination of the relationship between brain size and ecology is that folivorous animals tend to have smaller brains than frugivorous animals (Harvey & Bennett, 1983; Milton, 1981). Aiello and Wheeler (1995) propose the 'expensive tissue hypothesis' to explain the negative relationship between brain size and gut size in primates. They contend that because large brains are metabolically expensive, brain expansion could not occur without a corresponding reduction of other metabolically expensive organs. Because most other costly organs, such as the heart, kidney,

and liver, cannot be substantially altered, they suggest that the gut is the only costly organ that could have undergone such a reduction. However, this reduction is only possible in conjunction with a shift to a higher-quality, easily digestible diet. Thus, they conclude that big brains could only evolve in tandem with a shift to higher quality food resources and reduction of the gut.

While Aiello and Wheeler (1995) provide a compelling explanation of *how* primates could afford the metabolic costs of large brains, they do not address the question of *why* primates evolved large brains. As they explain, large brains are energetically expensive. Furthermore, the longer growth periods that occur as a consequence of large brains result in a long period within an individual's lifespan in which they are at risk for mortality, but they cannot reproduce. Thus, the evolution of large brains must confer some essential benefits or must evolve in conjunction with strategies to reduce the costs.

### **Ecological and Social Challenges**

Some of the theoretical explanations concerning the evolution of large brains within the primate order focus on ecological pressures. One theory is that primates, particularly frugivorous primates, developed larger brains in response to the greater cognitive demands associated with finding food resources (Martin, 1996; Milton 1988). The associated brain expansion could result in improved spatial and memory capacity for locating ripe fruit patches or in visual processing associated with seeing fruit resources in an arboreal environment (Barton, 1996; Milton 1988). However, because of the metabolic trade-offs between brain size and gut size, it is difficult to establish possible cause and effect relationships between frugivory and brain size.

Alternate explanations for the evolution of large brains focus on social pressures (Byrne, 1996; Byrne & Whitten, 1997; Dunbar, 1998; Dunbar, 2003; Kudo & Dunbar, 2001; Martin, 1996; Byrne, Whiten & Byrne, 1988). Dunbar (2003) put forth the ‘social brain hypothesis.’ This hypothesis rests on the argument that primates have larger brains because of expansions in the neocortex, and that neocortex size is related to social complexity. Dunbar (1998, 2003) notes that a variety of measures of social complexity have been shown to significantly correlate with neocortex size. For example, his research has found that grooming clique size and group size in primates increase with neocortex size (Dunbar, 1998; Dunbar, 2003). While his focus is on social causes, he does relate these to ecological causes. He suggests that group size may have evolved to solve ecological problems such as predation, but that the challenges that arose as a result of group-living may have driven brain expansion. He further suggests that this brain expansion occurred in the neocortex, which plays an important role in limiting the amount of social relationships an individual can keep track of and maintain within a social group. This relates to Byrne’s (1996) assertion that the ability to manage and manipulate social relations is dependent on memory, which puts great demands on neural capacities. Barrett et. al (2003) further note that the complexities of fission-fusion societies may pose additional social challenges beyond those faced by cohesive groups.

One of the key challenges in testing between the foraging efficiency and social brain hypotheses is the relationship between frugivory, large brains, and fission-fusion societies. While the trade-off between brain size and gut size complicates this relationship, the relationship between patchy, ephemeral food resources and fission-fusion social structure provide additional impediments to distinguishing between social and ecological causes.

However, as Milton (1988) notes, one pressure does not necessarily negate the importance of the other. Both types of selection may have acted on the evolution of the primate brain.

Nonetheless, there are some data that provide greater support for social hypotheses. Based on their extensive field experiments with vervet monkeys (*Cercopithecus aethiops*), Cheney and Seyfarth (1988, 1990) demonstrate that monkeys are able to demonstrate remarkable intelligence in social contexts but are unable to transfer these skills to non-social domains.

### **The Juvenile Period: Learning and Risks**

In addition to providing the time for large brains to grow, the developmental period is a key time to learn the social and ecological skills that this large organ presumably evolved to support (Godfrey et. al, 2001; Pagel & Harvey, 2002; Pereira & Fairbanks, 2002a). This may be the primary reason for the evolution of the extended juvenile period in primates. While the length of gestation and infancy are determined primarily by the constraints of body size, brain size, and metabolic needs, the transition to the juvenile period is more flexible and influenced by a variety of social factors (Lee, 1996). During this period, the immature is no longer dependent on the mother for support of its growth and development. While primate mothers, as well as other conspecifics, do continue to invest in juveniles, this investment is less metabolically taxing than gestation or lactation. Thus, extension of this period is less constrained than the previous growth periods. While lengthening the juvenile period would pose costs in terms of risking mortality while delaying reproductive maturity, these costs may be offset by the benefits gained in terms of acquiring social competency (Pagel & Harvey, 2002). Furthermore, anthropoid primates are unique in that the rate of somatic growth is delayed during the developmental period (Janson & van Schaik, 2002; Pereira & Fairbanks,

2002b). While this strategy may sound counterintuitive, it may be a way for juveniles to reduce some of the metabolic costs of this period.

While most theoretical discussions concerning the juvenile period focus on the acquisition of social skills, Janson and van Schaik (2002) propose an alternative explanation. They pose the ‘risk aversion hypothesis,’ stating that the slow growth period in the juvenile stage is a strategy to avoid starvation in unpredictable environments. Because juveniles cannot reproduce, their only way to maximize reproductive fitness is to ensure their own survival to reproductive maturity. Janson and van Schaik (2002) suggest that by delaying somatic growth, juveniles reduce the risk of starving. While the small body size may render them more susceptible to predation risks, such risks are compensated for via behavioral mechanisms. Janson and van Schaik (2002) consider this strategy an adaptation to the unique social and ecological conditions experienced by juvenile primates, in which they must compete for food resources with adults, who are more efficient foragers. Thus, Janson and van Schaik (2002) consider the social and behavioral benefits to be a byproduct of the long juvenile period, rather than a cause. However, they do acknowledge the interrelated nature of long juvenile periods, large brain sizes, and increases in social and behavioral complexity, noting that each may play a role in a “selective positive-feedback loop (Janson & van Schaik, 2002: 72).” While these authors provide an interesting hypothesis that accounts for the small body size of juvenile primates, it does not adequately address why the slow growth strategy would be more advantageous than a pattern of fast growth. If juveniles are at a disadvantage for foraging, why prolong the juvenile period at all? By delaying somatic growth, juveniles would simultaneously be putting themselves at a competitive disadvantage and delaying the digestive maturity that would allow them to achieve foraging and digestive efficiency, unless

this period was necessary to acquire associated social or technical skills. Furthermore, this hypothesis seems inadequate to account for the particularly long juvenile period of spider monkeys. Because spider monkeys live in fission-fusion societies and forage in smaller subgroups, most juveniles do not face significant competition for food resources with adult conspecifics. Thus, hypotheses associated with social skills and spatial learning seem far more compelling for this species. Nonetheless, Janson and van Schaik (2002) do provide a compelling explanation for how juveniles can lower some of their metabolic costs while supporting this lengthy learning period.

The strongest support for the hypothesis that social pressures are responsible for the evolution of the extended juvenile period comes from an analysis of the relationship between neocortex size and primate developmental periods. Joffe (1997) specifically examined this relationship by looking at the size of the non-visual neocortex in relationship to primate life history traits. By subtracting the size of the visual cortex, she utilized a measure that more directly corresponding to the area of the brain associated with solving social problems, while eliminating some of the confounds of the visual intelligence required in foraging. She then compared these values to the length of each developmental period. She found that only the length of the juvenile period correlated significantly and positively with non-visual cortex size. She also found that the length of the juvenile period was also significantly positively correlated with mean group size. She suggests that extension of the juvenile period is an adaptation specifically to the need to acquire social skills. While she stresses that these results do not exclude the importance of selection for foraging skills, she concludes that social pressures were the primary selective force for the long juvenile period.



## Conclusion

While most primates exhibit characteristics of slow life histories, spider monkeys are at the extreme end of the continuum. In order to contribute to their own reproductive success, these animals must survive the five or six years until they reach reproductive maturity. While part of the immature period can be accounted for by body size, allometric explanations are not sufficient to explain their extremely lengthy immaturity. However, the length of these periods, particularly gestation and infancy, can perhaps be explained by their large brain size. These large brains may have evolved in response to selection pressures associated with the cognitive demands of finding patchy fruit resources, and the social challenges posed by living in a dispersed social system. Such brain development was likely fueled by their high-quality, easily-digestible diets. While *Ateles* has relatively long gestation and infancy periods, it is the juvenile period that is longest, lasting for nearly four years. It is likely that this long period of immaturity evolved in order to provide adequate time to acquire the social and foraging skills needed to survive in this particular social system and ecological niche. The costs associated with such a long juvenile period may be offset by delayed somatic growth, in conjunction with more extensive maternal support, such as nursing and bridging, well into the juvenile period. Thus, while this period may be costly, both physiological and behavioral strategies lower the associated risks, while providing the individual adequate time to gain essential skills that will serve them in their reproductive futures.

## REFERENCES

Aeillo, LC, Wheeler, P. 1995. The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. *Current Anthropology*. 36(2):199-221.

- Altmann, J. 1980. *Baboon Mothers and Infants*. Princeton: Princeton University Press.
- Aureli, F, Schaffner, CM, Verpooten, J, Slater, K., Ramos-Fernandez, G. 2006. Raiding parties of male spider monkeys: Insights into Human Warfare? *American Journal of Physical Anthropology*. 131(4): 486-497.
- Barrett, L, Henzi, P, Dunbar, R. 2003. Primate Cognition: from ‘What Now?’ to ‘What if?’ *TRENDS in Cognitive Sciences*. 7(11): 494-497.
- Barton, RA, 1996. Neocortex Size and Behavioural Ecology in Primates. *Proceedings: Biological Sciences*. 263(1367):173-177.
- Bercovitch, FB. 2002. Sex-Biased Parental Investment in Primates. *International Journal of Primatology*. 23(4): 905-921.
- Byrne, RW. 1996. Machiavellian Intelligence. *Evolutionary Anthropology*. 5(5):172-180.
- Byrne, RW, Whitten, A. 1997. Machiavellian Intelligence. In *Machiavellian Intelligence II: Extensions and Evaluations*. Ed. Whiten, A, and Byrne, RW. Cambridge: Cambridge University Press. 1-23.
- Carpenter, CR. 1935. Behavior of Red Spider Monkeys in Panama. *Journal of Mammalogy*. 16(3):171-180.
- Chapman, CA. 1990. Association Patterns of Spider Monkeys: The Influence of Ecology and Sex on Social Organization. *Behavioral Ecology and Sociobiology*. 26: 409-414
- Chapman, CA, Fedigan, LM, Fedigan, L, Chapman, LJ. 1989. Post-weaning Resource Competition and Sex Ratios in Spider Monkeys. *OIKOS*. 54: 315-319.
- Chapman, CA, Chapman, LJ. 1990. Reproductive Biology of Captive and Free-Ranging Spider Monkeys. *Zoo Biology*. 9(1): 1-9.
- Chapman, CA, Wrangham, RW, Chapman, LJ. 1995. Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups. *Behavioral Ecology and Sociobiology*. 36(1): 59-70.
- Charnov, EL. 1991. Evolution of Life History Variation Among Female Mammals. *Proceedings of the National Academy of Sciences*. 88:1134-1137.
- Cheney, DL, Seyfarth, RM. 1988. Social and Non-social Knowledge in Vervet Monkeys. In *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Ed. Byrne, RW, and Whiten, A. Oxford: Oxford University Press. 255-270.

- Cheney, DL, Seyfarth, RM. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.
- Corner, BD, Richtsmeier, JT. 1993. Cranial Growth and Growth Dimorphism in *Ateles geoffroyi*. *American Journal of Physical Anthropology*. 92:371-394.
- Di Fiore, A, Campbell, CJ. 2007. The Atelines: Variation in Ecology, Behavior, and Social Organization. *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, KC, Panger, M, Bearder, SK. Oxford: Oxford University Press. 155-185.
- Dunbar, RIM. 1998. The Social Brain Hypothesis. *Evolutionary Anthropology*. 6:178-190.
- Dunbar, RIM. 2003. The Social Brain: Mind, Language, and Society in Evolutionary Perspective. *Annual Reviews of Anthropology*. 32: 163-181.
- Eisenberg, JF. 1976. Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contribution to Zoology*. 213: 1-108.
- Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.
- Fedigan, LM, Rose, LM. 1995. Interbirth Interval Variation in Three Sympatric Species of Neotropical Monkey. *American Journal of Primatology*. 37:9-234
- Froehlich, JW, Thorington, RW, Otis, JS. 1981. The demography of howler monkeys (*Alouatta palliata*) on Barro Colorado Island, Panama. *International Journal of Primatology*. 2: 207-236.
- Godfrey, LR, Samonds, KE, Jungers, WL, Sutherland, MR. 2001. Teeth, Brains, and Primate Life Histories. *American Journal of Physical Anthropology*. 114: 192-214.
- Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: The Bellknap Press.
- Harvey, PH, Bennett, PM. 1983. Brain size, energetics, ecology, and life history patterns. *Nature*. 306(24):314-315.
- Harvey, PH, Martin, RD, Clutton-Brock, TH. 1987. Life Histories in Comparative Perspective. In *Primate Societies*. Ed. Smuts, BB, Cheney, DL, Seyfarth, RM, Wrangham, RW, Struhsaker, TT. Chicago: University of Chicago Press. 181-196.

Janson, CH, Van Schaik, CP. 2002. Ecological Risk Aversion in Juvenile Primates: Slow and Steady Wins the Race. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 57-74.

Kudo, H, Dunbar, RIM. 2001. Neocortex Size and Social Network Size in Primates. *Animal Behavior*. 61:1-12.

Joffe, TH. 1997. Social Pressures have Selected for an Extended Juvenile Period in Primates. *Journal of Human Evolution*. 32: 593-605.

Lee, PC. 1996. The Meanings of Weaning: Growth, Lactation, and Life History. *Evolutionary Anthropology*. 5(3):87-98.

Lee, PC. 1999. Comparative ecology of postnatal growth and weaning among haplorhine primates. In *Comparative Primate Socioecology*. Ed. Lee, P.C. Cambridge: Cambridge University Press. 111-136.

Leigh, SR, Blomquist, GE. 2007. Life History. In *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, KC, Panger, M, Bearder, SK. Oxford: Oxford University Press. 396-407.

MacArthur, RH., Wilson, EO. 1967. *The Theory of Island Biogeography*. Princeton: Princeton University Press.

Martin, RD. 1996. Scaling of the Mammalian Brain: the Maternal Energy Hypothesis. *News in Physiological Sciences*. 11: 149-156.

Milton, K. 1981. Food Choice and Digestive Strategies of Two Sympatric Primate Species. *The American Naturalist*. 117(4): 496-505.

Milton, K. 1988. Foraging Behaviour and the Evolution of Primate Intelligence. In *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. Ed. Byrne, RW, and Whiten, A. Oxford: Oxford University Press.

Nunes, A, Chapman, CA. 1997. A Re-evaluation of Factors Influencing the Sex Ratio of Spider Monkey Populations with New Data from Maraca Island, Brazil. *Folia Primatologica*. 68: 31-33.

Pagel, MD., Harvey, PD. 2002. Evolution of the Juvenile Period in Mammals. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 28-37.

Pereira, ME. 2002. Juvenility in Animals. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 17-27.

- Pereira, ME, Fairbanks, LA. 2002a. Foreword 2002: Family, Friends, and the Evolution of Childhood. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. vii-xxiii.
- Pereira, ME, Fairbanks, LA. 2002b. Why be Juvenile? In *Juvenile Primates: Life History, Development, and Behavior*. . Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 13-15.
- Pereira, ME, Leigh, SR. 2003. Modes of Primate Development. In *Primate Life Histories and Socioecology*. Ed. Kappeler, P.M., Pereira, M.E. Chicago: University of Chicago Press. 149-176.
- Purvis, A, Webster, AJ., Agapow, P., Jones, KE., Isaac, NJB. 2003. Primate Life Histories and Phylogeny. In *Primate Life Histories and Socioecology*. Ed. Kappeler, P.M., Pereira, M.E. Chicago: University of Chicago Press. 25-40.
- Ramos-Fernandez, G. 2005. Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch with Close Associates? *International Journal of Primatology*. 26(5): 1077-1090.
- Robinson, JG., Janson, CJ. 1987. Capuchins, Squirrel Monkeys, and Atelines: Socioecological Convergence with Old World Primates. . In *Primate Societies*. Ed. Smuts, BB, Cheney, DL, Seyfarth, RM, Wrangham, RW, Struhsaker, TT. Chicago: University of Chicago Press. 69-82.
- Van Roosmalen, MGM., Klein, LL. 1988. The Spider Monkeys, Genus *Ateles*. *Ecology and Behavior of Neotropical Primates, Vol. 2*. Ed. Mittermeier, RA, Rylands, AB, Coimbra-Filho, AF, de Fonseca, AB. Washington, DC: World Wildlife Fund. 455-537.
- Rubenstein, DI. 2002. On the Evolution of Juvenile Life-Styles in Mammals. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 38-56.
- Sacher, GA. Staffeldt, E.F. 1974. Relation of Gestation Time to Brain Weight for Placental Mammals: Implications for the Theory of Vertebrate Growth. *The American Naturalist*. 108 (963). 593-615.
- Schaffner, CM., Aureli, F. (2005). Embraces and Grooming Captive Spider Monkeys. *International Journal of Primatology*. 26(5): 1093-1106.
- Schultz, AH. 1926. Studies on the variability of Platyrrhine Monkeys. *Journal of Mammalogy*. 7(4): 286-305.

Schultz, AH. 1941. The Relative Size of the Cranial Capacity in Primates. *American Journal of Physical Anthropology*. 28: 273-287.

Symington, MM. 1987. Sex Ratio and Maternal Rank in Wild Spider Monkeys: When Daughters Disperse. *Behavioral Ecology and Sociobiology*. 20: 421-425

Symington, MM. 1990. Fission-fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology*. 11(1): 47-61.

Watt, SL. 1994. Alloparental Behavior in a Captive Group of Spider Monkeys (*Ateles geoffroyi*) at the Auckland Zoo. *International Journal of Primatology*. 15: 135-151.

Whiten, A, Byrne, RW. 1988. The Machiavellian Intelligence Hypothesis. In *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Ed. Byrne, RW, and Whiten, A. Oxford: Oxford University Press. 1-9.

## **CHAPTER 3 LITERATURE REVIEW: SEX DIFFERENCES AND SOCIAL DEVELOPMENT**

### **Introduction**

Sex differences in immature primate social behavior and spacing have been found in many different species under a variety of social conditions (Wallen et. al, 2003). These differences may reflect both differential exposure to prenatal hormones and social influences at a young age (Wallen et. al, 2003). While certain sex differences may be reflective of general mammalian patterns (Roney & Mastripietri, 2003) and thus widespread throughout primate and other mammal species, other sex differences in development reflect the differential life histories of males and females in different species (Wallen et. al, 2003). Therefore, the developmental sex differences in spider monkeys (*Ateles spp.*) can only be understood in the context of their unique social structure and life history. Furthermore, the sex differences in matrilocal species, such as Old World monkeys, will be different from those of patrilocal species (Wallen et. al, 2003). Meaningful comparison of developmental sex differences in spider monkeys can only be made with other patrilocal species, such as those within the *Pan*, *Brachyteles*, and *Lagothrix* genera.

### ***Ateles* Sociality**

#### **Dispersal, Affiliation, and Aggression**

In spider monkey communities, males reside within their natal community, while the females disperse (Fedigan & Baxter, 1984; Chapman et. al, 1989; Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005; Strier, 1994; Symington, 1987; van Roosmalen & Klein, 1988). As a consequence of this dispersal, the males within spider monkey communities are assumed to be more closely related than the females (Strier, 2004). Fedigan and Baxter

(1984) describe spider monkey communities as a sex-segregated society. While the subgroups vary in size and composition, males and females differ in their level of association with conspecifics (Chapman, 1990; Fedigan & Baxter, 1984). Adult males tend to be more affiliative and range together in large subgroups (Chapman, 1990; Fedigan & Baxter, 1984). Furthermore, the adult males travel faster, range over larger areas, and frequent the boundaries of the community's range more often (Chapman, 1990; Fedigan & Baxter, 1984). Fedigan and Baxter (1984) report that males engage in more affiliative contact behaviors than females, and tend to direct affiliative behaviors to other males. While females can be found in subgroups with males or with other females, they are less affiliative with each other, and tend to be found in smaller subgroups (Chapman, 1990; Fedigan & Baxter, 1984). Furthermore, females, particularly mothers with dependent offspring, range over smaller areas within the core of the community's territory (Chapman, 1990; Fedigan & Baxter, 1984). Chapman notes that adult females are over three times more likely to be solitary than adult males (Chapman, 1990). The only constant association found in spider monkey societies is that between a female and her dependent offspring (Chapman, 1990; Eisenberg, 1976; Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988). Chapman (1990) reports that females with offspring tend to be in smaller subgroups than females without offspring. He suggests that aggression from conspecifics may pose a serious danger to infants and young juveniles, and that females avoid other conspecifics in order to protect their offspring (Chapman, 1990). Fedigan and Baxter (1984) report that males are more aggressive, and male aggression is often directed at adult females (Campbell, 2003; Fedigan & Baxter, 1984). While males have been considered to be generally affiliative with other males within their own community, whom are presumed kin, new research has challenged this assumption.



Lethal intragroup coalitionary attacks, initiated by adult males against subadult males, have been recently reported from two long-term study sites (Campbell, 2006; Valero et. al, 2006). Furthermore, like chimpanzees (*Pan troglodytes*), male raids into neighboring communities have also been reported, in which aggression is directed to neighbors of both sexes (Aureli, et. al, 2006). Despite these patterns of aggression, it should be noted that rates of aggression are nonetheless low in comparison to affiliative behavior (Fedigan & Baxter, 1984, Sussman & Garber, 2004). Furthermore, it is considered unlikely that adult males would pose a threat to immature individuals, since, in a patrilocal society, they are assumed related to the immatures (Strier, 2004). However, at least one case of infanticide by a resident male has been reported in spider monkeys (Vick et. al, 2001), and infanticide by resident males has been reported in chimpanzees (Arcadi & Wrangham, 1999; Hamai et. al, 1992; Otali & Gilchrist, 2006). While females are reported to be less aggressive and more submissive (Fedigan & Baxter, 1984), aggression against immature males may be exhibited by adult females. Chapman et. al (1989) suggest that this may be a method by which females can decrease competition for their own male offspring (*sensu* Silk, 1983). It should be noted that dominance rank may have an effect on both rates of aggression and rates of affiliation among females; low-ranking females are more likely to be solitary (Chapman, 1990) and it is likely that both they and their offspring face a greater risk of aggression.

### **Sex Ratios**

A female-biased sex ratio has been demonstrated among several spider monkey populations (Chapman et. al, 1989; Nunes & Chapman, 1997). Biases in secondary sex ratio may reflect differential investment in male and female offspring (Bercovitch, 2002). However, the source of this biased sex ratio remains unclear (Nunes & Chapman, 1997).

While the adult sex ratio remains biased in each of the populations examined, the birth sex ratios varied between populations (Nunes & Chapman, 1997). At Santa Rosa National Park in Costa Rica, Chapman and colleagues (1989) found a 1: 1 sex ratio at birth, which became increasingly skewed in the juvenile and adult populations. They also found evidence that at Santa Rosa, male immatures faced nearly twice as much aggression as female immatures, and faced a higher mortality rate, presumably as a result of that aggression (Chapman et. al, 1989). Furthermore, in an examination of sex ratio and habitat productivity in the nearby Guanacaste National Park, they found that more skewed female-biased sex ratios correlated with less productive habitats, as measured by rainfall (Chapman et. al, 1989). However, while spider monkeys at Manu National Park in Peru also have a female-biased sex ratio (2.67:1), it does not appear to be due to immature mortality, but rather begins at birth (Nunes & Chapman, 1997; Symington, 1990). Symington (1987) found that while high-ranking females had equal numbers of sons and daughters, low-ranking females produced only daughters. Symington (1987) suggests that the proximate explanation for the biased sex ratio is differential mortality of male embryos, as suggested by evidence that low-ranking females had a longer interbirth interval, and gave birth predominantly to females. This mechanism may ultimately function to reduce male competition in adulthood. Conversely, in Maraca Island, Brazil, Nunes and Chapman (1997) found a strongly male-biased (5: 1) sex ratio at birth. However, the adult sex ratio was still slightly female-biased (1:1.33), and immature males faced higher mortality than immature females, although there was no evidence of aggression towards these animals (Nunes & Chapman, 1997). Nunes and Chapman (1997) suggest that the high immature male mortality may be due to poor health, although the reasons for this sex difference were unclear. Finally, another factor that may differentially

affect immature male mortality is predation. Campbell and colleagues (2005) note that juveniles sometimes played on the ground, and tended to be unaware when absorbed in chase games. While other animals, particularly mothers and adult males, watch these animals vigilantly, spider monkeys face increased risk of predation when on the ground (Campbell et. al, 2005). Reports of sex differences in other primate species suggest that males engage in more active, rough-and-tumble play (*Homo sapiens*: Maccoby & Jacklin, 1974; *Macaca mulatta*: Hinde & Spencer-Booth, 1967; *Macaca fuscicularis*: Van Noorwijk et. al, 2002; *Saimiri sciuricus*: Biben, 1986). If male immatures are more likely to engage in active play on the ground, they may face increased risk of predation. It should be noted that data on causes of immature male mortality come from different habitats and different species (Nunes & Chapman, 1997); whether these reflect species differences, habitat differences, or a combination of the both factors remains unclear. Finally, it is possible that factors regulating the sex ratio occur after the infancy and juvenile period. Recent reports of adult males attacking and killing young males of their own community (Campbell, 2006; Valero, et. al, 2006) suggest that sex ratios may be adjusted via male coalitionary aggression. Such aggression may be exacerbated by equivalent sex ratios and a lack of reproductively available females (Campbell, 2006; Valero, et. al, 2006).

### **Social Behaviors**

The types of affiliative social behaviors prevalent among spider monkeys differ from those seen in other primate species. While grooming is considered to be the most prevalent form of affiliation and indicator of social relationships in primates, it is found at fairly low rates in free-ranging spider monkeys (Ahumada 1992; Fedigan & Baxter, 1984; van Roosmalen & Klein, 1988; Symington, 1990). This may be due to the fact that most research

on grooming and social relationships has focused on Old World primates (Schaffner & Aureli, 2005), while grooming is less prevalent in New World monkeys. While patterns and rates of grooming among spider monkeys are indicative of social relationships (Ahumada, 1992), embraces, pectoral sniffs, and whinny vocalizations may play a more important role in their social behavior (Ramos-Fernandez, 2005; Schaffner & Aureli, 2005). Embraces tend to occur in conjunction with pectoral sniffs, and these two behaviors may be considered a greeting behavior (Eisenberg, 1976; Fedigan and Baxter, 1984; Schaffner & Aureli, 2005; van Roosmalen & Klein, 1988). Schaffner and Aureli (2005) found that embraces often occurred following fusion events. Furthermore, females with infants are reported to have higher levels of embraces than females without infants (Fedigan & Baxter, 1984; Schaffner & Aureli, 2005). Schaffner and Aureli (2005) suggest that embraces serve to reduce tension and facilitate cooperation, and thus are an important factor in the regulation of social relationships. Whinny vocalizations, an affiliative contact call, may also play an important role in the social relationships of spider monkeys (Ramos-Fernandez, 2005). Whinnies provide a vocal signal that allows other subgroups to determine both the location and individual identity of the caller (Chapman & Weary, 1990; Ramos-Fernandez, 2005). In playback experiments, Ramos-Fernandez (2005) found that whinnies influence the movement and behavior of subgroups in auditory range. Furthermore, individuals approached the speakers more often when the recorded call was one from associate (Ramos-Fernandez, 2005). Ramos-Fernandez (2005) suggests that the whinny vocalizations in spider monkeys may have a similar function to the chimpanzee pant-hoot. Furthermore, as Fedigan and Baxter (1984) note, in an arboreal species, it is likely that individuals that may appear solitary may still be able to monitor the locations and presence of other individuals. As

females were found to be more solitary and engaged in more vocal behavior (Fedigan & Baxter, 1984) it is likely that these vocalizations play an important role in their social lives. Ramos-Fernandez (2005) notes that the dispersed social structure adds a level of complexity to the social relationships of spider monkeys; the social mechanisms that regulate relationships may be different from those found in cohesive groups. Furthermore, fission-fusion societies pose a cognitive challenge to monitoring and maintaining social relationships, and how spider monkeys negotiate these challenges remains unclear (Barrett et. al, 2003; Ramos-Fernandez, 2005). Finally, while rates of overt social behavior remain low among spider monkeys, spatial patterns follow those of social interactions, thus social spacing is indicative of the strength of affiliative social relationships (Di Fiore & Fleischer, 2005; Strier, 1994).

### **Comparisons to Other Species**

#### **Other Atelines**

Like spider monkeys, the closely related miquis ( *Brachyteles* spp.) and woolly monkeys ( *Lagothrix* spp.) are generally characterized by female dispersal and male residence, although some male dispersal does occur in woolly monkeys (Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005). However, despite these similar dispersal patterns and a close phylogenetic relationship, social relationships do differ between these species (Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005; Strier, 1994). Like spider monkeys, miquis are characterized by strong male-male social relationships (Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005; Strier, 2004). Male miquis demonstrate a strong preference for one another, in both spatial relations and in social interactions (Strier, 1994). However, unlike the hierarchical dominance relationships among male spider monkeys, miquis males have egalitarian relationships (Di Fiore & Campbell, 2007; Strier, 1994). This

may be due to the fact that muriqui males are unable to dominate muriqui females; thus there is no contest, or direct, competition for access to estrus females (Strier, 2004). Furthermore, muriqui females also have strong affiliative relationships, in contrast to the weak female-female relationships found in spider monkeys (Di Fiore & Fleischer, 2005; Strier, 1994). The patterns of social relationships in woolly monkeys differ from either spider monkeys or muriquis (Di Fiore & Campbell, 2007; Di Fiore & Fleischer, 2005; Strier, 1994). While, like spider monkeys, male dominance relationships are hierarchal (Strier, 1994), there is a lack of strong male-male relationships in woolly monkeys (Di Fiore & Fleischer, 2005). Di Fiore and Fleischer (2005) report that in this species, the strongest relationships are found between males and females. Furthermore, the females are generally responsible for actively maintaining these relationships (DiFiore & Fleischer, 2005).

### **Chimpanzees and Bonobos**

The mating patterns and dispersal patterns of the Ateline primates are a remarkable convergence with the African apes (Di Fiore and Campbell, 2007; Di Fiore & Fleischer, 2005). In particular, aspects of spider monkey social relationships and structure display striking parallels with chimpanzee (*Pan troglodytes*) sociality (Aureli et. al, 2006; Chapman, Chapman, & Wrangham, 1995; Fedigan and Baxter, 1984; Robinson & Janson, 1987; Symington, 1990). While bonobos (*Pan paniscus*) also display the same dispersal patterns and fission-fusion social structure, the prevalence of strong female-female bonds and lack of male dominance suggest that bonobos display greater behavioral convergence with the muriquis (Di Fiore & Campbell, 2007). Both spider monkeys and chimpanzees live in fission-fusion societies and are generally characterized by strong male social relationships and weak female bonds (Di Fiore & Campbell, 2007; Symington, 1990). However, it should

be considered that in chimpanzees, there is variability in the strength of bonds among geographical locations and subspecies. Western chimpanzees (*P.t. verus*, *P.t. vellerosus*) are reported to demonstrate greater female affiliation and stronger male-female bonds (Doran et. al, 2002; Lehmann & Boesch, 2005). Like spider monkey females, eastern chimpanzee females (*P.t. schweinfurthii*) tend to be less gregarious and range in smaller subgroups within the core of the community's territory (Nishida & Hiraiwa-Hasegawa, 1987; Symington, 1990; Watts & Pusey, 2002). Furthermore, in both spider monkeys and chimpanzees, males have a hierarchal dominance rank but nonetheless demonstrate strong affiliative relationships (Nishida & Hiraiwa-Hasegawa, 1987; Strier, 1994; Symington, 1990). Additionally, both lethal intragroup aggression and intergroup raids on neighboring communities have been reported for chimpanzees and spider monkeys (Aureli et. al, 2006; Campbell, 2006; Valero et. al, 2006). Symington (1990) notes that although females are less affiliative, among both spider monkey populations at Cocha Cashu, Peru, and chimpanzee populations at Gombe, Tanzania, some female-female dyads demonstrated strong associations. The behavioral convergence of these two species, especially in contrast to the social relationships found in close phylogenetic relatives characterized by similar life histories and dispersal patterns, provides opportunities to examine ecological factors that influence the evolution of social structure and relationships (Barrett et. al, 2003; Chapman, Wrangham, & Chapman, 1995; Di Fiore & Campbell, 2007).

## **Social Development**

### **Abnormal Rearing Conditions**

Certain studies have demonstrated that, in the absence of adult conspecifics, ex-pet/confiscated animals have nonetheless been able to develop species-typical behaviors

(Anaya-Huertas & Mondragon-Ceballos, 1998; Milton, 2002; Milton & Hopkins, 2005). In one study, 14 animals that were reared in abnormal conditions as pets were resocialized in a captive setting. Anaya-Huertas and Mondragon-Ceballos (1998) hypothesized that these animals would not develop species-typical social structure. However, they found results mirroring those of studies of natural populations. Males were far more affiliative than females, and although rates of agonism were low, females were the recipients of more aggression than males (Anaya-Huertas & Mondragon-Ceballos, 1998). Milton (2002) also reports that the population descended from an original group of spider monkeys purchased at a market and released onto Barro Colorado Island, Panama, developed species-typical behaviors. She notes that, without adult models, males developed preferential associations with each other, and females ranged in core areas and were more solitary. However, only a small number of the total animals released survived (four females and one male, out of 20 released animals) and all of these animals were juveniles (Milton, 2002, Milton and Hopkins, 2005). The effects of individual social experience, rearing condition, or health condition on the survival and social competency of these animals is unclear. Furthermore, the ability to develop and maintain species-typical behavior may be dependent on group composition and rearing history. In a group of three spider monkeys at Jungle Friends Primate Sanctuary, two females that were reared together consistently dominated and directed aggression toward a male with a particularly poor rearing history (personal observation). Milton (2002) and Anaya-Huertas and Mondragon-Ceballos (1998) suggest that there may be innate biological mechanisms that regulate patterns of species-typical behaviors. This is consistent with Wallen and colleagues' (2003) assertion that prenatal hormonal exposure shapes the differentiation of behavior in the sexes. However, they do note that early rearing



environment and social experience is equally important; rather than “programming” individuals for certain behavior, hormone-related differences in neural organization may make certain behaviors more or less rewarding for each sex (Wallen et. al, 2003).

### **Social Influences during the Juvenile Period**

The juvenile period is an important time period for learning, brain development, and social development (Fairbanks & Pereira, 2002; Roney & Mastriperi, 2003). Van Noordwijk et. al (2002) note that immature individuals exhibit sex-typical behavior earlier than those behaviors would be advantageous or could be explained in terms of differential social or nutritional needs. Rather, these differences seem to emerge in preparation for the demands of adult life. Furthermore, the differences exhibited in immature behavior are reflective of patterns of residence and dispersal (Strier, 2002; Wallen et.al, 2003). Watts and Pusey (2002) note that the social lives of immature chimpanzees are tremendously influenced by the mother’s social interactions and ranging patterns. The social lives of immature spider monkeys are most likely shaped in the same way. While immature individuals in group-living primates always have access to other individuals, individuals in fission-fusion societies are more limited (Watts & Pusey, 2002). Furthermore, Pusey (1983) notes that the transition from maternal dependence to integration within the adult community presents more of a challenge for individuals living in dispersed societies.

McDaniel (1994) suggests that the formation of species-typical behaviors and patterns of affiliation emerge early in spider monkeys. However, her data is somewhat conflicting. It indicates that while infant females engaged in more social behavior than infant males (females=26.6% vs. males=15%), this pattern was reversed amongst juveniles, as juvenile males engaged in more social behavior than juvenile females (females=18.1% vs.

males=22.8%). However, her data must be interpreted with caution, as she had only one infant in each sex category. Whether these trends indicate a developmental change between infancy and juvenility, or individual idiosyncrasies is unclear.

### **Development in Chimpanzees**

Immature chimpanzees have been shown to demonstrate many adult-like sex differences (Pusey, 1990; Watts & Pusey, 2002). Juvenile males are particularly interested in following and interacting with other individuals, particularly adult males and estrous females (Pusey 1983; Watts & Pusey, 2002). Furthermore, as immature males grow, they demonstrate increasing interest and association with adult males (Pusey, 1990; Watts & Pusey, 2002). While both male and female immatures devoted most of their grooming to their mother and maternal siblings, males groomed unrelated individuals more often than did females (Pusey, 1990). Male immatures were also observed to display more than females (Pusey, 1990). Male immatures were also more likely to groom adult males (Pusey, 1990). However, male and females engaged in equivalent amounts of social play, and males interacted with infants as often as females did (Pusey, 1990). Pusey (1990) notes that males would benefit more than females from social interaction with all community members, including adult males, adult females, and immatures, since they would be residing within that community. However, although the immature males play an active role in their social lives, they were also recipients of differential treatment from other individuals. Adult males demonstrated increasing aggression toward immature males as they grew (Pusey, 1990). Furthermore, Pusey (1983) notes that at food resources, daughters were more likely than sons to be supplanted by their mothers. Finally, while sex differences existed during the juvenile

period, Pusey (1990) notes that some differences became more apparent or first emerged at adolescence.

### **Development in Muriquis**

Sex differences in immature social behavior also exist in the spider monkey's closest relative, the muriqui (Strier, 2002). In addition to having similar residency and dispersal patterns, muriquis have a similar life history and developmental trajectory as spider monkeys (van Roosmalen & Klein, 1988; Strier, 2002). Strier (2002) looks specifically at sex differences in spatial proximity, as spatial relations generally mirror patterns of overt social behavior in Atelines (DiFiore & Fleischer, 2005; Symington, 1990). Both male and female immatures maintained close proximity to their mothers (Strier, 2002). However, males immatures were in proximity to other group members more often than female immatures (Strier, 2002). Strier (2002) notes that natal immature females as well as immigrant subadult females demonstrated weaker spatial relationships. Furthermore, there were differences in nearest neighbor preferences between juvenile and subadult females; juvenile females maintained proximity to adult males more often, while subadult females were more likely to have adult females as their nearest neighbor (Strier, 2002). Differences also existed between juvenile and subadult males; juvenile males maintained proximity with non-mother females, while subadult males were more often in proximity to adult males (Strier, 2002). Thus, both males and females exhibited a shift in nearest neighbor preferences between the juvenile and subadult period (Strier, 2002). This is consistent with Pusey's (1990) data on chimpanzees, suggesting that even though some sex differences may emerge at a young age, they may undergo developmental changes. Furthermore, Strier (2002) also notes that surprisingly, the juveniles did not preferentially associate with each other.

## **Sex Differences in Immature Spider Monkeys**

### **Early Experiences**

Data from long-term studies indicates that immature male and immature female spider monkeys face differential pressures and experiences from a young age. Symington (1987) reports that at Cocha Cashu, Peru, mothers invested more in male offspring than in female offspring. Male infants were carried for approximately three months longer than female infants, and males were allowed to nurse to a later age than females (Symington, 1987). Symington (1987) estimated this differential investment to be 24% greater for males. Furthermore, she notes that among the offspring of high-ranking mothers, sons benefited overall more than females (Symington, 1987). Additionally, Symington (1987) suggests females may preferentially intervene in social situations to support sons, but not daughters. If this is the case, females may be able to influence their male offspring's achievements in the male dominance hierarchy (Symington, 1987). Such maternal influence in male dominance rank has been reported in bonobos (Furuichi, 1989). Data on captive spider monkeys support this suggestion; a positive correlation between juvenile male's rank and mother's affiliation with males was found (Macintosh, 2001). As Watts and Pusey (2002) note, in a fission-fusion social system, an immature individual's opportunities to develop social relationships depends on the mother's ranging patterns and sociability. If high-ranking females are more likely to affiliate and range with adult males, as suggested by Chapman's (1990) assertion that high-ranking females are less solitary, then sons of high-ranking females would have more opportunities to develop relationships that could ease integration into the adult hierarchy.

## **Survival Challenges**

Evidence also suggests that male and female immatures face different survival challenges (Chapman et. al, 1989; Nunes & Chapman, 1997; Symington, 1987). Symington (1987) observed that low-ranking females produce mostly daughters; she suggests that this may be due to differential survival of male and female embryos. This suggestion is supported by the evidence that the interbirth interval for low-ranking females was longer than that for high-ranking females (Symington, 1987). Furthermore, at Maraca Island, Brazil, male immatures faced increased mortality rates that were assumed to be due to health (Nunes & Chapman, 1997). However, most striking is Chapman and colleagues (1989) assertion that immature male mortality was due to aggression. They report that at Santa Rosa National Park, in northwestern Costa Rica, infant and juvenile males faced nearly twice the amount of aggression that infant and juvenile females encountered (Chapman et. al, 1989). A similar pattern was also found at Tikal, Guatemala (Chapman et. al, 1989, Fedigan and Baxter, 1984). Furthermore, immature males were more likely to exhibit injuries, presumably as a result of this aggression (Chapman & Chapman, 1987; Chapman et. al, 1989). Chapman and Chapman (1987) describe the result of one such injury and the post-injury care given to the immature male. The incident causing the injury was not witnessed; the injured juvenile suffered a loss in locomotor abilities and exhibited signs of illness following the injury (Chapman & Chapman, 1987). Furthermore, the injured juvenile suffered a developmental regression compared to his previous behavior and another juvenile of comparable age; while previously more independent, his mother resumed carrying him and nursing him (Chapman & Chapman, 1987). Chapman and Chapman (1987) note that while his mother demonstrated the most care to compensate for the injury, other individuals did as well. However, while

Chapman and colleagues (1989) as well as Fedigan and Baxter (1984) report that immature males received greater aggression than females, this pattern has not been found at all sites. At Hacienda Los Innocentes, another site in northwestern Costa Rica, McDaniel (1994) found that juvenile males and juvenile females were involved in equivalent numbers of aggressive encounters. In most of these encounters, juvenile females were recipients of aggression, whereas juvenile males initiated aggression more often than they received it. While the reasons for the conflict patterns found by McDaniel (1994), Chapman and colleagues (1989), and Fedigan and Baxter (1984) remain unclear, they may be reflective of ecological differences. Tikal, Guatemala, and Santa Rosa, Costa Rica, are tropical dry forests, whereas Hacienda Los Inocentes is a moist forest that receives more rainfall. This is consistent with Chapman and colleagues (1989) suggestion that the severity of female-biased sex ratios, and presumably, severity of aggression directed toward immature males, is related to low habitat productivity.

If males do incur greater risks of injury, or are of poorer health, greater maternal investment may be necessary to compensate for these risks (*sensu* Silk, 1983). Immature males may face increased aggression through one of two factors; via direct harassment from adult females (*sensu* Silk, 1983), or through increased participation in social interactions that result in aggression. Silk (1983) suggests that in matrilocal societies, females can limit the number of the non-dispersing sex (in this case, females) by either limiting unrelated female immatures' access to resources or by direct aggression. Applying Silk's theory to a patrilocal society, females can limit the number of the non-dispersing sex (in this case, males) by either limiting unrelated immature male's access to resources, or by directing aggression toward them. This aggression can occur directly to the immature individuals or to the females

pregnant with male fetuses (*sensu*, Silk, 1983). In a fission-fusion society, limiting resources is likely to be difficult; therefore aggression may be a more likely strategy. Furthermore, in a patrilocal society, other females' offspring are most likely unrelated individuals. Thus, infanticide by females may be advantageous in spider monkey societies. While most research and theory has focused on males, since males are responsible for most cases of infanticide in primates (Van Schaik & Janson, 2000), infanticide by females has been documented across five different orders of mammal, including primates (Digby et. al, unpublished data, reported in Digby, 2000). Digby (2000) also notes that infanticide by females may pose a more persistent threat than infanticide by males. While the selective advantages and causes of infanticide, as well as its prevalence among primates and other mammalian species is highly controversial (van Schaik & Janson, 2000; Sommer, 2000), the threat of infanticide may be a strong selection pressure on patterns of social structure (Digby, 2000). As Chapman (1990) noted, females with dependent offspring may range in smaller subgroups as a counterstrategy against this threat. However, it could be argued that ranging with males who might be potential fathers of offspring, and forming friendships with particular adult males (*sensu* Smuts, 1985) could also be efficient counterstrategies, as affiliation with adult males might confer protection for immature offspring. However, such male-female relationships have not reported in spider monkeys, and run contrary to the persistent patterns of male affiliation, male aggression toward females, and female asociality reported for spider monkey societies. As for increased social participation, if immature males have an overall higher level of social interaction, both aggressive and affiliative behavior may be increased; thus, rather than higher levels of aggression directed particularly at immature males, this higher rate may simply be a result of higher levels of overall social

interaction. Furthermore, it is also possible that, like immature male chimpanzees, as male spider monkeys grow older, they might also face increased aggression as they start to become integrated in the male dominance hierarchy (*sensu* Pusey, 1990). Reports of lethal male coalitionary aggression toward male subadults support this possibility (Campbell, 2006; Valero et. al, 2006). In order to distinguish between these different possibilities, identifying the context, initiators of aggression, and levels of aggression received by immature males in comparison to overall social interactions may be a valuable step in teasing apart each of these possibilities.

### **Social Play**

Sex differences in social play are one of the most pervasive sex differences observed in a variety of primates (Fagen, 2002; Roney & Mastripieri, 2003; Wallen et. al, 2003). For example, immature males are reported to engage in active, ‘rough-and-tumble’ play more often than immature females (Wallen et. al, 2003). Roney and Mastripieri (2003) note that the differences observed in such rough-and-tumble play may be due to general mammalian patterns of male competition over mates; thus such differences should be observed across mammalian species characterized by male-male competition. The dominance hierarchies found among spider monkeys (Strier, 1994) do suggest that some form of male competition exists among spider monkeys. Recent data on adult male-subadult male competition and intragroup killings support this suggestion (Campbell, 2006; Valero et. al, 2006). However, data on male aggression toward females also indicates that males cooperate in aggressive attacks (Campbell, 2003). Strier (1994) suggests that cooperation among male spider monkeys allow them to achieve dominance over females, despite fairly equivalent body size. Campbell’s (2003) study provides some support for this hypothesis, although she cautions



that more data is needed to support this. The factors that influence competitive versus cooperative strategies in males requires further investigation as well, although both Campbell (2006) and Valero and colleagues (2006) suggest that it may relate to the operational sex ratio. The unresolved questions regarding the prevalence of male cooperation and competition in mating strategies suggests that male juveniles need to acquire the skills necessary to engage in both. While immature male chimpanzees must also prepare for competition as adults, Pusey (1990) found that immature males and immature females did not differ in social play behavior in chimpanzees, who experience similar social pressures due to their residence and dispersal patterns. However, in spider monkeys, Eisenberg (1976) observed that most instances of grappling, or play-fighting, were initiated by juvenile males. Since aspects of immature social behavior often mirror adult relationships, males would be expected to engage in social play with other males more often. However, data is conflicting on this subject. Van Roosmalen and Klein (1988) report that juveniles do not exhibit preferences for either males or females as play partners. However, individual juveniles do demonstrate preferences for particular individuals as play partners (van Roosmalen & Klein, 1988). McDaniel (1994) reports that among juveniles, social play occurred most often between males and females. She did however, observe that among single-sex play, male-male play occurred twice as frequently as female-female play.

### **Alloparenting**

Eisenberg (1976) reported that males sometimes carried young immatures in the period of transition from riding on the mother to locomotory independence. However, reports of alloparental behavior are rare among free-ranging spider monkeys (Watt, 1994). Watt (1994) does report that alloparental behavior was prevalent in a group of captive spider

monkeys. She observed that infant spider monkeys were carried by alloparents, left in the care of other group members, and occasionally nursed by non-mother females. Adult males and females engaged in more alloparental behavior than juveniles and older infants (Watt, 1994). Watt (1994) notes that the alloparental behavior on the part of nonmother females may be an artifact of the particular captive situation. The females had a long history of residence in the group together, and they may be related. Similarly, Link and colleagues (2006) observed alloparental behavior initiated by a natal subadult female towards younger siblings in a wild spider monkey community. However, most females are assumed to be unrelated, and thus unlikely to participate in alloparental behavior. Furthermore, if other females may be a danger to immature offspring (Chapman et. al, 1989; Chapman, 1990) mothers who left their offspring in the care of other females would risk lowering their reproductive fitness and this behavior would therefore be selected against. However, alloparenting by adult males would be consistent with the social behavior of free-ranging spider monkeys. Watt (1994) notes that adult males demonstrated significantly more alloparental behavior than other age-sex classes. Additionally, she notes that infants often actively initiated transfer to adult males (Watt, 1994). Link and colleagues (2006) also report that an adult male provided assistance to a female burdened with twins. In a patrilocal society, adult males are likely to be related to the immatures of the community; they may even be potential fathers (Strier, 2004; Watt, 1994). Watt (1994) remarks that adult males demonstrated marked interest in immatures of both sexes. In a captive setting, adult males may have had greater access to immatures than they do in wild populations. However, the patterns of affiliation are likely to be the same, even if their frequency is not (Watt, 1994). Furthermore, both adult males and immature males are known to demonstrate interest in each

other (Eisenberg, 1976; Milton, 2002; van Roosmalen & Klein, 1988; Watt, 1994).

Eisenberg (1976) reports that as immature males age, adult males devote increasing attention to them. Van Roosmalen and Klein (1988) report that juvenile males often initiate embraces with adult males, and that this behavior occurs in both wild and captive settings. Milton (2002) reports that around three to three and half years of age, juvenile males began to leave their mothers in order to range with adult males. Watt (1994) reports that adult males initiated interactions with older infant males and interacted with them in different ways than they did with younger males or infant females. She speculates that these interactions were the beginning of the process of male bonding, and that establishing affiliations at young age with adult males would assist immature males in integration in the adult male social structure (Watt, 1994). However, she stresses that more data from wild groups are necessary to corroborate this hypothesis.

### **Conclusion**

Spider monkeys share a phylogenetic history with their closest relatives, the marmosets, and a remarkable behavioral convergence with a very distant relative, the chimpanzees. Looking at evidence from studies on both adult and immature spider monkeys, as well as these other species, provides suggestions as to what social processes occur during immaturity, and to what kind of sex differences may emerge. This evidence suggests that immature spider monkeys are likely to receive differential treatment and display sex differences at a relatively young age. Nonetheless, data from chimpanzees and marmosets, as well as from spider monkeys, indicate that juveniles do not always display the sex differences and behavioral patterns that would be predicted. Just as many aspects of adult sociality remain unclear despite more extensive study, it is clear that more data is needed to

understand what social processes characterize the juvenile period amongst spider monkeys, and which behavioral sex differences do exist.

### References

- Ahumada, JA. 1992. Grooming Behavior of Spider Monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *International Journal of Primatology*. 13(1): 33-49.
- Anaya-Huertas, C, Mondragon-Ceballos, R. 1998. Social Behavior of Black-Handed Spider Monkeys (*Ateles Geoffroyi*) Reared as Home Pets. *International Journal of Primatology*. 19(4):767-784.
- Arcadi, AC, Wrangham, RW. 1999. Infanticide in Chimpanzees: Review of cases and a new within-group observation from the Kanyawara study group in Kibale National Park. *Primates*. 42: 337-351.
- Aureli, F, Schaffner, CM, Verpooten, J, Slater, K, Ramos-Fernandez, G. 2006. Raiding parties of male spider monkeys: Insights into Human Warfare? *American Journal of Physical Anthropology*. 131(4): 486-497.
- Barrett, L, Henzi, P, Dunbar, R. 2003. Primate Cognition: from ‘What Now?’ to ‘What if?’ *TRENDS in Cognitive Sciences*. 7(11): 494-497.
- Bercovitch, FB. 2002. Sex-Biased Parental Investment in Primates. *International Journal of Primatology*. 23(4): 905-921.
- Biben, M. 1986. Individual- and –sex-related strategies of wrestling play in captive squirrel monkeys. *Ethology*. 71: 229-241.
- Campbell, CJ. 2003. Female-directed Aggression in Free-ranging *Ateles geoffroyi*. *International Journal of Primatology*. 24(2): 223-237.
- Campbell, CJ, Aureli, F, Chapman, CA, Ramos-Fernandez, G, Matthews, K, Russo, SE, Suarez, S, Vick, L. 2005. Terrestrial behavior of *Ateles* spp. *International Journal of Primatology*. 26(5): 1039-1051.
- Campbell, CJ. 2006. Lethal Intragroup Aggression by Adult Male Spider Monkeys (*Ateles geoffroyi*). *American Journal of Primatology*. 68(12): 1197-1201.
- Chapman, CA. 1990. Association Patterns of Spider Monkeys: The Influence of Ecology and Sex on Social Organization. *Behavioral Ecology and Sociobiology*. 26: 409-414
- Chapman, CA, Chapman, LJ. 1987. Social Response to the Traumatic Injury of a Juvenile Spider Monkey (*Ateles geoffroyi*). *Primates*. 28(2): 271-275.

- Chapman, CA, Chapman, LJ. 1990. Reproductive Biology of Captive and Free-Ranging Spider Monkeys. *Zoo Biology*. 9(1): 1-9.
- Chapman, Ca, Weary, DM. 1990. Variability in Spider Monkey's Vocalizations May Provide Basis for Individual Recognition. *American Journal of Primatology*. 22(4): 279-284.
- Chapman, CA, Wrangham, RW, Chapman, LJ. 1995. Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups. *Behavioral Ecology and Sociobiology*. 36(1): 59-70.
- Chapman, CA, Fedigan, LM, Fedigan, L, Chapman, LJ. 1989. Post-weaning Resource Competition and Sex Ratios in Spider Monkeys. *OIKOS*. 54: 315-319.
- Digby, L. 2000. Infanticide by Female Mammals: Implications for the Evolution of Social Systems. Infanticide by Males: Prospectus. In *Infanticide By Males and its Implications*. Ed. van Schaick, CP, Janson, CH. Cambridge: Cambridge University Press. 423-446.
- Di Fiore, A, Campbell, CJ. 2007. The Atelines: Variation in Ecology, Behavior, and Social Organization. In *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, KC, Panger, M, Bearder, SK. Oxford: Oxford University Press. 155-185.
- Di Fiore, A, Fleischer, RC. 2005. Social Behavior, Reproductive Strategies, and Population Structure of *Lagothrix poeppigii*. *International Journal of Primatology*. 26(5): 1137-1173.
- Doran, DM, Jungers, WL, Sugiyama, Y, Fleagle, JG, Heesy, CP. 2002. Multivariate and Phylogenetic Approaches to Understanding Chimpanzee and Bonobo Behavioral Diversity. In *Behavioural Diversity in Chimpanzees and Bonobos*. Ed. Boesche, C, Hohmann, G, Marchant, LF. Cambridge: Cambridge University Press. 14-34.
- Eisenberg, JF. 1976. Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and Related Species. *Smithsonian Contribution to Zoology*. 213: 1-108.
- Fagen, R. 2002. Primate Juveniles and Primate Play. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 182-196.
- Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.
- Furiuchi, T. 1989. Social Interactions and the Life History of Female *Pan paniscus* in Wamba, Zaire. *International Journal of Primatology*. 10: 173-197.
- Hamai, M, Nishida, T, Takahasi, H, Turner, LA. 1992. New Records of Within-group Infanticide and Cannibalism in Wild Chimpanzees. *Primates*. 133-151-162.
- Hinde, RA, Spencer-Booth, Y. 1967. The Behavioral Development of Socially Living Rhesus Monkeys in their First Two and Half Years. *Animal Behavior*. 15: 169-196.
- Lehman, J, Boesch, C. 2005. Bisexually Bonded Ranging in Chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*. 57: 525-535.

- Link, A, Palma, AC, Velez, A, de Luna, A.G. 2006. Costs of twins in free-ranging white-bellied spider monkeys (*Ateles belzebuth belzebuth*) at Tinigua National Park, Columbia. *Primates*. 47: 131-139.
- MacIntosh, AJJ. 2001. Rank Relations in Captive Juvenile Spider Monkeys (*Ateles geoffroyi*): A Case Study. *Laboratory Primate Newsletter*. 40(2): 1-4.
- McDaniel, PS. *The Social Behavior and Ecology of the Black-handed Spider Monkey (Ateles geoffroyi)*. PhD Dissertation, St. Louis University.
- Milton, K. 2002. Diet and Social Organization of a Free-Ranging Spider Monkey Population: The Development of Species-Typical Behavior in the Absence of Adults. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 173-181.
- Milton, K, Hopkins, ME. 2005. Growth of a Reintroduced Spider Monkey (*Ateles geoffroyi*) Population on Barro Colorado Island, Panama. In *New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation*. Ed. Estrada, A, Garber, PA, Pavelka, MSM, Luecke, L. 417-435.
- Nishida, T, Hiraiwa-Hasegawa, M. 1987. Chimpanzees and Bonobos: Cooperative Relationships among Males. In *Primate Societies*. Ed. Smuts, BB, Cheney, DL, Seyfarth, RM, Wrangham, RW, Struhsaker, TT. Chicago: University of Chicago Press. 165-177.
- Van Noordwijk, MA, Hemelrijk, CK, Herremans, LAM, Sterck, EHM. 2002. Spatial Position and Behavioral Sex Differences in Juvenile Long-Tailed Macaques. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 77-85.
- Nunes, A, Chapman, CA. 1997. A Re-evaluation of Factors Influencing the Sex Ratio of Spider Monkey Populations with New Data from Maraca Island, Brazil. *Folia Primatologica*. 68: 31-33.
- Otali E, Gilchrist, JS. 2006. Why Chimpanzee (*Pan troglodytes schweinfurthii*) Mothers are less Gregarious than Nonmothers and Males: the Infant Safety Hypothesis. *Behavioral Ecology and Sociobiology*. 59: 561-570.
- Pereira, ME, Fairbanks, LA. 2002. Foreword 2002: Family, Friends, and the Evolution of Childhood. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. vii-xxiii.
- Pusey, AE. 1983. Mother-Offspring Relationships in Chimpanzees after Weaning. *Animal Behaviour*. 31(2): 363-377.
- Pusey, AE. 1990. Behavioural Changes at Adolescence in Chimpanzees. *Behaviour*. 115: 203-246.

Ramos-Fernandez, G. 2005. Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch with Close Associates? *International Journal of Primatology*. 26(5): 1077-1090.

Robinson, JG, Janson, CJ. 1987. Capuchins, Squirrel Monkeys, and Atelines: Socioecological Convergence with Old World Primates. . In *Primate Societies*. Ed. Smuts, BB, Cheney, DL, Seyfarth, RM, Wrangham, RW, Struhsaker, TT. Chicago: University of Chicago Press. 69-82.

Roney, JR, Maestripieri, D. 2003. Social Development and Affiliation. In *Primate Psychology*, ed. Maestripieri, D. Cambridge: Harvard University Press. 171-204.

Van Roosmalen, MGM, Klein, LL. 1988. The Spider Monkeys, Genus *Ateles*. *Ecology and Behavior of Neotropical Primates, Vol. 2*. Ed. Mittermeier, RA, Rylands, AB, Coimbra-Filho, AF, de Fonseca, AB. Washington, DC: World Wildlife Fund. 455-537.

Schaffner, CM, Aureli, F. 2005. Embraces and Grooming Captive Spider Monkeys. *International Journal of Primatology*. 26(5): 1093-1106.

Van Schaik, CP, Janson, CH. 2000. Infanticide by Males: Prospectus. *Infanticide By Males and its Implications*. Ed. van Schaick, CP, Janson, CH. Cambridge: Cambridge University Press. 1-6.

Silk, JB. 1983. Local Resource Competition and Facultative Adjustment of Sex Ratios in Relation to Competitive Abilities. *The American Naturalist*. 121(1): 56-66.

Smuts, BB. 1985. *Sex and Friendship in Baboons*. New York: Aldine.

Sommer, V. 2000. The Holy Wars on Infanticide. Which Side Are You On? In *Infanticide By Males and its Implications*. Ed. van Schaick, CP, Janson, CH. Cambridge: Cambridge University Press. 1-6.

Strier, KB. 1994. Brotherhood Among Atelins: Kinship, Affiliation, and Competition. *Behaviour*. 130: 151-167.

Strier, KB, 2002. Growing Up in a Patrifocal Society: Sex Differences in the Spatial Relations of Immature Muriquis. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 138-147.

Strier, KB, 2004. Sociality Among Kin and Nonkin in Nonhuman Primate Groups. In *The Origins and Nature of Sociality*. Ed. Sussman, RW, Chapman, AR. New York: Aldine de Gruyter. 191-214.

- Sussman, RW, Garber, PA. 2004. Rethinking Sociality: Cooperation and Aggression among Primates. In *The Origins and Nature of Sociality*. Ed. Sussman, RW, Chapman, AR. New York: Aldine de Gruyter. 161-190.
- Symington, MM. 1987. Sex Ratio and Maternal Rank in Wild Spider Monkeys: When Daughters Disperse. *Behavioral Ecology and Sociobiology*. 20: 421-425
- Symington, MM. 1990. Fission-fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology*. 11(1): 47-61.
- Valero, A, Schaffner, CM, Vick, LG, Aureli, F, Ramos-Fernandez, G. 2006. Intragroup Lethal Aggression in Wild Spider Monkeys. *American Journal of Primatology* 68: 732-737.
- Vick, LG, Ramos-Fernandez, G, Taub, DM. 2001. Infanticide among the spider monkeys (*Ateles geoffroyi yucatanensis*) of Punta Laguna, Mexico. Congreso Mexicano de Primatología, Merida, Yucatan, 2-5 Septiembre, 2001: Programa y Resúmenes. Merida, Yucatan, Mexico: Asociación Mexicana de Primatología. 8.
- Wallen, K, Zehr, JL, Herman, RA, Graves, FC. 2003. Sexuality. In *Primate Psychology*, ed. Maestripieri, D. Cambridge: Harvard University Press. 69-107.
- Watt, SL. 1994. Alloparental Behavior in a Captive Group of Spider Monkeys (*Ateles geoffroyi*) at the Auckland Zoo. *International Journal of Primatology*. 15: 135-151.
- Watts, DP, Pusey, AE. 2002. Behavior of Juvenile and Adolescent Great Apes. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 148-167.
- Wittig, RM, Boesche C. 2003. Food Competition and Linear Dominance Hierarchy among Female Chimpanzees of the Taï National Park. *International Journal of Primatology*. 24: 847-867.



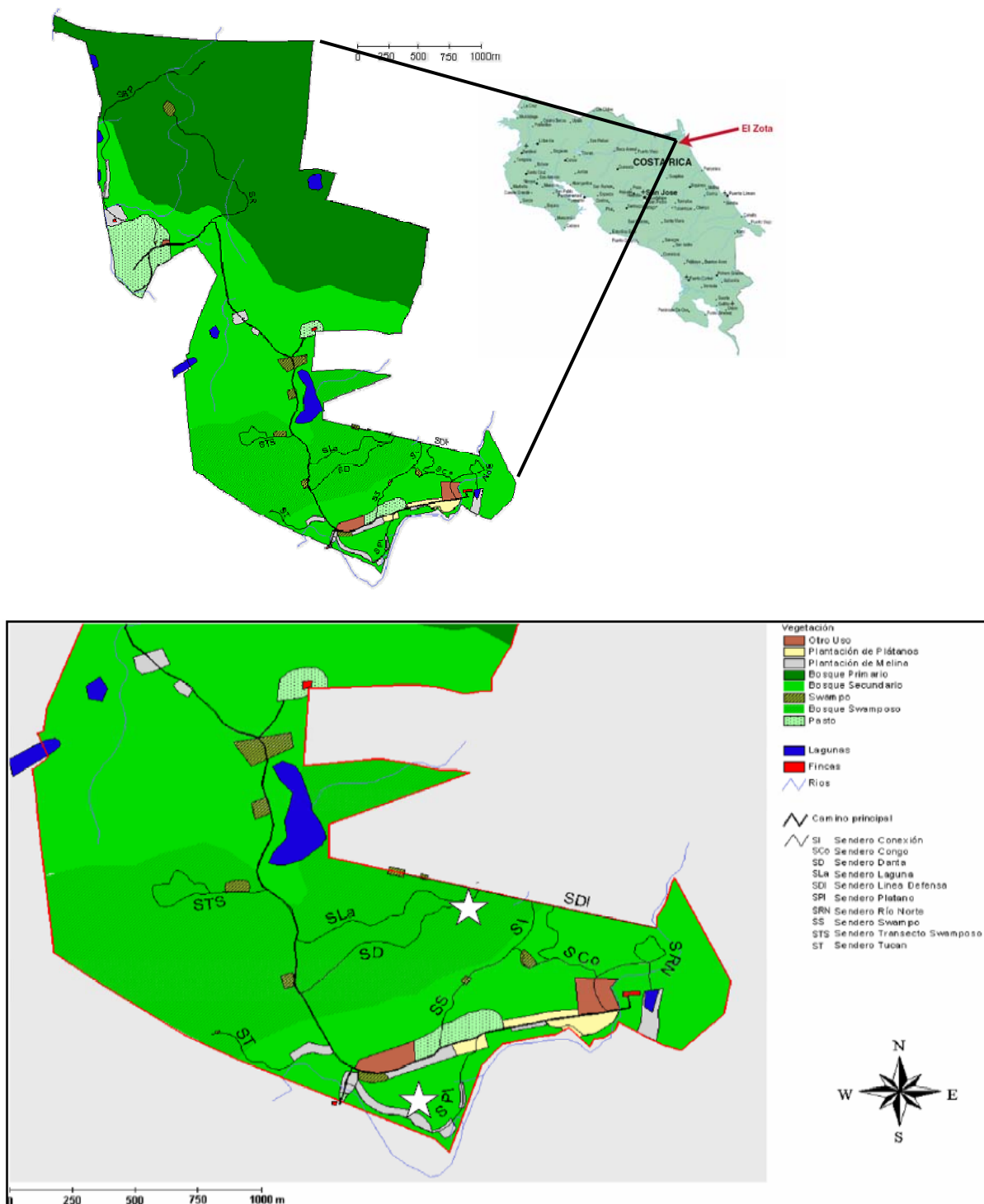
## **CHAPTER 4 RESEARCH METHODOLOGY**

### **Study Site**

Research was conducted at El Zota Biological Field Station (EZBFS) in Costa Rica. EZBFS is situated in the northeastern region of the country at 10°57.6 N, 83°75.9'W (Pruetz & LaDuke, 2001). The field station is one of the largest privately-owned biological field stations in Costa Rica and harbors greater diversity than other similar field stations (Pruetz & LaDuke, 2001). The station was founded through a collaboration between the landowner, Hiner Ramirez, Dr. Thomas LaDuke of East Strousburg University, Dr. Jill Pruetz of Iowa State University, and a non-profit organization, DANTA: Association for the Conservation of the Tropics. The field site is host to several field courses and student research projects each year.

El Zota includes 1000 hectares of land comprised of a mosaic landscape of lowland swamp forest, lowland wet forest, pasture, cropland and reforested areas (Pruetz & LaDuke, 2001; Lindshield, 2006). About 700 hectares of this land is predominated by mature and secondary forest, while approximately 300 hectares are a patchwork of pastures and plantation. Approximately 8.5 km of trails have been cut to facilitate research. These trails traverse several different types of habitat, including primary forest, swamp forest, secondary forest, gallery forest, and plantation (Lindshield, 2006). Both mature and secondary forests are comprised of lowland wet and swamp forest, and the low-lying areas are often seasonally inundated (Lindshield, 2006). This area receives approximately 4000 mm of rainfall annually (Sanford et. al, 1994; Lindshield, 2006). Seasonality is mild, with rainfall occurring year-round, but with slight peaks in early November-December and June-July. Most

Figure 1: Maps of El Zota Biological Field Station



Courtesy of Fiebelkorn and Busse (unpublished data). Lower map shows southern portion of the station where the Pilón community ranges. English interpretation of line transects are as follows: Sendero Transecto Swamposo (STS) = Swamp Forest Transect (SFT); Sendero Línea Defensa (SDI) = Fence Line Transect (FLT); Sendero Plátano (SPI) = (SP).

research on spider monkeys has been conducted at much drier study sites (Chapman et. al, 1989, Lindshield, 2006), although this type of habitat represents an important type of spider monkey habitat that has been understudied for logistical reasons (Lindshield, 2006).

El Zota is home to three primate species: white-faced capuchin monkeys (*Cebus capucinus*), mantled howling monkeys (*Alouatta palliata*) and black-handed spider monkeys (*Ateles geoffroyi*). Recent surveys conducted by Lindshield (2006) indicate densities of 6.0 individuals/km<sup>2</sup> for capuchin monkeys, 8.4 individuals/km<sup>2</sup> for howling monkeys, and 12.2 individuals/km<sup>2</sup> for spider monkeys. The density of spider monkeys is relatively high compared to other sites, although much higher densities have been reported at a few other sites (Lindshield, 2006). Both capuchin and howling monkeys have been observed to occasionally associate and interact with spider monkeys and thus can be considered potential social partners for both agonistic and affiliative interactions (Rose et. al, 2003; Pruett & LaDuke, 2001, personal observation). The subspecies of spider monkey (*A.g. ornatus*) found at EZBFS is endemic to northeastern Costa Rica and has recently been elevated from vulnerable to endangered status (Cuarón et. al, 2003). Thus, EZBFS is an important site for the study and preservation of this subspecies.

### **Study Community**

Two to three spider monkey communities are estimated to occur at El Zota (Lindshield, 2006). Research was conducted on the Pílon group, which is the best-habituated of the spider monkey communities present at EZBFS. This community ranges through the eastern region of the property, in an area composed of secondary and swamp forest, gallery forest, and plantation. This section of the EZBFS directly abuts the station buildings, and is the location of the majority of field course activities and student projects. As a result, while

behavioral research on the spider monkeys has only been undertaken recently (Howells & Pruettz, 2005; Lindshield, 2006, Lockett et. al, 2004), the Pilón community has had more exposure to with humans. While spider monkeys have traditionally been assumed to prefer primary forest (van Roosmalen and Klein, 1988), Lindshield's (2006) investigations suggest that the disturbed habitat utilized by the Pilón community provides adequate resources, and that densities in the disturbed and undisturbed habitats are fairly equivalent.

The Pilón community is estimated to include at least 30 members (personal observation). This estimate includes two to three adult males, one sub-adult male, three females and their dependent infants, and at least three adult females without dependent offspring. Nine juveniles and their mothers could be individually identified. This community size is comparable to the average community sizes reported elsewhere. In a recent synthesis of the existing literature, Di Fiore and Campbell (2007) report that average community size for *Ateles* species is 28 individuals (n=13), with a range of 12-42 individuals. The average community size for *Ateles geoffroyi* is slightly smaller, with about 25 individuals per community (Di Fiore & Campbell, 2007).

Infants are defined as individuals aged approximately 0-15 months, which cling to the mother's ventrum or back during travel (van Roosmalen and Klein, 1988). Juveniles are defined as individuals approximately 15-50 months old who travel independently of the mother but still remain in close contact and range with her (van Roosmalen and Klein, 1988). They can be further subdivided into three categories, including juvenile-one, juvenile-two, and juvenile-three (Table 3), following Roosmalen and Klein (1988). The sex of immatures can be easily distinguished due to the pendulous clitoris of the females. The original research proposal called for the study of both infants and juveniles. However, upon beginning this

study, the decision was made to conduct research only on juveniles. The females with infants were far more skittish than females with more independent offspring, and the former immediately fled upon contact with the observer. The stress and metabolic costs of both fleeing and disruption of resting and foraging were considered too great to incur upon females with dependent infants. Thus, research focused on juveniles, who were habituated enough for focal observation. Juvenile focal subjects could be identified on the basis of size, sex, facial characteristics, and pelage (Table 4). Juvenile's mothers were also identified based on facial characteristics and pelage.

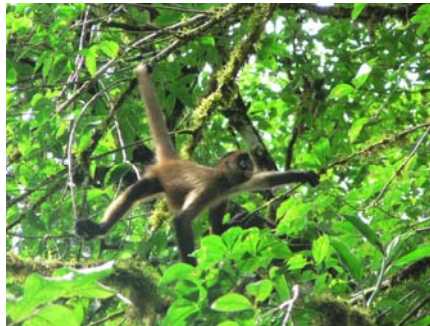
*Figure 2: Focal Subjects*



*Anya (Juvenile Female)*



*Iris (Juvenile Female)*



*Tristan (Juvenile Male)*

*Table 3: Juvenile Age Classes*

<b>Age Class</b>	<b>Age Range</b>	<b>Distinguishing Features</b>
Juvenile-1	15 to 24 months	relatively small size; large pink circles around eyes and mouth; independent locomotion; frequent bridging, occasional nursing and dorsal clinging
Juvenile-2	24 to 36 months	relatively medium size; decreasing pink circles; independent locomotion increases; infrequent bridging and nursing
Juvenile-3	36 to 50 months	larger size; decreasing pink circles; rapid locomotion; bridging rare

**Adapted from van Roosmalen and Klein (1988)**

*Table 4: Focal Subjects*

<b>Subject</b>	<b>Sex</b>	<b>Age Class</b>	<b>Distinguishing Characteristics</b>
Buttercup	F	Juvenile-1	small, golden, very large pink circle around mouth
Iris	F	Juvenile-1	small, caramel brown, large pink circle around mouth
Lena	F	Juvenile-2	medium, dark brown, dark face, very small pink circles around eyes and mouth
Piper	F	Juvenile-2	medium, reddish brown, medium pink circles
Anya	F	Juvenile-3	large, dark brown, white chinstraps
Oliver	M	Juvenile-1	small, golden, dark face
Tristan	M	Juvenile-1	small, golden, large pink circles
Freddie	M	Juvenile-2	medium, caramel brown, medium pink circles
Miguel	M	Juvenile-2	medium-large, golden

## **Procedure**

### **Data Collection**

Data was collected on focal animals using a two-minute instantaneous recording technique (Altmann, 1974). Additionally, all social interactions that the focal engaged in were recorded. The first focal animal encountered at the beginning of each day was followed for as long as visual contact could be continued. If multiple focal animals were present, subjects were chosen so as to equalize the amount of data collected for each individual. Weekly data summaries were conducted to identify priority focal subjects. Observations were terminated if the subject was lost for ten consecutive sample points (20 minutes).

Binoculars were used to confirm identity and aid in observation. During each sampling interval the following information was collected: 1) time of day, 2) location in the forest (estimated distance to and number of nearest trailmarker), 3) identity and activity of focal animal, 4) identity of all party members, 5) nearest neighbor distance, 6) initiator/recipients of social interaction, and 7) type of social interaction. Distance to the nearest neighbors was visually estimated and recorded as the following categories: contact, within 1 meter, 1-5 meters, or >5 m. Nearest neighbors and party members were identified individually whenever possible, and if not possible, age/sex class of individual was recorded. A party is defined as a group of individuals associating with each other and maintaining proximity of 30 m or less with each other (Chapman, 1990; Ramos-Fernandez, 2005). Party composition was recorded and all changes in composition were noted during focal observation. Activities include travel, rest, feed/forage, social interactions, and other behaviors (Table 5-7).

*Table 5: Behavioral Categories*

<b>Behavior</b>	<b>Definition</b>
Travel	movement within the crown of a tree or between the crowns of trees that is not related to food acquisition or play
Rest	any period of inactivity
Feed/forage	any localized movement within the tree crown associated with the procurement, handling of, and ingestion of food items
Social	any behavior that involves interaction or contact with conspecifics or other animals
Other	any behavior that does not fall into the above categories; includes observer-directed behavior, and solitary play

**Adapted from van Roosmalen & Klein (1988); McDaniel (1994); and personal observations**

### **Research Schedule**

Data was collected from 23 December 2005-5 January 2006 (two weeks), and from 12 May 2006, to 2 August 2006 (12 weeks). The initial field season was spent familiarizing myself with the field site, identifying focal subjects, and testing the proposed methodology.

Pilot data was collected at this time and, as individual recognition could be carried out, this data was included for analysis. Approximately 5-6 days per week were spent collecting data

**Table 6: Affiliative Behaviors**

<b>Behavior</b>	<b>Definition</b>
Huddle	sitting in contact, may include tail- or limb-wrapping around conspecific
Embrace	clasping arms around a conspecific; often in conjunction with pectoral sniffing
Touch	reaching out and making contact with a conspecific
Grooming	parting of a conspecific's hair and picking out insects or foreign objects out of hair with hands or mouth
Pectoral sniff	leaning in and sniffing the pectoral region of a conspecific; often in conjunction with embracing
Nurse	suckling from the mother or another lactating female
Cling	clinging to the mother or another conspecific during travel
Bridge	using the mother or another conspecific to cross large gaps
Social Play	includes grappling, wrestling, lunging, and chase games; may be accompanied by head-shaking, play-faces, or panting
Whinny	contact call with a 'wave-like frequency;' usually occurs in response to visual or auditory contact

**Adapted from Eisenberg (1976); Van Roosmalen & Klein (1988); Fedigan & Baxter (1984); Schaffner & Aureli (2005); Ramos-Fernandez (2005); and personal observations**

**Table 7: Agonistic Behaviors**

<b>Behavior</b>	<b>Definition</b>
Avoid	Retreat from a conspecific's approach
Displace	Assuming a conspecific's spatial position, forcing the conspecific to move
Chase	following or lunging at a retreating conspecific
Harass	Hitting, poking, or tail-pulling a conspecific
Fight	Biting, wrestling, and slapping that results in screaming and fear responses
Display	aggressive visual signals that may include branch-shaking, head-shaking, and arm-swaying; may be accompanied by open-mouth threats and pilo-erection
Weaning rejection	any aggressive response as a result of immature's attempts to nurse
Distress vocalizations	squawks, whoas, and cries associated with distress

**Adapted from Eisenberg (1976); Van Roosmalen and Klein (1988); and personal observations**

with an average of 42 hours spent in the field each week. The remaining time was devoted to data entry, data summary, and rest. A total of 76.8 hours of focal data were obtained, and 116.2 hours were spent in contact with *Ateles* parties.

## **Data Analysis**



Data was analyzed regarding the values listed in Table 8. For each of these variables, individual means were calculated. This data was then compared using two-sample t-tests with SAS statistical analysis software. All relevant tests were carried out, including and excluding mothers as conspecifics. Significance levels were set initially at 0.05, and adjusted with a Bonferroni correction to account for Type I errors associated with multiple tests. One-tailed p-values were reported for all variables testing directional hypotheses, while two-tailed p-values were used for nondirectional hypotheses.

*Table 8: Data variables Examined*

<b>Category</b>	<b>Variable</b>
Social Behavior	Time engaged in each behavioral category
Social Behavior	Time engaged in each type of social interaction
Social Behavior	Rate of each type of social interaction
Social Behavior	Events/hr of agonism received from conspecifics
Social Behavior	Events/hr of agonism initiated toward conspecifics
Social Behavior	Frequency of grooming received from conspecifics
Social Behavior	Frequency of grooming initiated toward conspecifics
Social Behavior	Direct care behaviors (cling, bridge, nurse) provided by mother
Social Behavior	Indirect care behaviors (groom, huddle) provided by mother
Social Behavior	Indirect care behaviors (groom, huddle) provided by nonmothers
Social Behavior	Time engaged in play with each age/sex class
Proximity Patterns	Time spent in proximity to each age/sex class
Proximity Patterns	Time spent in proximity to mothers vs. nonmothers
Proximity Patterns	Distance categories maintained to mother
Proximity Patterns	Distance categories maintained to nonmothers
Proximity Patterns	Mean Party Size
Proximity Patterns	Time spent in different party compositions

## References

- Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*. 49(3):227-67.
- Chapman, CA. 1990. Association Patterns of Spider Monkeys: The Influence of Ecology and Sex on Social Organization. *Behavioral Ecology and Sociobiology*. 26: 409-414
- Cuarón, AD, de Grammont, PC, Cortés-Ortiz, L, Wong, G, Silva, JCS. 2003. *Ateles geoffroyi* ssp. *ornatus*. In: IUCN 2004. *2004 IUCN Red List of Threatened Species*. [www.iucnredlist.org](http://www.iucnredlist.org). Downloaded on 09 March 2007.

Di Fiore, A, Campbell, CJ. 2007. The Atelines: Variations in Ecology, Behavior, and Social Organization. In *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, K, Panger, M, Bearder, SK. Oxford: Oxford University Press. 155-185.

Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.

Lindshield, SM. 2006. The Density and Distribution of *Ateles geoffroyi* in a Mosaic Landscape at El Zota Biological Field Station, Costa Rica. Masters Thesis. Iowa State University, Ames.

Luckett, J, Danforth, E, Linsenhardt, K, Pruett, J. 2004. Planted Trees as Corridors for Primates at El Zota Biological Field Station, Costa Rica. *Neotropical Primates*. 12(3): 143-146.

McDaniel PS. 1994. The Social Behavior and Ecology of the Black-handed Spider Monkey (*Ateles geoffroyi*). Ph.D. dissertation, Saint Louis University, Saint Louis.

Pruetz, JD, LaDuke, TC. 2001. New Field Site: Preliminary Census of Primates at El Zota Biological Field Station, Costa Rica. *Neotropical Primates*. 9(1): 22-23.

Ramos-Fernández, G. 2005. Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch with Close Associates? *International Journal of Primatology*. 26(5): 1077-1090.

Van Roosmalen, MGM, Klein, LL. 1988. The Spider Monkeys, Genus *Ateles*. *Ecology and Behavior of Neotropical Primates, Vol. 2*. Ed. Mittermeier, RA, Rylands, AB, Coimbra-Filho, AF, de Fonseca, AB. Washington, DC: World Wildlife Fund. 455-537.

Rose, LM, Perry, S, Panger, MA, Jack, K, Manson, JH, Gros-Louis, J, Mackinnon, JC, Vogel, E. 2003. Interspecific Interactions between *Cebus capucinus* and Other Species: Data from three Costa Rican sites. *International Journal of Primatology*. 24(4): 759-796.

Sanford, RLJ, Paaby, P, Luvall, JC, Phillips, E. 1994. Climate, Geomorphology, and Aquatic Systems. In *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. Ed. McDade LA, Bawa KS, Hespdenheide HA, Hartshorn GS. Chicago: The University of Chicago Press. 19-33.

Schaffner, CM, Aureli, F. (2005). Embraces and Grooming Captive Spider Monkeys. *International Journal of Primatology*. 26(5): 1093-1106.

## CHAPTER 5 RESULTS AND DISCUSSION: SOCIAL BEHAVIOR

### Quantitative Results

A total of 71 hours of instantaneous focal data (2130 sample points) were analyzed (males=1062 sample points; females=1068 sample points) after out-of-sight sample points were discarded. While fairly equivalent amounts of data were collected on males and females, the amount of focal data collected on each individual varied (Table 9). One female was not observed to engage in any social behavior and was thus excluded from analyses of social behavior beyond the activity budget. One-tailed t-tests were used for directional hypotheses, while two-tailed tests were used for all non-directional hypotheses. To account for the increased likelihood of a Type I error when using multiple t-tests, a Bonferroni adjustment was used. This reduces the significance level of 0.05 to account for the number of t-tests used in each comparison.

*Table 9: Focal Data per Individual*

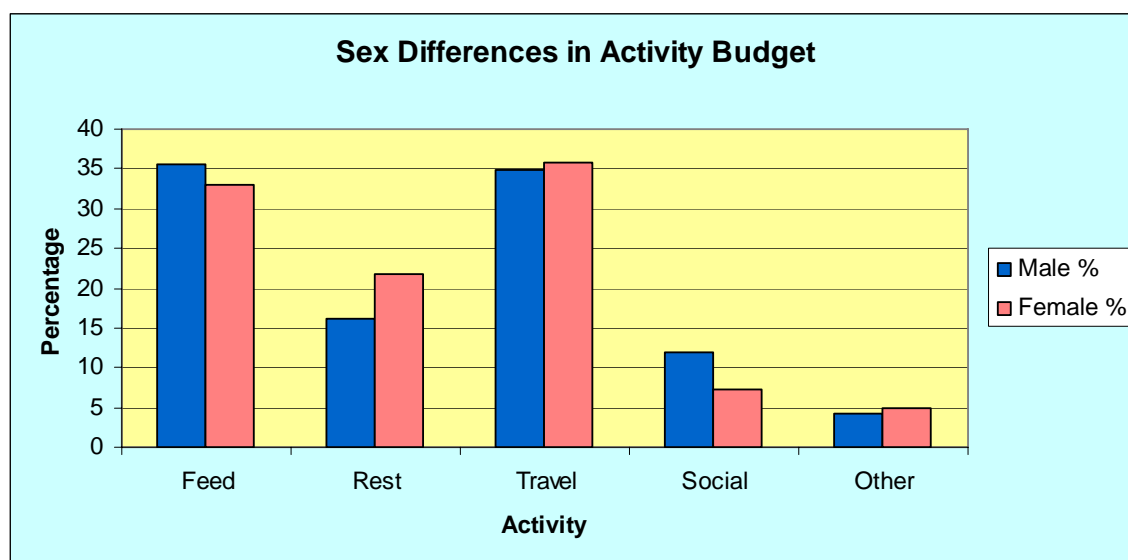
<b>Focal</b>	<b>Anya (F)</b>	<b>Lena (F)</b>	<b>Buttercup (F)</b>	<b>Iris (F)</b>	<b>Piper (F)</b>	<b>Freddie (M)</b>	<b>Miguel (M)</b>	<b>Oliver (M)</b>	<b>Tristan (M)</b>	<b>Total</b>
Sample points	134	170	387	357	20	311	31	53	667	2130
Minutes	268	340	774	714	40	622	62	106	1334	4260
Hours	4.47	5.67	12.9	11.9	0.67	10.37	1.03	1.77	22.23	71.0

### Activity Budget

In a comparison of male and female activity budgets (Figure 3), observable differences were noted for rest (males=16.1%; females=21.7%) and social behavior (males=11.9%; females=7.3%), while feed/forage (males=35.5%; females=33%), travel (males=34.8%; females=35.8%), and other behaviors (males=4.1%; females=4.9%) were similar (Figure 3). The Bonferroni-adjusted significance level is 0.01 for these tests. No

statistical differences were found for feed/forage ( $T=-2.7$ ,  $df=7$ , one-tailed  $p=0.3967$ ), travel ( $T=.14$ ,  $df=7$ , one-tailed  $p=0.4456$ ), rest ( $T=.76$ ,  $df=7$ , one-tailed  $p=0.2355$ ), or other behaviors ( $T=.21$ ,  $df=7$ , one-tailed  $p=0.4188$ ). The difference for social behavior approaches significance ( $T=-1.77$ ,  $df=7$ , one-tailed  $p=0.0603$ ).

*Figure 3*



### **Social Behaviors**

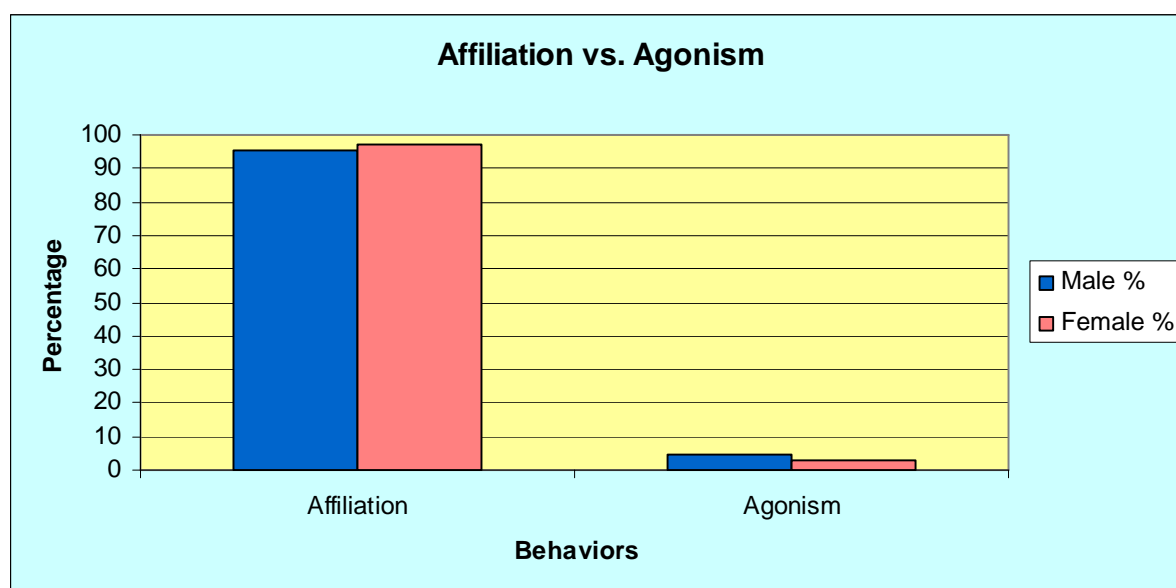
Both focal data and all-occurrence behavior was used to investigate whether males and females differ in the types of social behaviors that they exhibited. Social behaviors recorded using instantaneous sampling were calculated as a frequency of the individual's total social behavior, while all occurrences of social behavior were calculated as a rate of events per hour of observation.

#### *Affiliation vs. Agonism*

In order to compare the frequency of affiliation versus agonism, all affiliative and agonistic behaviors observed during instantaneous focal sampling were combined and

compared (Figure 4). Both males and females engaged predominantly in affiliative behavior (males=95.4%; females=96.9%) and rarely engaged in agonism (males=4.6%; females=3.1%). The Bonferroni-adjusted significance level is 0.025 for these tests. No difference was found in either category (affiliation:  $T=.27$ ,  $df=6$ , two-tailed  $p=0.7967$ ; agonism:  $T=-.27$ ,  $df=6$ , two-tailed  $p=0.7967$ ).

*Figure 4*

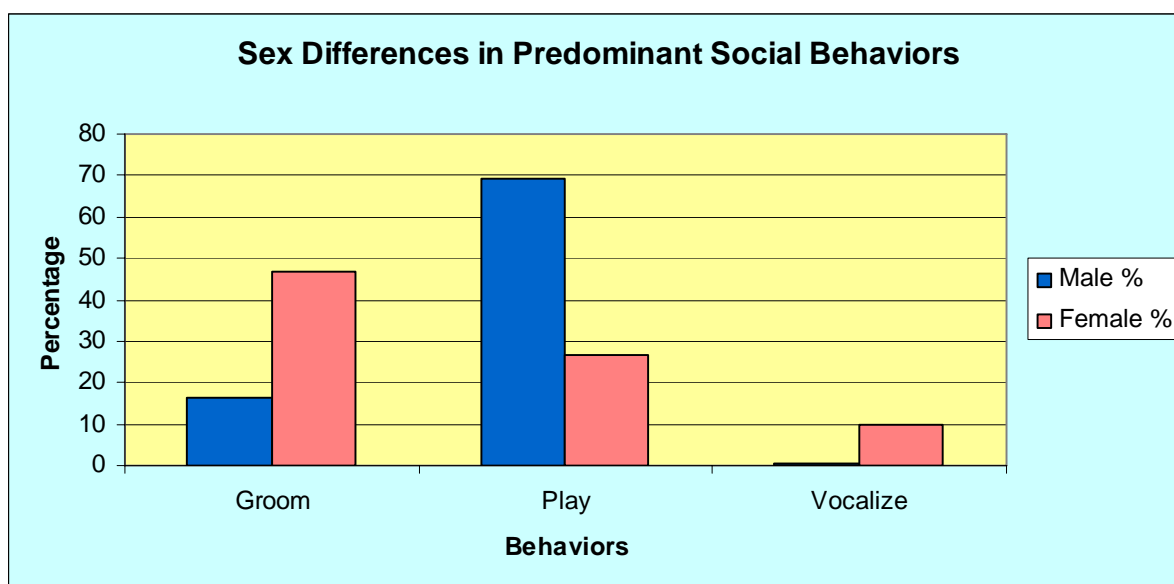


### *Instantaneous Social Behaviors*

In an analysis of predominant social behaviors recorded during instantaneous sampling, observable differences were noted in all three categories. Females engaged in grooming (males=16.2%; females=46.7%) and vocalizing (males=0.7%; females=9.8%) more often than males, while males engaged in play (males=69.3%; females=26.7%) more often than females (Figure 5). The Bonferroni-adjusted significance level is 0.016 for this test. No statistically significant differences were found for grooming ( $T=1.92$ ,  $df=6$ ,

$p=0.1039$ ), play ( $T=-2.28$ ,  $df=6$ ,  $p=0.0626$ ) or vocalizing ( $T=2.15$ ,  $df=6$ ,  $p=0.0746$ ). In an analysis of specific social behaviors, vocal behavior was broken down into affiliative (males=0.7%; females=11.11%) and distress (males=0.07%; females=3.1%) vocalization categories (Figure 6). T-tests were performed for all specific behavioral categories, and the Bonferroni-adjusted significance level for these tests was 0.0055. The frequencies of observations of most behaviors were low (Table 10), and none of these differences were significant (Table 11).

*Figure 5*



### *All-occurrence Social Behaviors*

All-occurrence records of behaviors may provide a better measure of behaviors that are rare, especially for those that are short in duration and therefore frequently missed by instantaneous sampling. Play and grooming were not included in all-occurrence analyses because these behaviors were intermittent states with frequent starts and stops, and instantaneous samples provide a better measure of these behaviors. The Bonferroni-

Figure 6

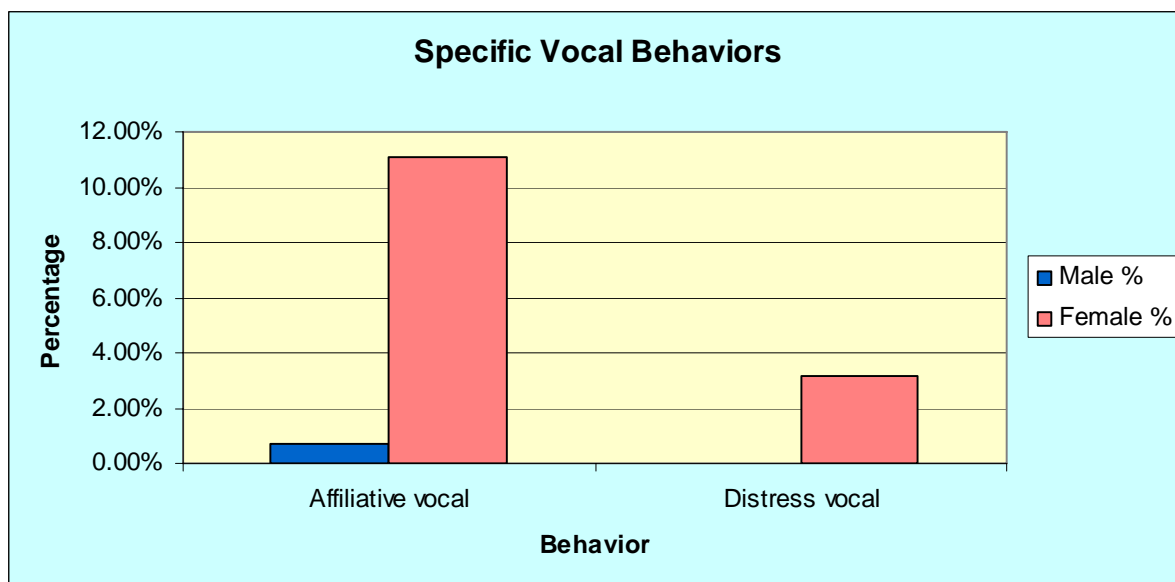


Table 10: Instantaneous Social Behaviors

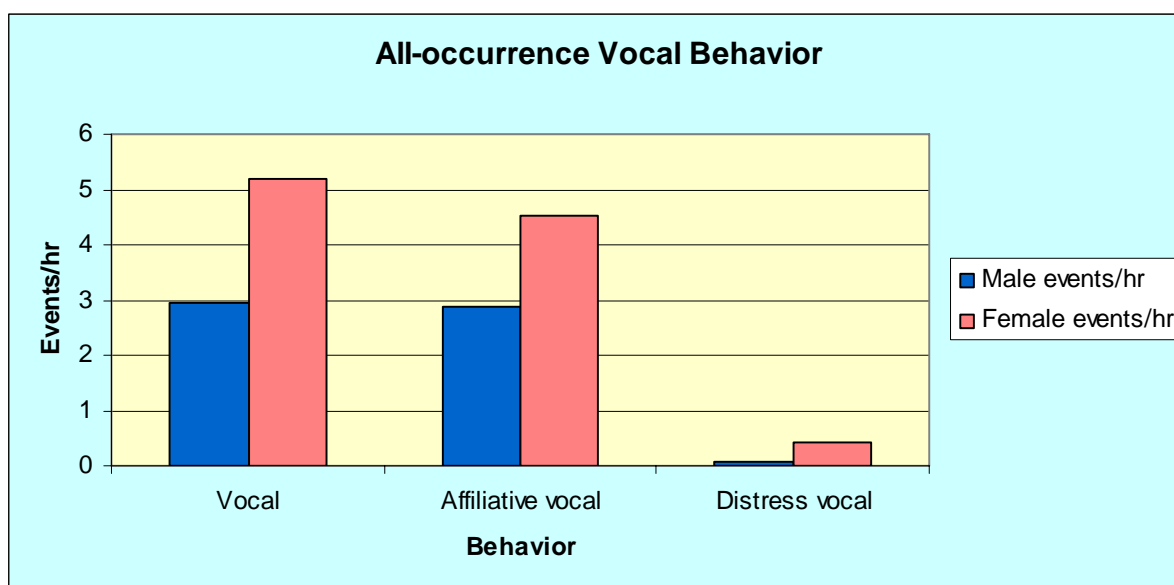
Behavior	Male %	Female %
Affiliative vocal	0.70	11.11
Distress vocal	0.00	3.13
Chase	2.78	0.00
Harass	0.93	0.00
Avoid	0.93	0
Cling	1.16	0
Bridge	4.51	2.30
Nurse	2.33	3.72
Huddle	1.16	3.87

Table 11: T-tests for Instantaneous Social Behaviors

Behavior	df	T	two-tailed p-value
Affiliative vocal	6	.214	0.0762
Distress vocal	6	1	0.3559
Chase	6	-1	0.3559
Harass	6	-1	0.3559
Avoid	6	-1	0.3559
Cling	6	-1.32	0.2339
Bridge	6	-0.6	0.5715
Nurse	6	0.45	0.6751
Huddle	6	1.12	0.3042

adjusted significance level was 0.0036, and no significant differences were found for any of the behavioral categories. The patterns of all-occurrence vocal behaviors followed the same pattern as the instantaneous data, with females vocalizing more than males (Figure 7). However, these differences were not significant ( $T=1.74$ ,  $df=6$ ,  $p=0.1327$ ).

*Figure 7*



*Table 12: All-occurrence Social Behaviors*

Behavior	Male events/hr	Female events/hr
Embrace	0.1415	0.06
Fight	0	0.14
Vocal	2.9445	5.20
Affiliative vocal	2.8724	4.54
Distress vocal	0.0723	0.41
Bridge	1.4237	0.81
Chase	0.0836	0.02
Cling	0.2122	0.20
Harass	0.0482	0.08
Huddle	0.1269	0.18
Nurse	0.1719	0.23
Touch	0	0.04
Weaning reject	0	0.04
Avoid	0.0241	0



*Table 13: T-tests for All-occurrence Social Behaviors*

<b>Behavior</b>	<b>df</b>	<b>T</b>	<b>two-tailed p-value</b>
Embrace	6	-0.56	0.5944
Fight	6	1.65	0.1498
Vocal	6	1.74	0.1327
Affiliative vocal	6	1.24	0.2603
Distress vocal	6	1.21	0.2716
Bridge	6	-0.79	0.4578
Chase	6	-0.89	0.4072
Cling	6	-0.07	0.9470
Harass	6	0.6	0.5692
Huddle	6	0.57	0.5902
Nurse	6	0.37	0.7237
Touch	6	1	0.3559
Weaning reject	6	1	0.3559
Avoid	6	-1	0.3559

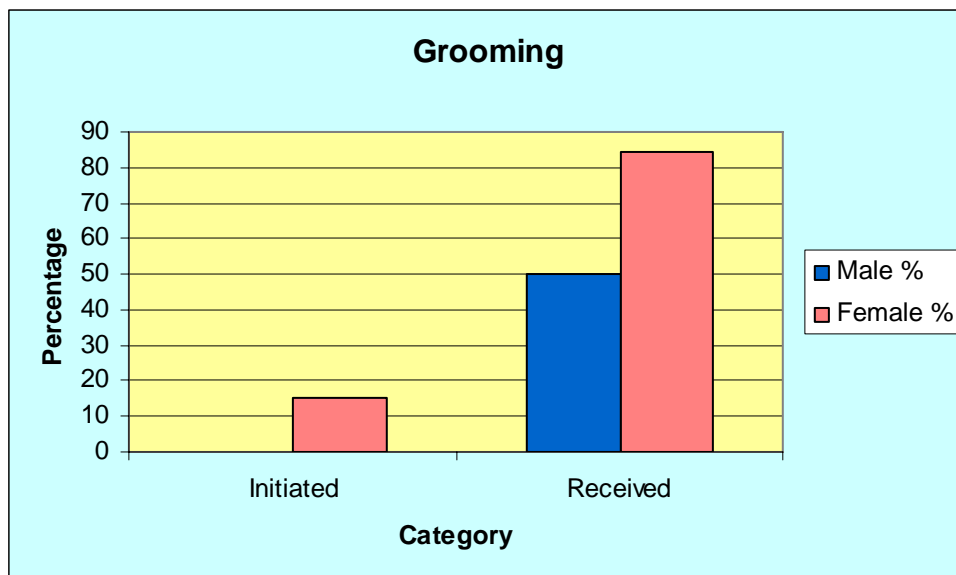
### ***Grooming***

Grooming behavior was further broken down into the percentage of total grooming received (males=50%; females=84.4%) versus percentage of total grooming initiated (males=0.0%; females=15.3%) (Figure 8). Only instantaneous measures in analyses of grooming. The Bonferroni-adjusted significance level was 0.025. No statistical difference was found for grooming received ( $T=1.17$ ,  $df=6$ , two-tailed  $p=0.2859$ ). However, males did not initiate any grooming, and therefore the amount of grooming initiated between the sexes approached significance ( $T=6$ ,  $df=6$ , two-tailed  $p=0.0343$ ).

### ***Care Behaviors***

Several behaviors were combined as measures of direct and indirect care. The behavioral categories ‘cling,’ ‘bridge,’ and ‘nurse,’ were combined into a category entitled ‘Direct Maternal Care’ (see qualitative results below for a discussion of direct nonmaternal

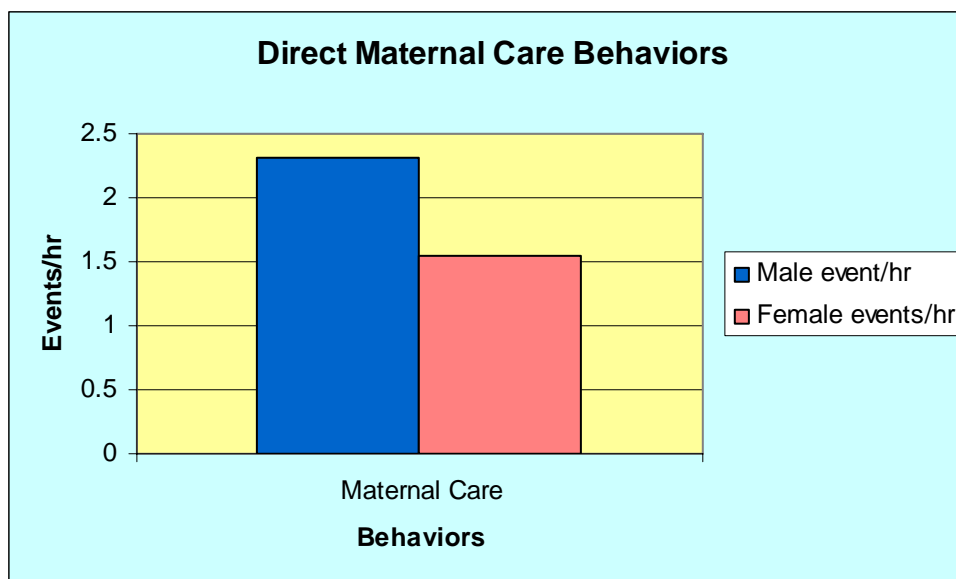
Figure 8



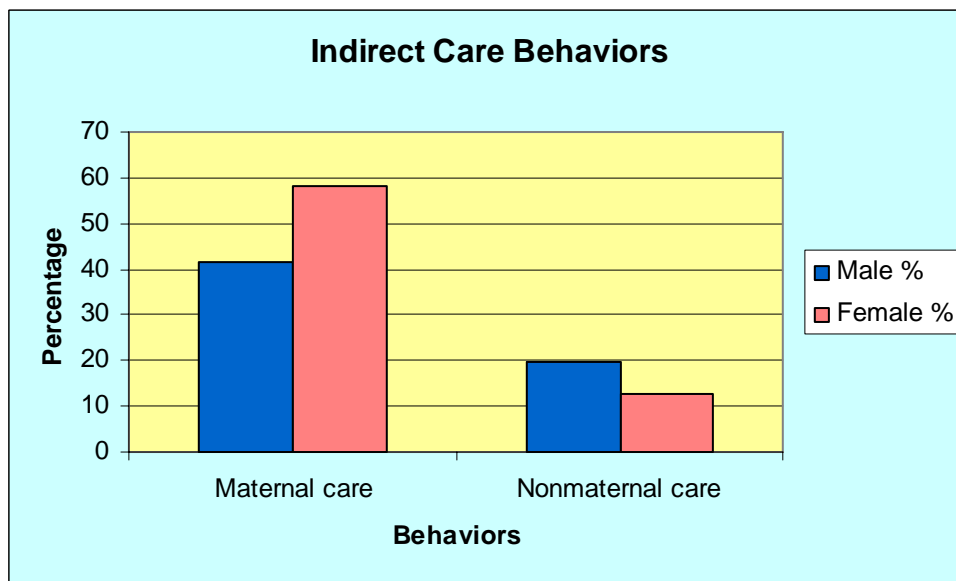
care). All-occurrence data was used in analyses of this category, as many of these behaviors are short in duration and missed by instantaneous sampling. The behavioral categories 'groom' and 'huddle' were combined into a category entitled 'Indirect Care,' and both maternal and nonmaternal contributions were examined. Instantaneous data was used to examine this category, as these are state behaviors that are most accurately measured with this type of sampling (Altmann, 1974). This test required no adjustment, so the significance level remained at 0.05. Only a slight observable difference in direct maternal care was observed (males=2.30 events/hr; females=1.55 events/hr) (Figure 9), and this difference was not significant ( $T=-.41$ ,  $df=6$ , two-tailed  $p=0.695$ ). Thus, it can be concluded that direct maternal care was equivalently distributed between males and females. For the t-test investigating indirect care, the Bonferroni-adjusted significance level was 0.025. Females received more indirect maternal care (males=41.4%; females=58.4%), while males received

more indirect nonmaternal care (males=19.8%; females=12.6%) (Figure 10), but neither of these differences were significant (maternal:  $T=1.38$ ,  $df=6$ , two-tailed  $p=0.2177$ ; nonmaternal:  $T=-.3$ ,  $df=6$ , two-tailed  $p=0.7736$ ).

*Figure 9*



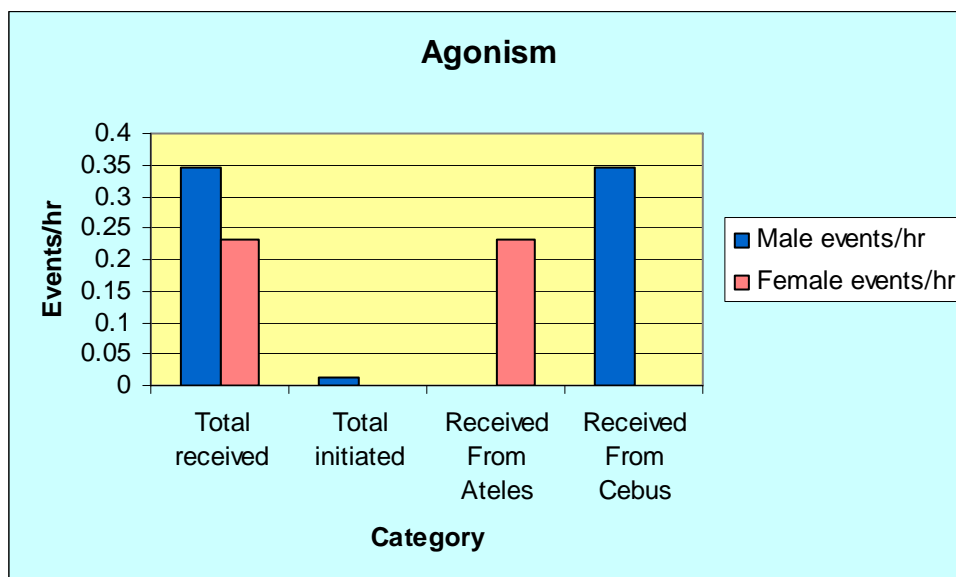
*Figure 10*



### *Agonism*

As agonistic events were short and infrequent, all-occurrence data was used to examine this behavior. While males received slightly more overall agonism than females, this difference was not significant ( $T=-.41$ ,  $df=6$ , two-tailed  $p=0.6934$ ). However, while the amounts of agonism received between the sexes was fairly equivalent, the patterns of agonism were different (Figure 11). Females received agonism from conspecifics, while males received agonism only from capuchin monkeys (*Cebus capucinus*). When this data was reanalyzed to separately examine agonism received from each species, these differences were not significant (*Ateles*:  $T=1.4$ ,  $df=6$ , two-tailed  $p=0.2119$ ; *Cebus*:  $T=-1.59$ ,  $p=6$ , two-tailed  $p=0.2095$ ). See ‘qualitative results’ for a further discussion of patterns and contexts of agonistic behavior.

*Figure 11*



*Table 14: Agonism*

Category	Male events/hr	Female events/hr
Total received	0.35	0.23
Total initiated	0.01	0
Received From <i>Ateles</i>	0	0.23
Received From <i>Cebus</i>	0.35	0

*Table 15: T-tests for Agonism*

Category	df	T	two-tailed p-value
Total received	6	-0.41	0.6934
Total initiated	6	-1	0.3559
Received From <i>Ateles</i>	6	1.4	0.2119
Received From <i>Cebus</i>	6	-1.59	0.2095

## Social Interactions

### *Interaction Partners*

Frequency of interactions with each age-sex class was calculated using instantaneous data. Mothers were considered a separate category from other adult females. Female juveniles concentrated their social interaction with female conspecifics, particularly mothers (males=8.0%; females=71.3%), other juvenile females (males=1.8%; females=25.2%), and subadult females (males=0.0%; females=9.87%) (Figure 12). Females did not interact with males of any age-sex class. Male juveniles distributed their social interactions across a wider range of age-sex classes, including both males and females. Males interacted more often with adult females (males=18.8%; females=1.3%), adult males (males=28.3%; females=0.0%), and juvenile males (males=24.6; females 0.0%). However, males did not interact with infants (males=0.0%; females=1.92%), subadult males (males=0.0%; females=0.0%) or subadult females. Only males interacted with capuchin monkeys

(males=18.8%; females=0.0%). The Bonferroni-adjusted significance level was 0.0056 for these tests. The difference in interaction with mothers approached significance, as juvenile females spent more interacting with mothers than did juvenile males ( $T=5.3$ ,  $df=6$ , two-tailed  $p=0.0059$ ). Additionally juvenile males spent more time interacting with other juvenile males than did juvenile females but this difference was not significant ( $T=-3.11$ ,  $df=6$ , two-tailed  $p=0.0209$ ).

Figure 12

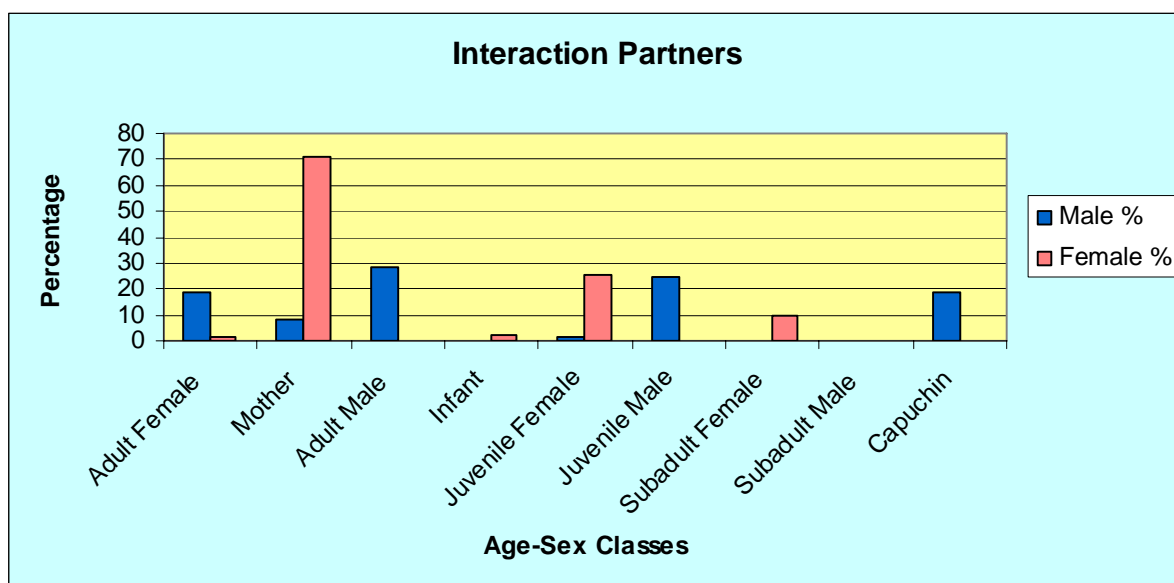


Table 16: T-tests for Interaction Partners

Age-Sex Class	df	T	two-tailed p-value
Adult Female	6	-1.33	0.2325
Mother	6	5.3	0.0059
Adult Male	6	-1.76	0.1282
Infant	6	1	0.3559
Juvenile Female	6	1.59	0.164
Juvenile Male	6	-3.11	0.0209
Subadult Female	6	1	0.3559
Subadult Male	N/A	N/A	N/A
Capuchin	6	-1.42	0.2499

### ***Play Partners***

Instantaneous data was used to investigate the frequency of play interactions with different age-sex classes. Mothers were considered a separate category from other adult females. The percentage of play with each age-sex class relative to total play was calculated and compared. The patterns observed for play are similar to those total social interactions. Juvenile females only played with other juvenile females (males=8.3%; females=50%) and subadult females (males=0.0%; females=25%) (Figure 13). Males played with a wider variety of male and female conspecifics, including their mothers (males=6.8%; females=0.0%) and adult females (males=1.7%; females=0.0%). However, male play was most often with other juvenile males (males=40.5%; females=0.0%), adult males (males=29.2%; females=0.0%), and capuchins (males=19.6%; females=0.0%). Neither sex was observed to play with infants or subadult males. The Bonferroni-adjusted level of significance was 0.0056, and none of these differences were significant. However, the difference in time spent playing with juvenile males approached significance, as male juveniles spent more time playing with other juvenile males than did juvenile females ( $T=3.48$ ,  $df=6$ ,  $p=0.0132$ ).

### ***Interactions Initiated and Received***

Instantaneous data was analyzed to see if there were sex differences in the frequency with which juveniles initiated and received social interactions. However, for some interactions, particularly play, it was difficult to discern which individual initiated or received the interaction. These interactions were coded as unknown. Females both initiated and received more social interactions while, for many of the males' interactions, the initiator and

Figure 13

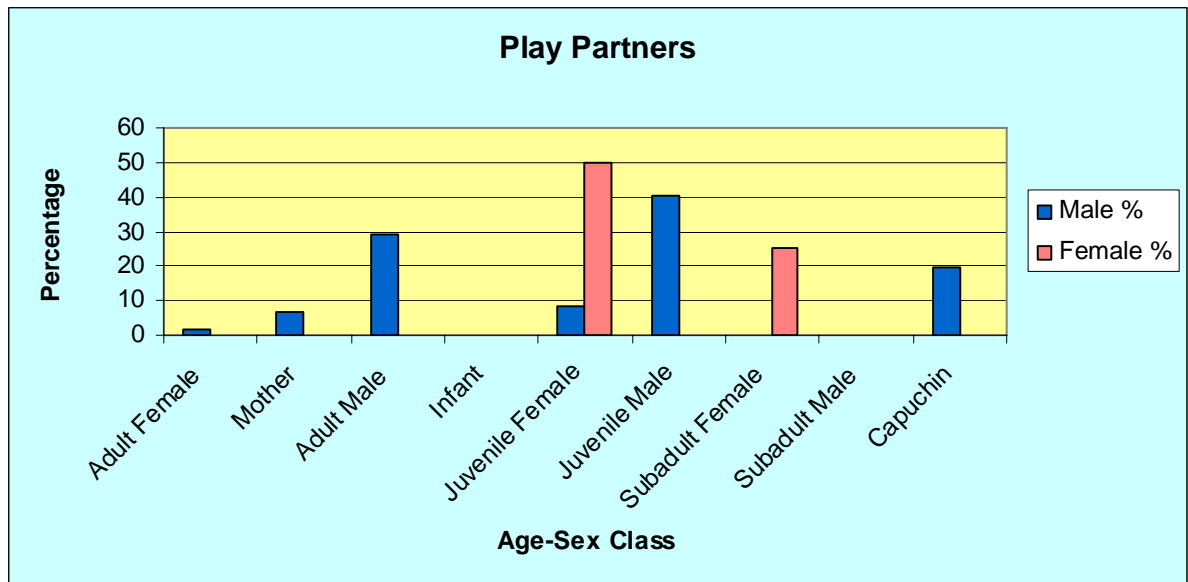


Table 17: T-tests for Play Partners

Age-sex Class	df	T	two-tailed p-value
Adult Female	6	-1	0.3559
Mother	6	-1	0.3559
Adult Male	6	-1.7	0.1405
Infant	N/A	N/A	N/A
Juvenile Female	6	1.39	0.2148
Juvenile Male	6	-3.48	0.0132
Subadult Female	6	1	0.3559
Subadult Male	N/A	N/A	N/A
Capuchin	6	-1	0.2559

recipient were unknown. None of the differences were significant, although the p-values for the 'received' category and the 'unknown' category were low (received:  $T=1.46$ ,  $df=6$ ,  $p=0.0973$ ; unknown:  $T= 1.52$ ,  $df=6$ ,  $p=0.0778$ ). However, because of the high frequency of 'unknown' values, the results are not conclusive regarding the presence of sex differences in the initiation and reception of social interactions.



## Qualitative Results

Qualitative notes were taken when observing unusual or important behaviors using *ad libitum* sampling. The following observations were considered valuable in a comprehensive understanding of the social lives of juvenile spider monkeys.

### Kidnapping

On 6 June 2006, a juvenile female, Lena, was observed carrying a newborn infant, which was easily identified due to a gray natal coat, which lasts for only a week after birth. While the source of the newborn infant is unclear, it is unlikely that it was Lena's mother's infant. Observations of both nursing and weaning conflict indicate that Lena was going through the process of weaning, so it is unlikely that her mother would have been able to give birth at that point. Although the procurement of the infant was not observed, it is likely that the infant was kidnapped. While kidnapping has been reported for other species of primates, particularly macaques (*Macaca radiata*: Silk, 1980, *Macaca mulatta*: Maestriperieri, 1993), kidnapping has never been reported in spider monkeys. Lena was observed from 0602h to 0606h without the infant, and then later recontacted at 1040 h with the newborn infant and her mother, Lynn. She carried the infant in an odd position on her side, which deviated from the normal methods of carrying infants, either ventrally on the belly, or dorsally on the back. The infant's position was precarious but it was able to cling, and both Lena and Lynn traveled very slowly. The sex of the infant could not be determined. While Lena carried the infant oddly and the infant continued to cry the entire time, Lena was very gentle with the infant and tried to soothe and groom the infant during rest. The gentle manner in which she handled the infant was very different from the rough manner in which rhesus macaques usually handle kidnapped infants (personal observation). The party was lost at 1150h, but

recontacted at 1349h, at which point Lena was still carrying the infant. Lynn was observed to bridge gaps for Lena and the clinging infant and generally seemed tolerant of the infant for most of the time. However, at 1407h, Lynn lunged at and harassed Lena, and it was unclear if this was directed at Lena or the infant. A few minutes later, at 1412h, they made contact with another party, which immediately attacked them. The party consisted of two adult males and two adult females. An adult female attacked Lena, while an adult male attacked Lynn. After that, the events of the fight could not be observed, the females immediately dispersed, and the whereabouts of the infant could not be determined. Lena was never seen carrying an infant again, and the newborn infant was not observed for the rest of the week. After the natal coat changed, it would be impossible to recognize the infant, so the fate of the infant cannot be determined.

### **Agonism**

While instances of agonism were rare, the patterns of agonism observed in this study were different for males and females. While females received agonism from spider monkeys, males received agonism only from capuchin monkeys. Five agonistic events were observed for two females, and all of these events were initiated by adult females. Only one agonistic event was observed for Anya, a juvenile-3. In this case, her mother, Anita, lunged and bit her during a feeding bout when Anya approached. Anya responded with screams and a retreat. This agonistic event may have been a case of feeding competition. Four agonistic events were observed for Lena, a juvenile-2. The first agonistic event was apparently mother-offspring weaning conflict. Lena first approached her mother, Lynn, and groomed her for approximately three minutes. Lena then attempted to nurse. Lynn rejected this attempt to nurse and fled to the other side of the tree crown. When Lena attempted to follow

her, Lynn then fled to another tree. The second agonistic event was observed while Lena was engaged in a play bout with Anya. Anya's mother, Anita, attacked while the two juveniles were engaged in play, and Lena responded with distressed shrieks and fleeing. The two juveniles were part of a large party that fissioned immediately after this event. While Anya exhibited no sign of distress during play, it is possible that Anita intervened in play that was too rough. The last two agonistic events occurred during the kidnapping of the newborn infant, and are described above. Both of the juvenile-1 females, Iris and Buttercup, were never observed to receive any agonism.

Five agonistic events were observed for Freddie, a juvenile-2. All of these events occurred on the same day, while both spider monkeys and capuchin monkeys were feeding in a large *Ficus* tree in December. On three separate occasions, Freddie was chased by capuchin monkeys. In two of these chases, Freddie was chased out of a tree and fell into a nearby tree. Two of these chases were initiated by adult capuchins, while one chase was initiated by a juvenile capuchin. In another agonistic event, an adult capuchin swatted at Freddie while he was feeding within close proximity of the capuchin. In one agonistic event, Freddie quickly retreated when a juvenile capuchin approached. Two agonistic events were observed for Tristan, a juvenile-1. These events were observed on separate days, but both occurred while spider monkeys and capuchins were feeding at the same *Ficus* tree in July. In the first event, an adult capuchin approached Tristan while he was resting and chased him. In the second event, an adult male capuchin attacked Tristan. While the events precipitating this attack was not observed, Tristan immediately screamed, and his mother Trina intervened by threatening and chasing the capuchin. All of these agonistic events can be considered a result of interspecies feeding competition at a popular food resource. However, it should be

considered that Tristan played frequently with juvenile capuchins and occasionally tried to approach adults, so it is possible that the attack Tristan received was a result of approaching capuchins in an attempt to solicit play.

### **Nonmaternal Care**

Only two events of direct nonmaternal care were observed, and both of these were instances in which animals bridged for a juvenile. In one instance, Lena, a Juvenile-2, bridged for Buttercup, a Juvenile-1. In another instance, an adult female, Lynn, bridged for her own daughter, Lena, and then waited and bridged for another juvenile, Tristan. However, instances of indirect care behavior, such as huddling and grooming, were observed. However, these behaviors were not very common and were only between certain individuals. Iris, a female juvenile-1, was observed to concurrently huddle with both her mother, Ingrid, and a subadult female, for approximately 12 minutes. The subadult female is an individual that traveled frequently with Iris and her mother and one that she frequently played with. The subadult females may have been an older sibling who has not yet dispersed. Freddie, a male juvenile-2, was observed to huddle with an adult male for six minutes. Tristan, a male juvenile-1, was observed to huddle with an adult female that frequently traveled with him and his mother for four minutes. Tristan was also the only recipient of non-maternal grooming and received grooming from the same adult female for a total of 28 minutes. Tristan was also observed to play with this adult female. From these events it can be inferred that alloparental care is generally rare, and generally consists of affiliative behaviors with specific individuals that travel frequently with the juvenile's mother.

## Discussion

### General Patterns

The results of this study indicate that juvenile spider monkeys do exhibit some sex differences in social behavior. Males tended to engage in social behavior more than females. Also, males tended to engage in play more often than females, while females engaged in vocal behavior more often. Females spend more time engaged in grooming, and only females initiated grooming. Furthermore, patterns of agonism were different, as females received aggression from adult females, while males received aggression only from capuchin monkeys. Finally, sex differences are apparent in the general patterns of social interaction and play. Females tended to concentrate social interaction with their mother, with most other interactions occurring with other females, particularly juvenile females. However, males interacted with a wider variety of conspecifics, especially juvenile and adult males. Furthermore, females played predominantly with other immature females, while males played with a wider variety of age/sex classes, including adult males, juvenile males, and even another primate species.

These data support some of the patterns of sex differences reported for adult spider monkeys. For example, Fedigan and Baxter (1984) consider spider monkey societies to be “sex-segregated.” The patterns of social interaction observed in this study suggest that the tendency towards sex-segregation begins at a young age. Juvenile males and females do appear to demonstrate a preference for their own sex. Furthermore, while juvenile females appear to have a restricted social network that is centered around their mothers and other immature females, juvenile males appear to have a wider social network that is comprised of both immatures and adults of both sexes.

The patterns of vocal behavior found in this study are consistent with the patterns reported by Fedigan and Baxter (1984) for adult spider monkeys. They report that adult females vocalized significantly more than males, and that differences were found in both affiliative (whinny) and distress (whine, squeak) vocalizations. The strong trend observed in this study indicates that these differences in vocal behaviors emerge at a young age. However, why this pattern emerges is unclear. Fedigan and Baxter (1984) suggest that females engaged in vocal behavior more often because they are more solitary and dispersed. Engaging in vocal behavior allows females to monitor the presence of other individuals, remain in greater social contact, and make subgrouping decisions. However, at the juvenile stage, when both males and females travel with the mother and are dependent on her for travel and foraging decisions, there is no immediate reason why vocal behavior might be more beneficial for females. This may be one pattern that emerges before it has any tangible benefits for the individuals.

The patterns of maternal care behavior recorded in this study contradict those suggested by previous studies. Symington (1987) observed that females invested more in male offspring and were more likely to intervene in support of sons. While interventions were rare in the current study, with only one event observed for each sex, patterns of direct and indirect maternal care indicate that mothers are providing fairly equivalent levels of care behaviors to offspring of each sex. These results suggest that sex differences in juvenile behavior are not a result of differential maternal treatment. However, the levels of maternal care invested in each offspring may vary at sites in relation to the severity of sex ratio skew and the factors that cause it. Previous studies (Chapman et. al, 1989; Chapman & Nunes, 1997; Symington, 1987) have reported skewed juvenile sex ratios that are a result of

differential mortality of male and female offspring. However, at El Zota, the juvenile sex ratio is fairly equivalent, and there was no visual indication that male juveniles faced greater aggression or nutritional stress. At sites where males face greater survival challenges, mothers may be investing more in male offspring to compensate for those challenges. The lack of differential care observed at El Zota suggests that, in a highly productive habitat, where post-weaning resource competition is assumed to be low, greater maternal investment may not be necessary. This supports the hypothesis that greater male investment is a strategy to deal with specific social or environmental pressures that face male offspring, rather than a strategy to invest more in the resident sex simply because they are socially more valuable to the mother.

### **Patterns of Agonism**

One of the most prevalent debates in primatology is the importance of affiliation and cooperation versus agonism in structuring primate societies. While Sussman and colleagues (Sussman & Garber, 2004; Sussman et. al, 2005) argue that affiliative behaviors are more prevalent and thus are a stronger force in shaping primate social dynamics, others (Koenig et. al, 2006) argue that while affiliative behaviors account for a greater proportion of activity budgets, the severity of agonistic behavior has a greater impact on social dynamics. The percentage of time that both males and females were engaged in affiliative versus agonistic behavior support Sussman and colleagues' (Sussman & Garber, 2004; Sussman et. al, 2005) argument. Both sexes engaged primarily in affiliative behavior, and agonistic behavior was rare. Nonetheless, although agonism is rare, it can have important social consequences and should be considered an important force in affecting social dynamics. In this study, while agonism was rare and sex differences were not significant, the patterns exhibited by male and

female juveniles are striking. Only females received agonism from other conspecifics, and these agonistic behaviors were directed by mothers and other adult females.

Males received agonism only from capuchin monkeys. These patterns contradict findings reported by Chapman and colleagues (1989) and Fedigan and Baxter (1984), who report that immature males received twice the amount of aggression immature females receive from other spider monkeys. However, these patterns may be more consistent with patterns observed by McDaniel (1994) at Hacienda Los Inocentes. While McDaniel (1994) found that male and female juveniles were involved in equivalent amounts of aggressive encounters, she reports that females were recipients of aggression more often while males were initiators. While the patterns observed in this study and McDaniel's do not support Chapman and colleagues' (1989a) assertions that males face increased aggression, they nonetheless may be consistent with the post-weaning resource competition hypothesis (Silk, 1983) as Chapman and colleagues (1989) articulate it. Chapman and colleagues (1989) posit that the severity of sex ratio skew and patterns of aggression towards immature males are related to habitat productivity. El Zota is much wetter, and therefore presumably a more productive habitat, than Santa Rosa and Tikal, the two sites where greater aggression towards immature males was observed. Thus, competitive pressures for food resources may be less severe at this site in comparison to drier forests at Santa Rosa and Tikal.

The adult sex ratio at El Zota is consistent with the skewed proportions reported at other sites, despite the equivalent sex ratios observed in juveniles. This finding challenges Chapman and colleagues' (Chapman et al., 1989; Nunes & Chapman, 1997) assertion that increased mortality of immature males is responsible for the sex ratios observed in adult populations. However, recent evidence from Punta Laguna, Mexico and Barro Colorado,



Panama suggest that subadult males face severe and sometimes lethal aggression from adult males of their own community (Campbell, 2006; Valero et. al, 2006). While no direct aggression was observed against subadult males at El Zota, anecdotal observations suggest that loud distress vocalizations are sometimes emitted by subadult males (personal observation; S. Lindshield, personal communication). In each of these situations (n=4), the subadult males appeared distressed and were alone when we encountered them after following their vocalizations. The events that prompted this distress, however, were not observed. While this is an area that needs further investigation, the disparity of juvenile and adult sex ratios suggest that such aggression towards subadult males may be a plausible mechanism of sex ratio adjustment at El Zota. While direct lethal aggression may be rare and unlikely, it is possible that aggressive behavior could lead to increased stress that renders subadult males more susceptible to mortality. At this point, this hypothesis is purely speculative but warrants further investigation.

The patterns of agonism received by juvenile females at El Zota indicates that despite their greater affiliation with females, particularly mothers, juvenile females may face less tolerance from conspecifics than male juveniles. This is consistent with evidence reported by Symington (1987) for spider monkeys and Pusey (1990) for chimpanzees. At least one agonistic event observed was clearly a case of mother-offspring weaning conflict (Trivers, 1974). This is a common form of agonism experienced by weaning primates (Maestriperi, 2002), and further investigation is needed to determine if the level of weaning conflict differs between male and female offspring. However, only older juvenile females received agonism from conspecifics, suggesting that this is a pattern related to the increased marginalization and agonism that the dispersing sex may face. In howling monkeys (Pope, 2000), maturing

females are evicted from the group due to increased aggression from female conspecifics. The pressures that force female spider monkeys to disperse have not been adequately studied, and this is an area that warrants future research. However, as only a few agonistic events were observed, and several of these events may have been related to the unusual instance of infant kidnapping, no clear conclusions can be drawn.

### **Grooming**

Grooming is considered one of the most predominant and important forms of affiliative social behavior within the Primate Order (Henzi & Barrett, 1999). Grooming may serve a variety of purposes. On a proximate level, grooming serves the practical purpose of the removal of ectoparasites (Tanaka & Takefushi, 1993) and the release of endorphins (Keverne et. al, 1989). However, a variety of other benefits have been proposed for engaging in grooming behavior, including access to coalitionary support, as a means of testing or solidifying a relationship (Dunbar, 1998), or as a commodity traded for tolerance from dominant individuals (Henzi & Barrett, 1999). Henzi and Barrett (1999) suggest that evidence from baboons supports the hypothesis that grooming is traded as a commodity for either tolerance or reciprocal grooming. However, they do acknowledge that the immediate benefits of grooming may be sufficient enough to promote reciprocal grooming, and that it may be used as a currency only in differential power relationships. Additionally, Kinzey and Wright (1982) suggest grooming to be an important form of parental investment.

Most of the studies investigating grooming behavior have focused on Old World monkeys, while New World monkeys are reported to engage less frequently in grooming behavior (DiFiore & Campbell, 2007; Schaffner & Aureli, 2005; Strier, 1994.). The importance of grooming within spider monkey society has been debated. Ahumada (1992)

argues that although rates of grooming are relatively low, it is still one of the most important indicators of social relationships within *Ateles* society. These findings are supported by Pastor-Nieto (2001), who found grooming significantly related to food-sharing relationships among captive spider monkeys (*A. geoffroyi*). However, based on another study of captive spider monkeys (*A. geoffroyi*), Schaffner and Aureli (2005) argue that grooming does not play an important role in regulating social relationships. They argue that within a fission-fusion social structure, greeting behaviors such as whinnies, embraces, and pectoral-sniffing are of greater importance due to the frequency in which community members separate and reunite. These assertions are supported by their findings that embraces, but not grooming, were significantly associated with fusion events.

The findings of the current study suggest that grooming is a predominant, and thus important, social behavior among juvenile spider monkeys, while embraces were rare. Grooming may be a much more important behavior for immatures, who are in constant association with their mothers. Furthermore, most grooming behavior occurred with mothers and was initiated by mothers. This suggests that grooming is an important form of social bonding and investment between mothers and offspring. Furthermore, the finding that only females initiated grooming indicates that this behavior is a more important social behavior for females. While Fedigan and Baxter (1984) found no sex differences in grooming among adult spider monkeys, Ahumada (1992) found that adult females groomed the most, while juveniles received the most grooming. These findings are consistent with Ahumada's (1992) results. However, why juveniles females initiated grooming, while males did not, remains unclear. One possibility is that among adults females, grooming is more important for social bonding than it is for males. Another possibility is that these patterns can be considered

practice for adult life, as grooming is an important way for females to invest and care for their own offspring. One interesting question raised by this possibility is whether the neuroendocrine mechanisms underlying grooming behavior differ between males and females. While this is beyond the scope of the current study, this question may be particularly suited to further study in a captive setting.

### **Play**

The patterns of grooming and play observed in this study are reminiscent of the patterns of social play reported for human children. Amongst humans, boys are reported to engage in more active, rough-and-tumble play, and play in larger groups, while females are reported to engage in quieter play in smaller groups (Maccoby & Jacklin, 1974; Roney & Mastriperi, 2003). Furthermore, girls are reported to engage in activities that promote social bonding (Maccoby & Jacklin, 1974), which presents an interesting parallel to the grooming behavior observed in the juvenile female spider monkeys. If patterns of both play and grooming are considered together, some of the sex differences observed in these behaviors amongst spider monkeys provide a parallel situation to the sex differences in patterns of social bonding and affiliation observed in human children. These patterns may support Dunbar's (1993) assertion that human verbal behavior serves the same social bonding purposes that grooming does in other primates. However, whether play patterns are a result of human socialization practices or biological sex differences is a widely debated subject (Maccoby & Jacklin, 1974; Roney & Mastriperi, 2003). Roney and Maestriperi (2003) contend that male participation in greater rough-and-tumble play may be a preparation for male mate competition and reflects a general mammalian pattern. They suggest that neurochemical mechanisms may make certain activities, such as rough-and-tumble play,

more rewarding for one sex. However, while play is often considered practice for competition and fighting, theoretical discussions on the immediate and delayed benefits of play consider a variety of other explanations for the evolution of this behavior (Bekoff & Allen, 1998; Biben, 1998; Fagen, 2002; Palagi et. al, 2004; Palagi et. al, 2006; Pellis & Pellis, 1998; Siviy, 1998; Thompson, 1998). Based on studies of play-fighting among juvenile squirrel monkeys (*Saimiri sciureus*), Biben (1998) supports the idea that play-fighting provides opportunity to practice skills related to physical competition and establishing dominance. However, Pellis and Pellis (1998) argue that play fighting has features that make it an inefficient means of practicing fighting skills. Bekoff and Allen (1998) suggest that play is related to reading social signals and inferring intentionality. They note that ritualized play signals communicate that play is different from aggression. Rather than serving as practice for fighting, they argue that play provides opportunity to practice cooperation and to learn to read the intentions and behaviors of others (Bekoff & Allen, 1998; Biben, 1998). Furthermore, play may function to serve immediate social needs, such as testing and solidifying present relationships (Pellis & Pellis, 1998). Additionally, play may provide feedback on an individual's abilities in relation to other conspecifics, and repeated play bouts over time may provide information on both the individual and partner's overall abilities (Thompson, 1998). Play may also play a role in providing experience in stress and subordination. Dopamine, norepinephrine, and serotonin are three neurotransmitters that regulate aspects of play, and Siviy (1998) suggests that play during development may impact the individual's neuroendocrine function. This may affect the animal's ability to deal with stressors later in life. Studies of humans have supported the role that play is an important part of social and emotional development, as studies among human

men have found that the absence of normal play behavior during childhood is associated with violent and antisocial behavior as adults (Brown, 1998). Biben (1998) asserts that role reversals during play may provide opportunities to practice the behaviors associated with being subordinate. She states that these experiences “may later save his hide for another day,” (Biben 1998:174). She suggests this practice in subordination may help to deal with the stressors associated with losing contests and occupying a subordinate role as an adult.

Additionally, Pellis and Iwankiuk (2000) suggest that play may be an important feature of adult social life among fluid social systems. They suggested that play may function as a means of social assessment that is particularly important in situations where conspecifics are not in daily association. Furthermore, Palagi and colleagues (2004) argue that while grooming plays less of a role in reducing tension amongst juveniles, play may be an extremely valuable mechanism for juveniles to relieve stress and conflict. Additionally, Palagi et. al (2004) suggest juvenile play provides the means to assess both the abilities of the individual (self-assessment) and play partners (social assessment). Finally, Palagi and colleagues (2004) also suggest that adult-juvenile play functions to strengthen social bonds between immature’s adult relatives and the adult playing with the immature. They suggest that adult-immature play functions as an honest signal that communicates information about relationships within the wider social network.

The patterns of play observed in this study indicate that while play is a predominant social behavior of both sexes, it may be more important for males. Males engage in play behavior more often, engage in play with a greater range of social partners, and include both adult and juvenile males as play partners. Furthermore, the patterns of play partner choice suggest that females prefer playing with immature female partners, while males play

significantly more with other juvenile males. These findings support Eisenberg's (1976) findings that juvenile males engage in play more often. However, they are contradictory to the patterns that Fedigan and Baxter (1984) reported for adults. They found that adult females played significantly more than adult males. Whether this pattern is consistent across different sites has yet to be examined, but if it holds, it may present an interesting case in which the sex-typical patterns of behavior switch during development. Furthermore, the patterns of play partner preferences conflicts previous findings by Van Roosmalen and Klein (1988) and McDaniel (1994) that juveniles do not exhibit a preference for play partners of the same sex.

The finding that juvenile male spider monkeys at El Zota engage in play more often is consistent with play patterns reported for a variety of primate species (Fagen, 2002; Van Noordwijk et. al, 2002; Roney & Maestriperi, 2003). Additionally, it is also consistent with the social structure of spider monkeys, as males would be expected to engage in greater amounts of behavior related to social bonding. However, this may not be necessarily related to the need to develop competitive skills. As Bekoff and Allen (1998), Pellis and Pellis (1998), Palagi and colleagues (1994) and others discuss, play may be an opportunity to develop skills for self and social assessment as well as cooperative skills. Such social skills may provide the foundations for developing and evaluating relationships with other community members. As males remain in their natal community, the juvenile period provides time for males to develop and maintain relationships that will continue for the duration of their lives. This may be one reason why juvenile males engage in play with a wider variety of conspecifics. Additionally, as male-male bonding is particularly important for spider monkeys, play provides opportunity to test and solidify relationships with both

peers and adult males that will become increasingly important as males reach maturity. However, the fact that males engage in play with capuchin monkeys suggests that play provides rewards beyond those related to the establishment of specific social relationships. Play may provide immediate neuroendocrine rewards (Roney & Maestripieri, 2003), that make play enjoyable to juveniles, as well as provide the delayed rewards in neuroendocrine function suggested by Siviy (1998).

While juvenile males' choice of play partners can be easily related to the social needs and pressures they will face in adult life, juvenile females' choices are more difficult to explain. Female spider monkeys normally disperse to other communities, so there is no apparent reason why they should prefer playing with other immature females over other conspecifics. However, Biben's (1998) observations of playfighting amongst squirrel monkeys provide one plausible explanation. Biben (1998) asserts that while role reversals occur in male-male and female-female play, when males and females play role reversals are rare. Rather, males consistently dominate females in play, which Biben (1998) cites as the reason that females play less than males and prefer other females as play partners. However, she also relates these patterns to two different play strategies. The first, which she terms 'directional wrestling' involves play on a flat surface where one partner can be pinned. The second, 'nondirectional wrestling' refers to play while hanging from a branch. While she states that male squirrel monkeys favor directional wrestling, while females prefer nondirectional wrestling, the pattern of play observed amongst the spider monkeys of both sexes fit the definition of nondirectional wrestling. Nonetheless, Biben's (1998) dominance hypothesis provides the best explanation of the play partners patterns observed in spider monkeys.



## **Kidnapping**

The observation of possible infant kidnapping is a rare event that may provide an opportunity to compare the relatively rare demonstration of nonmother females' interest in infants within the Atelines to the common occurrences of kidnapping and alloparenting among Old World monkeys. Extreme interest in infants is thought to be a general trait of primate females (Hrdy, 1976; Paul, 1999). However the extent to which females are allowed access to other female's infants greatly varies amongst species. Paul (1999) notes that socioecological models that explain the frequency of infant-handling focus on the degree of maternal tolerance predicted by the strength of female dominance hierarchies. However, he argues that these models are generated from evidence from a few colobines and cercopithecines and do not explain the variety of infant-handling behaviors across the primate order. In macaques, infant kidnapping is a relatively common event (Maestripieri, 1993; Silk, 1980). Silk (1980) explains that kidnapping amongst bonnet macaques (*Macaca radiata*) can best be understood as a form of female competition. She suggests that interest in infants and infant-carrying behavior may be a way for young primate females to gain experience handling infants (Silk, 1980). However, this behavior may be considered a form of mutualism if the infant and its mother benefit from this care, or a form of parasitism if the infant and its mother incur costs related to this care. Kidnapping amongst macaques appears to be detrimental to infants and their mothers (Maestripieri, 1993; Silk, 1980) and thus could be considered a form of parasitism. However, as parous females kidnap infants just as frequently as nulliparous females, Silk (1980) argues that alloparental experience is not an adequate explanation for this behavior. Rather, she argues that infant kidnapping is a form of

female competition, in which females attempt to lower the reproductive success of their conspecifics.

Infant kidnapping has also been reported in red howlers monkeys (Agoramoorthy, 1998). In this situation, an adult female with infant twins acquired an infant from another group during an intergroup encounter. While she primarily carried the infant, a juvenile female of her group was also observed to carry the infant as well. For the following two days, the infant's mother was observed away from her group, and made several attempts to approach the group containing her infant until she was able to successfully retrieve it. Agoramoorthy (1998) attributes the kidnapping to within-group competition. However, it should be considered that the kidnapping female was a lactating female with two infants of her own. Lactating females have higher levels of prolactin, a hormone associated with parental behavior (Ziegler, 2000). It is likely that this incident may have been a result of heightened interest in infants as a result of hormonal influences, rather than a case of competition.

The observation of presumed infant kidnapping in this study seems to follow a similar pattern as the howler case. Unlike kidnapers observed in macaques, the juvenile female observed carrying the newborn infant attempted to carry the infant in a secure manner and tried to groom and comfort the infant. This is in marked contrast to the infant-handling practices exhibited by macaque kidnapers, who often handle infants in a rough and careless manner (Maestriperi, 1993; personal observations). Furthermore, the attack that Lena received when encountering another party may have been an attempt by the infant's mother to retrieve the infant. While this cannot be determined for certain, the severity of the attack and the lack of provocation prior to the attack is consistent with this assumption. If so, this

contrasts the patterns observed in macaques, in which females do not attempt to rescue their infants (Maestripieri, 1993). Both the frequency of occurrence and the patterns observed in these cases suggest that the ultimate mechanism underlying their occurrence may be different. While the kidnapped infant may have undergone severe stress and possibly death as a result of this incident, the manner in which Lena treated the infant, as well the fact that she is an immature individual who will eventually migrate out of the community, is inconsistent with the female competition hypothesis. Rather, it is more likely that this incident was an isolated event that may have been caused by the particular female's interest and attraction in the infant, which may not be part of a broader social pattern.

### **Comparisons with Chimpanzees**

Given the remarkable behavioral convergence between spider monkeys and chimpanzees, it would be expected that patterns of sex differences and social behaviors would be the same amongst the two taxa. Pusey (1990) reports that juvenile female chimpanzees spend more time with their mothers than do their male counterparts. This is similar to the pattern observed in the present study, as juvenile females spent significantly more time interacting with their mothers. However, patterns of grooming and vocal behavior appear to differ between juvenile chimpanzees and spider monkeys. Pusey (1990) found no sex differences in grooming for juvenile and adolescent chimpanzees. Furthermore, males initiated grooming towards both mothers and nonmothers. However, like the spider monkeys, both males and females received most of their grooming from the mother. Additionally, females groomed mothers and siblings more than other conspecifics, suggesting that juvenile female chimpanzees' relationships are more centered around their mothers (Pusey, 1990). Amongst juvenile chimpanzees, males pant-hooted more than

females (Pusey, 1990). Although Ramos-Fernandez (2005) asserts that the spider monkey whinny vocalization serves a similar function to a chimpanzee pant-hoot, juvenile spider monkeys exhibit the reverse pattern, with females vocalizing more than males. However, the differences observed in both species are reflective of patterns of adult behavior. While adult female spider monkeys whinny more often than adult males (Fedigan & Baxter, 1984), adult and subadult males chimpanzees are the initiators of pant-hoots (Goodall, 1986). Thus, the social patterns regarding the use of the whinny and pant-hoot may be different, despite their similar function in greeting behavior.

The literature regarding sex differences in immature play amongst juvenile chimpanzees is conflicting. Pusey (1990) did not find any obvious sex differences in play at Gombe, Tanzania. However, Hayaki (1985) found slight differences in play at Mahale, Tanzania, and studies on captive groups have also demonstrated sex differences in play (Nadler & Braggio, 1974; Nadler et. al, 1987). When differences have been observed, they follow the same pattern observed in the juvenile spider monkeys, with males engaging in play more often than females. The patterns of interaction and play partners exhibited by the juvenile spider monkeys mirror many of the general trends exhibited by juvenile chimpanzees. While the female spider monkeys centered their social interaction around their mothers, and their play around other immature females, the males interacted and played with a wider variety of conspecifics, including juvenile and adult males. Pusey (1983, 1990) found that immature male chimps are particularly interested in associating and interacting with a wider variety of conspecifics. She explains that immature males benefit from interacting with adults of their community, while immature females can acquire the skills they require by associating with their mothers. The bond between immature males and adult

males may be particularly important. Pruettz and Bloomsith (1995) found that in a captive setting, adult male chimpanzees engaged in affiliative interactions significantly more often with immature males than with females. This pattern is similar to the pattern observed in the present study with spider monkeys, as only juvenile males interacted with and played with adult males. Pruettz and Bloomsith (1995) suggest that the theory of reciprocal altruism (Trivers, 1971) provides the best explanation for why adult males interact more often with immature males, as this may be a form of investment in future social alliances.

Given that males are philopatric, it would be expected that the adult males within the community are likely to be related (Pope, 2000), and therefore likely to be related to the immatures of the community. However, research on chimpanzees has produced conflicting results on this subject. Morin and colleagues (1994) found that male chimpanzees at Gombe were on average related at the level of being half-brothers. However, Vigilant and colleagues (2001) research on the relatedness between male chimpanzees at Tai National Park, Ivory Coast, found that males were not significantly closer related than females. Furthermore, they point out flaws in Morin and colleagues (1994) data and caution that it may not be accurate. If male chimpanzees vary greatly in average relatedness to immatures, it would be expected that if they can recognize kin, they would preferentially associate with closely related immatures. While paternal kin recognition has not been demonstrated in chimpanzees, there is evidence that captive chimpanzees can recognize relatedness in unfamiliar mother-son pairs using facial phenotypic matching (Paar & de Waal, 1999). Furthermore, Widdig and colleagues (2001) have demonstrated that amongst rhesus macaques (*Macaca mulatta*), females affiliate significantly more with paternal half-sisters than with non-related females, and that paternal kin recognition is greatest within the peer group. They suggest that the

rhesus macaques recognized paternal kin through phenotypic matching based on behavioral traits. Thus, it seems feasible that male chimpanzees, as well as male spider monkeys, might be able to recognize paternal kin. However, the data on paternity and association have not supported this. Pruettz and Bloomsith (1995) found that paternity had no significant effect on interactions between adult males and immatures in a captive setting. Furthermore, in a study of maternal relatedness, Goldberg and Wrangham (1997) found that male chimpanzees at Kibale, Uganda do not preferentially associate with maternal kin. Rather, the peer group appears to be the most important factor influencing affiliation. While research comparing spider monkey relatedness and behavior has yet to be carried out, it is likely that the spider monkeys are following the same patterns as chimpanzees. The mutual interest demonstrated between immature and adult males in both spider monkeys and chimpanzees is likely to be based on the importance of forming social bonds with lifetime social partners rather than preferential association with kin. However, as spider monkeys tend to have more skewed female-biased sex ratios (Chapman, Chapman, & Richardson, 1989) it is possible that spider monkeys males are, on average, more closely related than chimpanzee males. Thus, these hypotheses require future testing. Additionally, data from chimpanzees suggest that age proximity, rather than genetic relatedness, may be one of the most important factors in chimpanzee social bonds. This is consistent with the findings of this study, as the juvenile males both interacted and played significantly more with other juvenile males. This suggests that like chimpanzees, the bonds formed within the peer group during development may be extremely important to male spider monkeys throughout their lives.

### **Social Implications of the Juvenile Period for Spider Monkeys**

In late juvenility and adolescence, spider monkey males must make a transition toward integration into the adult male hierarchy. However, the results of this and other studies suggest that, like chimpanzees, this process starts early through increased association and interaction with adult males at an early age. Due to the dispersal patterns of spider monkeys, male and female juveniles face different social pressures. While males have the opportunity to develop the social bonds that will continue throughout their lives, juvenile females must prepare for emigration and integration within a new community. For juvenile females, the acquisition of social skills rather than the development of specific social relationships may be more important. In addition to the important ecological challenges of finding adequate food resources, females' greatest challenges may be the integration within a community of unfamiliar conspecifics and the successful rearing of offspring. Thus, interactions with female conspecifics in the natal group may be considered preparation for later interactions within a new community. Grooming relationships with mothers could provide the opportunity to practice behaviors that will be beneficial in investing in their own offspring. Furthermore, play with other immature females may provide opportunities to develop skills in assessing relationships, reading the social behavior of conspecifics, and in dealing with stress. Additionally, forming relationships with female peers may also provide emigration partners. While this has not been documented in spider monkeys, immigration with a close peer or sibling has been reported in species characterized by male dispersal, such as squirrel monkeys (Mitchell, 1994), lemurs (*Lemur catta*; Sussman, 1991) and macaques (*Macaca mulatta*; Meikle & Vessey, 1981). Even if females do not immigrate with a conspecific, within a forest such as El Zota, where there are only one or two accessible

neighboring communities, it is likely that a female immigrant may be reunited with other females from her natal community. Thus, for both males and female spider monkeys, the juvenile period provides opportunities to develop sex-typical social skills as well as develop social bonds that may be beneficial later in life.

### References

- Agoramoorthy, G. 1998. Intergroup Infant Transfer among Red Howlers, *Alouatta seniculus*, in Venezuela: Adoption or Kidnapping? *Neotropical Primates*. 6(4): 121-123.
- Ahumada, JA. 1992. Grooming Behavior of Spider Monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *International Journal of Primatology*. 13(1): 33-49.
- Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour*. 49(3):227-67.
- Bekoff, M, Allen, C. 1998. Intentional Communication and Social Play: How and Why Animals Negotiate and Agree to Play. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 97-114.
- Biben, M. 1998. Squirrel Monkey Play-fighting: Making the Case for a Cognitive Training Function for Play. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 161-182.
- Brown, S. 1998. Play as an Organizing Principle: Clinical Evidence and Personal Observations. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 243-259.
- Campbell, CJ. 2006. Lethal Intragroup Aggression by Adult Male Spider Monkeys (*Ateles geoffroyi*). *American Journal of Primatology*. 68(12): 1197-1201.
- Chapman, CA, Fedigan, LM, Fedigan, L, Chapman, LJ. 1989a. Post-weaning Resource Competition and Sex Ratios in Spider Monkeys. *OIKOS*. 54: 315-319.
- Chapman, CA, Chapman, LJ, Richardson, KS. 1989. Sex Ratio in Primates: A Test of the Local Resource Competition Hypothesis. *OIKOS*. 56: 132-134.
- Di Fiore, A, Campbell, CJ. 2007. The Atelines: Variation in Ecology, Behavior, and Social Organization. In *Primates in Perspective*. Ed. Campbell, CJ, Fuentes, A, MacKinnon, KC, Panger, M, Bearder, SK. Oxford: Oxford University Press. 155-185.



- Dunbar, RIM. 1993. Coevolution of Cortical Size, Group Size, and Language in Humans. *Behavioral and Brain Sciences*. 16: 681-735.
- Dunbar, RIM. 1998. The Social Brain Hypothesis. *Evolutionary Anthropology*. 6: 178-190.
- Eisenberg, JF. 1976. Communication Mechanisms and Social Integration in the Black Spider Monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian Contribution to Zoology*. 213: 1-108.
- Fagen, R. 2002. Primate Juveniles and Primate Play. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 182-196.
- Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.
- Goldberg TL, Wrangham RW. 1997. Genetic Correlates of Social Behavior in Wild Chimpanzees: Evidence from Mitochondrial DNA. *Animal Behavior*. 54: 559-70.
- Goodall J. 1986. *The Chimpanzees of Gombe*. Cambridge (MS): Belknap Press.
- Koenig, A, Borries, C, Doran-Sheehy, DM, Janson, CH. 2006. How Important are Affiliation and Cooperation? A reply to Sussman et. al. *American Journal of Physical Anthropology*. 131(4): 522-523.
- Hayaki, H. 1985. Social Play of Juvenile and Adolescent Chimpanzees in the Mahale Mountains National Park, Tanzania. *Primates*. 26:343-360.
- Henzi, SP, Barrett, L. 1999. The Value of Grooming to Female Primates. *Primates*. 40(1): 47-59.
- Hrdy, SB. 1976. Care and Exploitation of Nonhuman Primate Infants by Conspecifics other than the Mother. In *Advances in the Study of Behavior*. Ed. Rosenblum, LA. New York: Academic Press. 101-158.
- Keverne, EB, Martensz, N, Tuite, B. 1989. Beta-endorphin Concentrations in Cerebrospinal Fluid of Monkeys are Influenced by Grooming Relationships. *Psychoneuroendocrinology*. 14: 155-161.
- Kinzey, W.G. and Wright, P.C. 1982. Grooming Behavior in the Titi Monkey (*Callicebus torquatus*). *American Journal of Primatology*. Vol. 3, 267-275.
- Maccoby, EE, Jacklin, CN. 1974. *The Psychology of Sex Differences*. Stanford: Stanford University Press.

- Maestriperi, D. 1993. Infant Kidnapping amongst Group-living Rhesus Macaques: Why Don't Mothers Rescue their Infants? *Primates*. 34(2): 211-216.
- Maestriperi, D. 2002. Parent-offspring Conflict in Primates. *International Journal of Primatology*. 23:923-951.
- McDaniel, PS. *The Social Behavior and Ecology of the Black-handed Spider Monkey (Ateles geoffroyi)*. PhD Dissertation, St. Louis University.
- Meikle, DB, Vessey, SH. 1981. Nepotism among Rhesus Monkey Brothers. *Nature*. 294: 160-161.
- Mitchell, CL. 1994. Migration Alliances and Coalitions among Adult Male South American squirrel monkey (*Saimiri sciureus*). *Behaviour*. 130: 169-190.
- Morin, PA, Moore, JJ, Chakraborty, R, Jin, L, Goodall, J, Woodruff, DS. 1994. Kin Selection, Social Structure, Gene Flow, and the Evolution of Chimpanzees. *Science*. 265: 1193-1201.
- Nadler, RD, Braggio, JT. 1974. Sex and Species Differences in Captive-reared Juvenile Chimpanzees and Orang-utans. *Journal of Human Evolution*. 3: 541-550.
- Nadler, RD, Wallis, J, Roth-Meyer, C, Coer, RW, Baulieu, EE. 1987. Hormones and Behavior of Prepubertal and Peripubertal chimpanzees. *Hormones and Behavior*. 21: 118-131.
- Van Noordwijk, MA, Hemelrijk, CK, Herremans, LAM, Sterck, EHM. 2002. Spatial Position and Behavioral Sex Differences in Juvenile Long-Tailed Macaques. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 77-85.
- Nunes, A, Chapman, CA. 1997. A Re-evaluation of Factors Influencing the Sex Ratio of Spider Monkey Populations with New Data from Maraca Island, Brazil. *Folia Primatologica*. 68: 31-33.
- Paar, LA, de Waal, FBM. 1999. Visual Kin Recognition in Chimpanzees. *Nature*. 399: 647.
- Palagi, E, Paoli, T, Tarli, SB. 2006. Short-term Benefits of Play Behavior and Conflict Prevention in *Pan paniscus*. *International Journal of Primatology*. 27(5):1257-1270.
- Paul, A. The Socioecology of Infant Handling in Primates: Is the Current Model Convincing? *Primates*. 40(1): 33-46.
- Pastor-Nieto, R. 2001. Grooming, Kinship, and Co-feeding in Captive Spider Monkeys. *Zoo Biology*. 20(4): 293-303.

- Pellis, SM, Iwaniuk, AN. 2000. Adult-adult Play in Primates: Comparative Analyses of its Origin, Distribution, and Evolution. *Ethology*. 106: 1083-110.
- Pellis, SM, Pellis, VC. 1998. The Structure-Function Interface in the Analysis of Play Fighting. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 115-140.
- Pruetz, JD, Bloomsmith, MA. 1995. The Effects of Paternity on Interactions between Adult Male and Immature Chimpanzees in Captivity. *Folia Primatologica*. 65: 174-180.
- Pope, TR. 2000. The Evolution of Male Philopatry in Neotropical Monkeys. In *Primate Males: Causes and Consequences of Variation in Group Composition*. Ed. Kappeler, PM. Cambridge: Cambridge University Press. 219-235.
- Pusey, AE. 1983. Mother-Offspring Relationships in Chimpanzees after Weaning. *Animal Behaviour*. 31(2): 363-377.
- Pusey, AE. 1990. Behavioural Changes at Adolescence in Chimpanzees. *Behaviour*. 115: 203-246.
- Ramos-Fernandez, Gabriel. 2005. Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch with Close Associates? *International Journal of Primatology*. 26(5): 1077-1090.
- Roney, JR, Maestripieri, D. 2003. Social Development and Affiliation. In *Primate Psychology*, ed. Maestripieri, D. Cambridge: Harvard University Press. 171-204.
- Van Roosmalen, MGM, Klein, LL. 1988. The Spider Monkeys, Genus *Ateles*. *Ecology and Behavior of Neotropical Primates, Vol. 2*. ed. Mittermeier, RA, Rylands, AB, Coimbra-Filho, AF, de Fonseca, AB. Washington, DC: World Wildlife Fund. 455-537.
- Silk, JB. 1980. Kidnapping and Female Competition among Captive Bonnet Macaques. *Primates*. 21(1):100-110.
- Schaffner, CM, Aureli, F. (2005). Embraces and Grooming Captive Spider Monkeys. *International Journal of Primatology*. 26(5): 1093-1106.
- Silk, JB. 1983. Local Resource Competition and Facultative Adjustment of Sex Ratios in Relation to Competitive Abilities. *The American Naturalist*. 121(1): 56-66.
- Siviy, SM. 1998. Neurobiological Substrates of Play Behavior: Glimpses into the Structure and Function of Mammalian Playfulness. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 221-242.

Strier, KB. 1994. Myth of the Typical Primate. *Yearbook of Physical Anthropology*. 37: 233-271.

Sussman, RW, Garber, PA. 2004. Rethinking Sociality: Cooperation and Aggression among Primates. In *The Origins and Nature of Sociality*. Ed. Sussman, RW, Chapman, AR. New York: Aldine de Gruyter. 161-190.

Sussman, RW, Garber, PA, Cheverud, JM. 2005. Importance of Cooperation and Affiliation in the Evolution of Primate Sociality. *American Journal of Physical Anthropology*. 128: 84-97.

Sussman, RW. 1991. Demography and Social Organization of Free-ranging *Lemur catta* in the Beza Mahafaly Reserve, Madagascar. *American Journal of Physical Anthropology*. 84: 43-58.

Symington, MM. 1987. Sex Ratio and Maternal Rank in Wild Spider Monkeys: When Daughters Disperse. *Behavioral Ecology and Sociobiology*. 20: 421-425

Tanaka, I, Takefushi, H. 1993. Elimination of External Parasites (lice) is the Primary Function of Grooming in Free-ranging Japanese Macaques. *Anthropological Sciences*. 101: 187-193.

Thompson, KV. 1998. Self Assessment in Juvenile Play. In *Animal Play: Evolutionary, Comparative, and Ecological Perspectives*. Ed. Bekoff, M, Byers, JA. Cambridge: Cambridge University Press. 183-204.

Trivers, RL. 1971. The Evolution of Reciprocal Altruism. *Quarterly review of Biology*. 46: 35-57.

Trivers, RL. 1974. Parent-offspring Conflict. *American Zoologist*. 14: 249-264.

Valero, A, Schaffner, CM, Vick, LG, Aureli, F, Ramos-Fernandez, G. 2006. Intragroup Lethal Aggression in Wild Spider Monkeys. *American Journal of Primatology* 68: 732-737.

Vigilant, L, Hofreiter, M, Siedel, H, Boesch, C. 2001. Paternity and Relatedness in Wild Chimpanzee Communities. *Proceedings of the National Academy of Sciences*. 98 (23): 12890-12895.

Widdig, A, Nürnberg, Krawczak, M, Streich, WJ, Bercovitch, FB. 2001. Paternal Relatedness and Age Proximity Regulate Social Relationships among Adult Female Rhesus Macaques. *Proceedings of the National Academy of Sciences*. 2001. 98: 13768-13773.

Ziegler, T. E. 2000. Hormones Associated with Non-maternal Infant Care: A Review  
Mammalian and Avian studies. *Folia Primatologica*. 71: 6-21.

## **CHAPTER 6**

### **RESULTS AND DISCUSSION: PROXIMITY PATTERNS**

#### **Results**

In species that exhibit low rates of interaction, proximity patterns are valuable in elucidating information about social relationships. Furthermore, within a fission-fusion social structure, social opportunities are limited by party size and composition. For this reason, both proximity patterns and party characteristics were examined to determine if sex differences exist between male and female juvenile's social networks. One-tailed p-values are reported for all tests that are testing directional hypotheses; two-tailed p-values are reported for all other tests. To account for the increased likelihood of a Type I error when using multiple t-tests, a Bonferroni adjustment was used. This reduces the significance level of 0.05 to account for the number of t-tests used in each comparison.

#### **Nearest Neighbor Patterns**

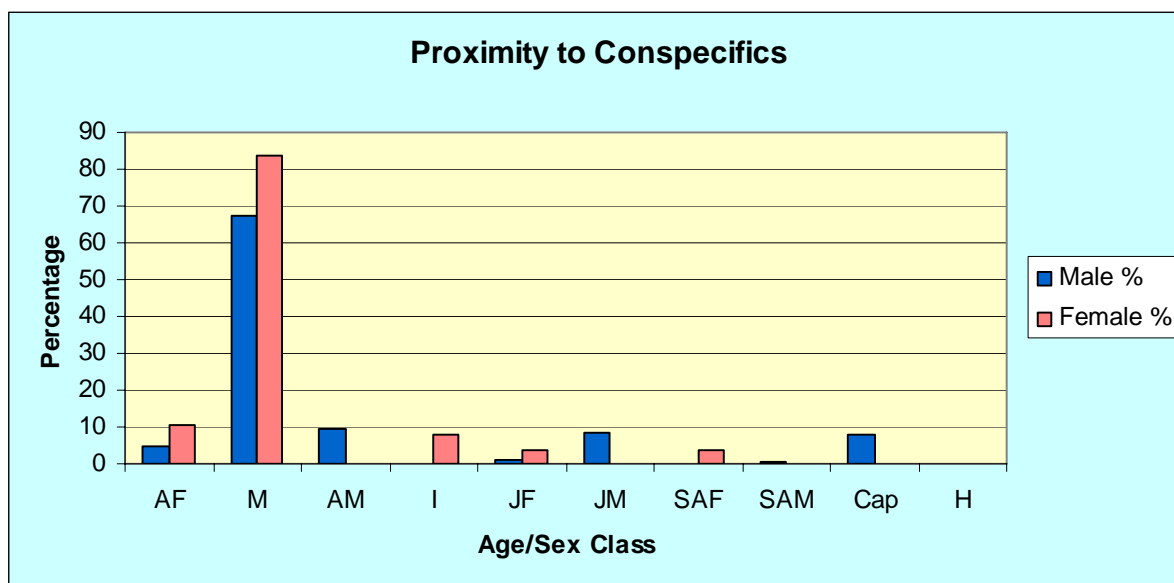
##### *Proximity to Conspecifics*

The frequency of time spent in proximity to each age/sex class was compared using instantaneous data. Both male and female juveniles spent the majority of their time in proximity to their mothers (males=67.6%; females=83.71%) (Figure 14). However, juvenile females spent more time in proximity to adult females (males=4.7%; females=10.7%) and juvenile females (males=1.2%; females=3.5%). Additionally, only juvenile females spent any time in proximity to subadult females (males=0.0%; females=3.6%) and infants (males=0.0%; females=8.0%), while only juvenile males spent any time in proximity to adult males (males=9.7%; females=0.0%), juvenile males (males=8.4%; females=0.0%), capuchin

monkeys (males=7.8%; females=0.0%), and howler monkeys (males=0.2%; females=0.0%).

The Bonferroni-adjusted significance level was 0.005. Differences in the time spent in proximity to adult males ( $T=-2.67$ ,  $df=7$ , one-tailed  $p=0.0155$ ) and juvenile males ( $T=-2.39$ ,  $df=7$ ,  $p=0.0242$ ) were not statistically significant, although  $p$ -values were low.

*Figure 14*



Abbreviations are as follows: AF=Adult Female, M=Mother, AM=Adult Male, I=Infant, JF=Juvenile Female, JM=Juvenile Male, SAF=Subadult Female, SAM=Subadult Male, Cap=Capuchin, H=Howler

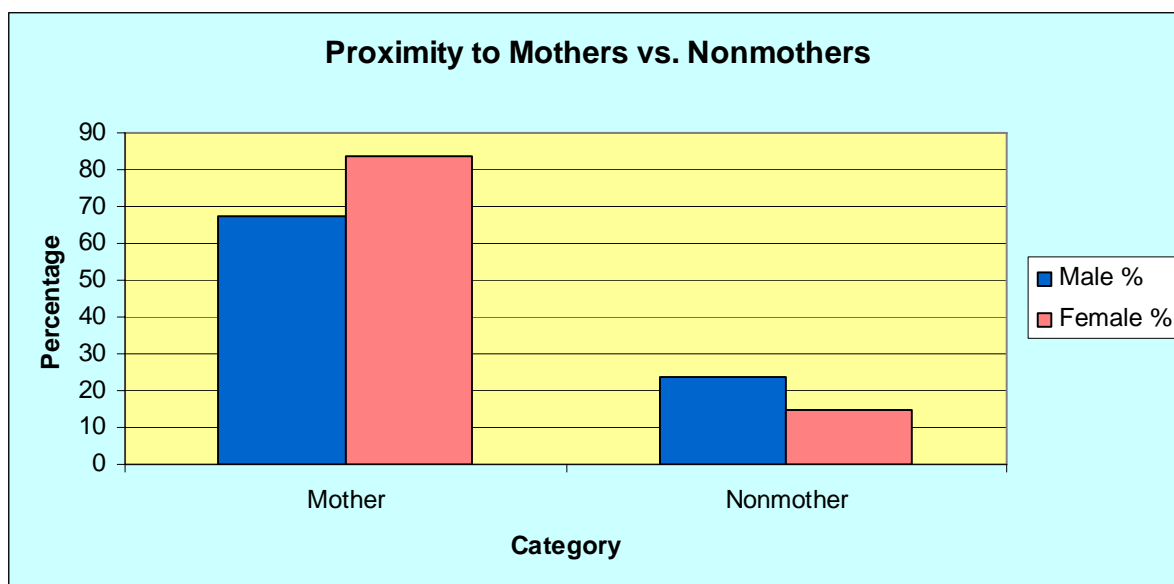
*Table 18: T-tests for Proximity to Conspecifics*

Age/Sex Class	df	T	one-tailed p-value
Adult Female	7	0.49	0.3193
Mother	7	1.42	0.0995
Adult Male	7	-2.69	0.0155
Infant	7	0.88	0.2036
Juvenile Female	7	0.84	0.2152
Juvenile Male	7	-2.39	0.0242
Subadult Female	7	0.88	0.2036
Subadult Male	7	-1.14	0.1462
Capuchin	7	-1.63	0.0733
Howler	7	-1.14	0.1462

### *Proximity to Nonmother Conspecifics*

The time spent in proximity to all nonmother conspecifics was combined into a single category in order to determine whether male juveniles spent more time in proximity to nonmothers. The time spent in proximity to mothers was also compared. Juvenile males spend more time in proximity to nonmother conspecifics (males=23.6%; females=14.9%), and less time in proximity to their mothers (males=67.6%; females=83.7%) than do juvenile females (Figure 15). The Bonferroni-adjusted significance level was 0.025, and these differences were not significant (mothers:  $T=1.43$ ,  $df=7$ , one-tailed  $p$ -value=0.0978; nonmothers:  $T=-0.75$ ,  $df=7$ , one-tailed  $p$ -value=0.2379).

*Figure 15*



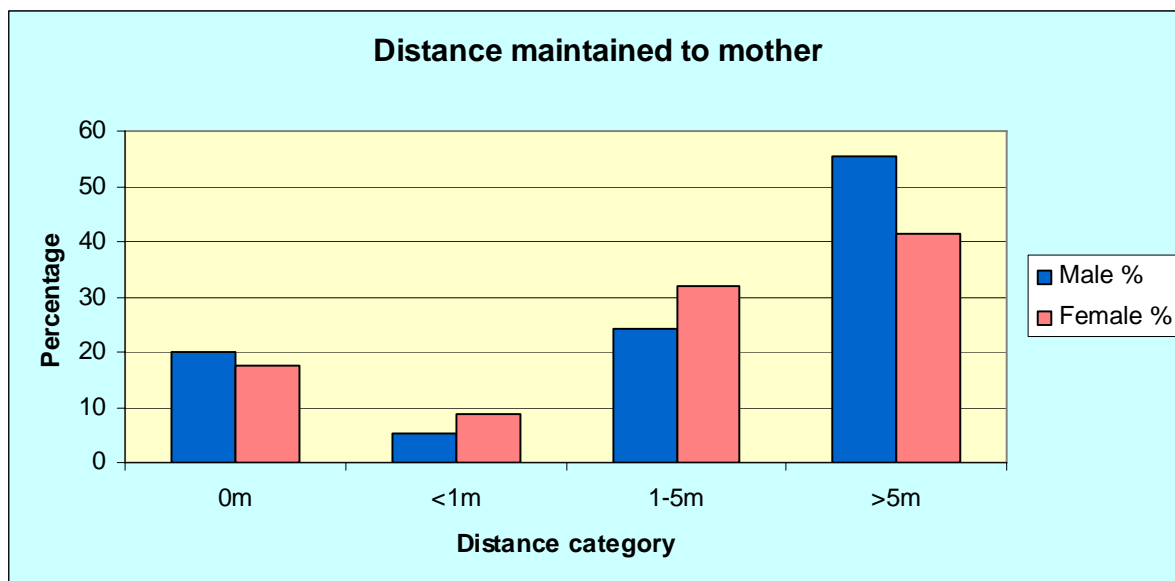
### *Distance Maintained to Mother*

The time spent in each distance category with the mother as nearest neighbor were compared to determine if male or female juveniles spend time in closer proximity to the



mother. The Bonferroni-adjusted significance level was 0.0125. No consistent pattern or significant differences were found between male and female juveniles (Figure 16).

*Figure 16*



*Table 19: Distance Maintained to Mother*

Distance	Male %	Female %
0m	20.0	17.6
<1m	5.3	8.9
1-5m	24.1	32.0
>5m	55.3	41.6

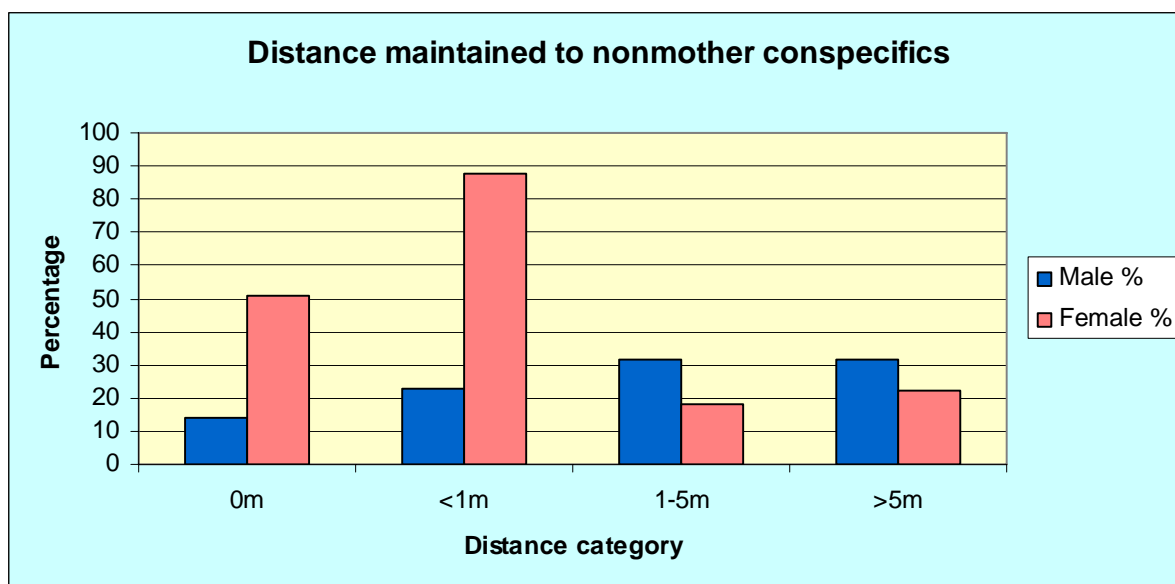
*Table 20: T-tests for Distance Maintained to Mother*

Distance	df	T	one-tailed p-value
0m	7	-0.23	0.4137
<1m	7	0.98	0.1797
1-5m	7	1.42	0.0979
>5m	7	-0.87	0.2092

### *Distances Maintained to Nonmother Conspecifics*

The time spent in each distance category when nonmothers were the nearest neighbor were compared to determine if male or female juveniles maintain closer distances to other conspecifics. Two females did not spend any time with nonmother conspecifics as nearest neighbors and were eliminated from this analysis. Juvenile females spent more time in the two closest distance categories and less time in the furthest distance categories, indicating that females maintain closer distances to nonmother conspecifics (Figure 17). The Bonferroni-adjusted significance level was 0.0125. Only the difference found for the 0m category approached significance ( $T=2.89$ ,  $df=5$ , one-tailed  $p=0.0172$ ).

*Figure 17*



*Table 21: Distances Maintained to Nonmother Conspecifics*

Distance	Male %	Female %
0m	14.25	51.05
<1m	23	87.8
2-5m	31.3	18.21
>5m	31.45	21.97

*Table 22: T-tests for Distances Maintained to Nonmother Conspecifics*

Distance	df	T	one-tailed p-value
0m	5	2.89	0.0172
<1m	5	-1.03	0.3491
2-5m	5	-1.93	0.0555
>5m	5	-0.67	0.2652

## Party Characteristics

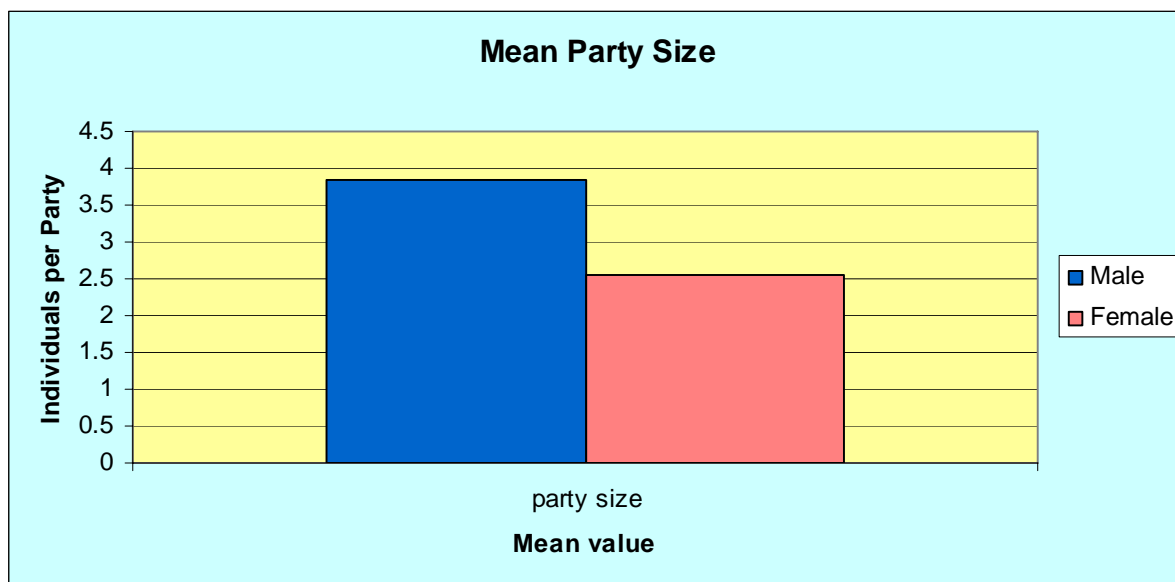
### *Party Size*

The mean party sizes of male and female juveniles (including the focal animal itself) were calculated and compared. Male juveniles were observed in parties that contained a mean of 3.83 individuals, while females were observed in parties that contained a mean of 2.56 individuals (Figure 18). No adjustment was necessary for this test, and this difference is significant ( $T=-2.59$ ,  $df=7$ , two-tailed  $p=0.036$ ).

### *Party Composition*

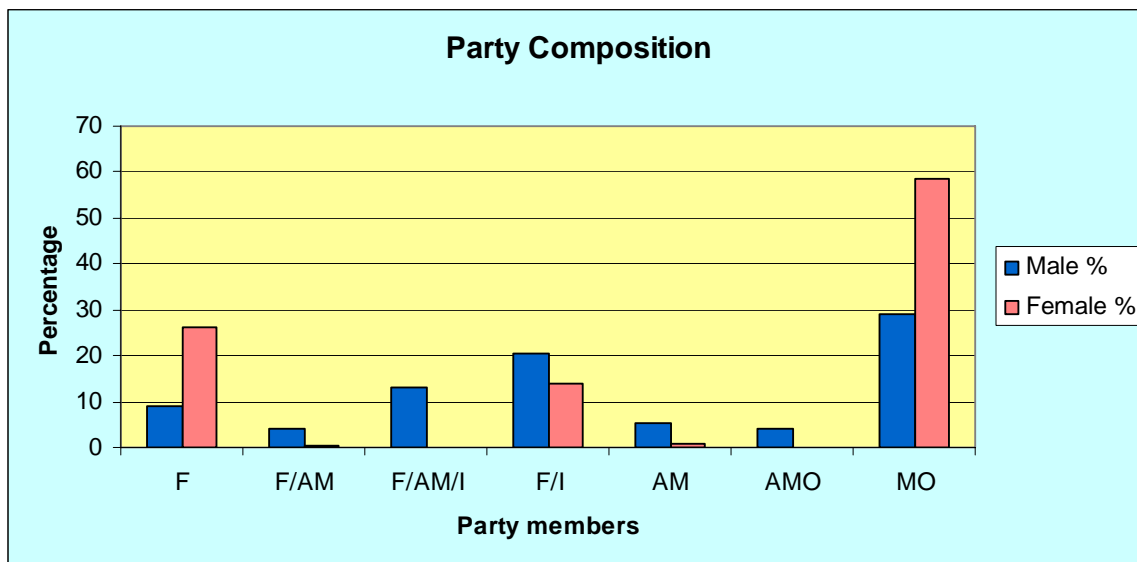
Party composition was determined by classifying each party based on the age and sex of the individuals represented besides the focal and its mother. For simplicity, infants and juveniles were considered in the general category ‘immatures,’ while subadults of both sex were considered adults due to their greater independence. All of these categories include the mother and the focal animal, with the exception of the ‘Males only’ category, in which the mother was not present. Females spent more time in parties that had only the mother present

Figure 18



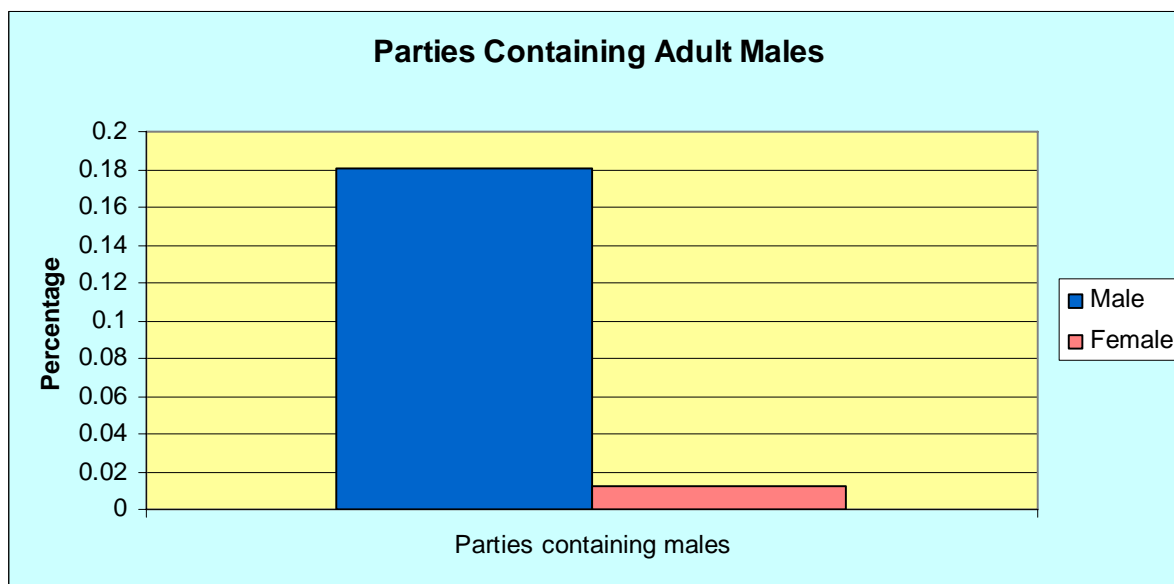
(males=29.2%; females=58.7%), and in parties with only adult females (males=9.1%; females=26.3%) (Figure 19). Conversely, juvenile males spent more time in all types of parties where adult males were present. This data was reassessed by recombining the categories initially used. All of the parties containing adult males were combining into a single category in order to provide a more direct assessment of the time each sex spent in parties including adult males. Juvenile males spent more time in parties containing males (males=18.1%; females=1.2%). No Bonferroni adjustment was needed for this test, so significance level was 0.05, and this difference was significant ( $T=2.47$ ,  $df=7$ ,  $p=0.0340$ ).

Figure 19



Abbreviations are as follows: F=Females, F/AM=Females/Adult Males, F/AM/I=Females/Adult Males/Immatures, F/I=Females/Immatures, AM=Adult Males, AMO=Adult Males Only (Mother not present), MO=Mother Only

Figure 20



*Table 23: Party Composition*

<b>Party composition</b>	<b>Male %</b>	<b>Female %</b>
Females	9.2	26.3
Females/Males	4.3	0.2
Females/Males/Immatures	13.1	0.1
Females/Immatures	20.4	13.8
Males	5.1	0.9
Males only	4.0	0
Mother only	29.2	58.7

*Table 24: T-tests for Party Composition*

<b>Party composition</b>	<b>df</b>	<b>T</b>	<b>two-tailed p-value</b>
Females	7	0.92	0.3868
Females/Males	7	-1.23	0.26
Females/Males/Immatures	7	-1.98	0.088
Females/Immatures	7	-0.68	0.5198
Males	7	-1.29	0.2386
Males only	7	-1.14	0.2924
Mother only	7	1.43	0.197

## **Discussion**

### **General Patterns**

The results of these analyses indicate that male and female juvenile spider monkeys do exhibit some sex differences in proximity patterns. Juvenile males spent more time in proximity with adult males and other juvenile males. Additionally, male juveniles were found in parties that were significantly larger than the parties containing juvenile females. However, when in proximity to nonmother conspecifics, juvenile females spent more time than juvenile males in contact with nonmothers. When in proximity to nonmother conspecifics, females spent more time in closer distance categories to nonmothers, while males spent more time in larger distance categories. Additionally the patterns in subgrouping composition indicate that juvenile males spent significantly more time in subgroups

containing adult males, while female juveniles spent more time in subgroups containing only adult females. These trends support the patterns found in overt social behavior, indicating limited social opportunities for juvenile females. Overall, male juveniles appear to have stronger spatial relationships with juvenile males and adult males, while females have stronger spatial relationships with their mothers and other females. These spatial relationships are strongly reflective of subgrouping patterns, as party composition limits the availability of social and spatial partners.

### **Comparisons to Other Species**

The patterns observed in this study are consistent with the patterns of adult social relationships as well as the immature spatial relations reported for other Atelines. Strier (2002) reported that juvenile muriqui males were in proximity to other group members more often than female juveniles. Furthermore, she found that immature females have weaker spatial relationships than immature males. Stevenson (1998) found sex differences in the proximity patterns of juvenile woolly monkeys. He reports that juvenile males older than three years old had looser association with their mothers than juvenile females, and spent more time in association with juvenile and subadult males. Each of these studies support the trend that, among Atelines characterized by female dispersal, males begin to exhibit stronger spatial associations with other males at an early age. Furthermore, the results of this study suggest that the patterns of sex-segregation observed by Fedigan and Baxter (1984) have their roots early in life.

These patterns mirror those found in other species. Nikolei and Borries (1997) found that in immature hanuman langurs (*Presbytis entellus*), a species characterized by female residence and male dispersal, female immature exhibited stronger spatial relationships to

other group members. Additionally, immature males received aggression more often than immature females. They argue that the social and spatial relationships exhibited by immatures suggest that the juvenile period serves as training for adult social relationships. Thus, the resident sex develops social bonds that will become advantageous in adulthood, while the dispersing sex develops skills that will serve them in emigration. The patterns observed in the present study support their training-for-adulthood hypothesis. However, why juvenile female spider monkeys maintain closer distances to nonmother conspecifics remains unclear. It is possible that juvenile females develop closer relationships with specific individuals and maintain stronger spatial associations to those individuals, while males interact more widely with a greater variety of conspecifics.

### **Ranging and Subgrouping**

In fission-fusion societies, proximity and subgrouping patterns provide valuable information about social structure and relationships (Symington, 1990). Previous studies indicate that adult male spider monkeys (*A. paniscus*) tend to be found in larger parties, but Symington (1990) notes that this is due to the differences in the time that each sex is found alone. Adult female spider monkeys tend to be solitary more often than adult males (Chapman, 1990; Symington, 1990). However, Chapman and colleagues (1995) note that spider monkey females (*A. geoffroyi*) tend to be less solitary than chimpanzee females. Additionally, Fedigan and Baxter (1984) report that males tend to associate with other males, while females tend to associate with other females. The results of the present study indicate that juvenile spider monkeys exhibit many of the same patterns observed in adult spider monkeys in terms of party size and composition. While the party sizes observed for both male and female juveniles were smaller than those observed for adults at other sites (*Ateles*



*geoffroyi*: 4.9 individuals, Chapman, 1990; 3.7 individuals, McDaniel, 1994; *Ateles paniscus*: 3.65-4.05 individuals; Symington, 1990) this is not surprising, given the observation that females with offspring tend to range in smaller parties (Chapman, 1990; Chapman et. al, 1995; Symington, 1990). However, the finding that male juveniles are found in significantly larger parties than female juveniles is surprising, given most of the theoretical discussions addressing differences in ranging patterns and party size.

Sex-segregation in ranging patterns is usually thought to reflect the differential needs of males and females. Females are thought to be limited by food resources, and thus focus on foraging to gain adequate nutrition, while males are thought to be limited by reproductive opportunities, and thus focus on monitoring and monopolizing territories and reproductive females (Fedigan and Baxter, 1984; Kortsjens et. al, 2005; Wrangham, 1980; Wrangham, 2000). For this reason, female ranging patterns are tied to resource abundance and distribution (Kortsjens et. al, 2005). Symington (1990) suggests that feeding competition is the most important factor determining fission-fusion dynamics among spider monkey communities. Spider monkeys and chimpanzees follow a scramble competition model, in which subgrouping is a way to reduce direct competition for patchy resources (Wrangham, 1980; Wrangham, 2000). While males are also limited by ecology, the presence and distribution of reproductively available females may be their limiting resource. Thus patterns of male ranging and association are considered a response to optimize access to females (Kortsjens et. al, 2005; Wrangham, 1980). However, both males and females are affected by patterns of food abundance, and Chapman (1990) notes that average party size is related to rainfall.

Another important constraint on subgroup size is the time cost associated with traveling from one food patch to the next (Chapman et. al, 1995; Kortsjens et. al, 2005; Pontzer & Wrangham, 2006; Wrangham, 2000). This is one variable that may affect males and females differently, as the females bear greater time and travel costs associated with dependent young. While the burden of carrying infants has been cited as the greatest burden on maternal energetics and travel time, Pontzer and Wrangham (2006) suggest that the presence of independently locomoting juveniles may constrain maternal foraging more than the presence of clinging infants. In examining the ranging patterns of juvenile chimpanzees (*P. t. schweinfurthii*), they found that day range was positively correlated with juvenile age. Mother-juvenile dyads leave parties when the day range increases past the distance they are able to travel. However, the presence of a clinging infant did not affect the mother's day range (Pontzer & Wrangham, 2006). The authors suggest that the presence of juveniles, particularly younger juveniles, constrain ranging patterns and thus the mother's social opportunities (Pontzer & Wrangham, 2006). They further suggest that in a species with a long period of immaturity, this factor has a large effect on the social lives of both immatures and mothers.

Another factor that may influence party size and composition is the risk of predation (Lehmann & Boesch, 2005; Symington, 1990). While reports of predation are rare, this may be an important pressure in shaping party size and composition. Based on observations of successful and attempted predation on adult spider monkeys, Matsudo and Izawa (in press) suggest that jaguars, (*Panthera onca*), pumas (*Puma concolor*), and tayras (*Eira barbara*) all pose a risk to adult spider monkeys. Juveniles would be more vulnerable to threats from these predators, as well as smaller carnivores and raptors. Additionally, reports from

observations of predation of red-handed howling monkeys (*Alouatta belzebul*) support the assertion that tayras pose a risk to monkeys of this size (Camargo & Ferarri, 2007). Both tayra and jaguar are present at El Zota (Lindshield, 2006). While tayras appear abundant and are frequently sighted (personal observation), traces and sightings of jaguar are currently rare (Lindshield, personal communication). If the presence of these predators poses greater risks to juveniles, females with offspring would be expected to range in large subgroups.

Additionally, females with offspring might be expected to range with adult males more often. In an analysis of spatial relations of immature mantled howling monkeys (*Alouatta palliata*) Arroyo-Rodríguez (2007) suggests that the proximity of males to immatures may be a form of protection against predation. This factor is likely to hold true for spider monkey parties as well. However, unless juvenile males are engaging in behaviors that render them more susceptible to predation, there is no reason why they would be at greater risk than female juveniles. While play on the ground has been reported at other sites (Campbell et. al, 2005) there was no indication that juvenile males were putting themselves at greater risk in this study. Thus, differential predation risks cannot account for why male juveniles were found in parties that were larger and contained males more often.

Conradt and Roper (2000) argue that sex segregation in fission-fusion social organization may occur because of the different ecological needs of different age/sex classes. However, in a study of social segregation in red deer (*Cervus elaphus*), they tested the hypothesis that sex segregation could be accounted for by differences in activity, and found that social segregation could not be explained solely by these differences. They suggest that social factors may also contribute to patterns of segregation. Otali and Gilchrist (2006) note that fission-fusion sociality provides the opportunity for individuals to optimize their social

environment as well as their foraging efficiency. Such social pressures may act to either limit party size or to increase it. The availability of playmates (Lehman & Boesch, 2005) and greater social opportunities (Otali & Gilchrist, 2006) for offspring may be benefits for mothers with immatures to ranging in larger subgroups, as long as ecological variables permit them to do so. However, social factors may also serve to discourage large social aggregations. Chapman (1990) argues that ecological factors are responsible for setting an upper limit on party size, and determining the general ranging patterns of males and females. However, he also argues that females with offspring range in smaller subgroups to protect immatures from aggression. Such an assertion is supported by Otali and Gilchrist's (2006) study on chimpanzee party sizes at Kibale, Uganda. They argue that female chimpanzees are less gregarious because of the risks of injury and stress that are posed by aggressive males. While females without offspring are not affected, females with dependent offspring avoid males to protect them. They found that females with offspring associate with fewer males and maintain closer distances to offspring when in the presence of males. Furthermore, as offspring age, their probability of associating with males increases. Otali and Gilchrist (2006) do however suggest that male offspring would benefit more than female offspring by socializing with the community's males. However, although they predicted that mother-son dyads would be in more frequent association with males than mother-daughter dyads, they found no significant difference.

Adult sex differences in subgrouping patterns can be explained through a variety of ecological factors and social factors. However, most of these factors should affect juvenile males and females similarly. Juveniles of both sexes have similar body sizes, and grow at the same rate, although females do have a growth spurt that results in reaching maturity slightly

before males do (Corner & Richtsmeier, 1993). It is likely that, for most of immaturity, males and females have the same nutritional requirements, travel costs, and predation risks. Thus an ecological explanation cannot account for these differences.

Social pressures may be one reason why males and females are found in parties of different size and composition. However, the finding that males are found in larger parties conflicts with Chapman's (1990) assertion that females with immature offspring range in smaller groups as a counterstrategy against aggression towards immature males. If this were the case, we would expect juvenile males to be found in smaller, rather than larger parties. Rather, the smaller groups that females and offspring travel in can be better explained as a strategy to deal with the greater travel costs incurred when traveling with slow-moving offspring. Although this was not specifically examined, it appeared as though larger party sizes, and parties containing adult males, were found more often at large fruiting resources, such as *Ficus* trees. This is consistent with data from other sites that correlate seasonal variations in fruit abundance, and fruit patch size, with larger party sizes (Chapman, 1990, Chapman et. al, 1995, Symington, 1990).

The differences found in the present study reflect the differential needs of male and female juveniles. In addition to receiving adequate nutrition to support growth, immatures need to learn the necessary social and ecological skills for survival. Sex differences in adulthood suggest that juvenile females might benefit more from learning ecological skills, while males would benefit from the acquisition of social skills. Lonsdorf (2005) suggests that the sex differences she found in the acquisition of termite-fishing skills in chimpanzees may be related to these pressures. While female immatures spent more time with their mothers learning to acquire these skills, males may have taken longer to achieve proficiency

in termite-fishing because they were focusing on acquiring social skills related to increasing future reproductive fitness. These results support Van Noordwijk's (2002) assertion that the emergence of sex-typical behaviors occurs before these differences can be explained by immediate social or nutritional needs. Rather, these differences occur in preparation of juvenile males' future social needs. However, how this occurs is not clear. One possibility is that mothers of male offspring make ranging decisions that allow their offspring greater social opportunities, as Otali and Gilchrist (2006) suggested for chimpanzees. Another possibility is that male juveniles may demonstrate a greater interest in other conspecifics, particularly adult males, and exert greater influence in their mother's ranging decisions. Finally, it may be possible that other conspecifics, particularly males, are more attracted to subgroups containing immature males and are more likely to join these subgroups than parties with immature females. While the factors that mediate these ranging decisions are not clear, it does appear that patterns of party size and composition do afford male juveniles greater social opportunities than are available to female juveniles. Furthermore, these opportunities allow juvenile males to develop the social relationships that will be advantageous later in life.

### References

- Arroyo-Rodríguez, V, Serio-Silva, JC, Alamo-García, J, Ordano, M. 2007. Exploring Immature-to-Mother Social Distances in Mexican Mantled Howler Monkeys at Los Tuxtlas, Mexico. *American Journal of Primatology*. 69: 173-181.
- Camargo, CC, Ferrari, SF. 2007. Interactions between Tayra (*Eira barbara*) and Red-handed Howlers (*Alouatta belzebul*) in Eastern Amazonia. *Primates*. 48: 147-150.
- Campbell, CJ, Aureli, F, Chapman, CA, Ramos-Fernandez, G, Matthews, K, Russo, SE, Suarez, S, Vick, L. 2005. Terrestrial behavior of *Ateles* spp. *International Journal of Primatology*. 26(5): 1039-1051.

Chapman, CA. 1990. Association Patterns of Spider Monkeys: The Influence of Ecology and Sex on Social Organization. *Behavioral Ecology and Sociobiology*. 26: 409-414.

Chapman, CA, Wrangham, RW, Chapman, LJ. 1995. Ecological Constraints on Group Size: An Analysis of Spider Monkey and Chimpanzee Subgroups. *Behavioral Ecology and Sociobiology*. 36(1): 59-70.

Conradt, L, Roper, TJ. 2000. Activity synchrony and Social Cohesion: A Fission-Fusion Model. *Proceedings of the Royal Society of London*. 267:2213-2218.

Corner, B.D., Richtsmeier, J.T. 1993. Cranial Growth and Growth Dimorphism in *Ateles geoffroyi*. *American Journal of Physical Anthropology*. 92:371-394.

Fedigan, LM, Baxter, MJ. 1984. Sex Differences and Social Organization in Free-Ranging Spider Monkeys (*Ateles geoffroyi*). *Primates*. 25(3): 279-294.

Korstjens, AH, Verhoeckx, IL, Dunbar, RIM. 2006. Time as a Constraint on Group Size in Spider Monkeys. *Behavioral Ecology and Sociobiology*. 60: 683-694.

Lehman, J, Boesch, C. 2005. Bisexually Bonded Ranging in Chimpanzees (*Pan troglodytes verus*). *Behavioral Ecology and Sociobiology*. 57: 525-535.

Lindshield, SM. 2006. The Density and Distribution of *Ateles geoffroyi* in a Mosaic Landscape at El Zota Biological Field Station, Costa Rica. Masters Thesis. Iowa State University, Ames.

Londorf, EV. 2005. Sex Differences in the Development of Termite-fishing Skills in Wild Chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour*. 70: 635-683.

Matusda, I, Izawa, K. (In press). Predation of Wild Spider Monkeys at La Macarena, Columbia. *Primates*.

McDaniel, PS. *The Social Behavior and Ecology of the Black-handed Spider Monkey (Ateles geoffroyi)*. PhD Dissertation, St. Louis University.

Nikolei, J, Borries, C. 1997. Sex Differential Behavior of Immature Hanuman Langurs (*Presbytis entellus*) in Rannagar, South Nepal. *International Journal of Primatology*. 18(3): 415-437.

Van Noordwijk, MA, Hemelrijk, CK, Herremans, LAM, Sterck, EHM. 2002. Spatial Position and Behavioral Sex Differences in Juvenile Long-Tailed Macaques. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 77-85.

- Otali, E, Gilchrist, JS. 2006. Why Chimpanzee (*Pan troglodytes schweinfurthii*) Mothers are Less Gregarious than Nonmothers and Males: the Infant Safety Hypothesis. *Behavioral Ecology and Sociobiology*. 59:561-570.
- Pontzer, H, Wrangham, RW. 2006. Ontogeny of Ranging in Wild Chimpanzees. *International Journal of Primatology*. 27(1): 295-309.
- Stevenson, PR. 1998. Proximal Spacing between Individuals in a Group of Woolly Monkeys (*Lagothrix lagotricha*) in Tinigua National Park, Colombia. *International Journal of Primatology*. 19(2): 299-311.
- Strier, KB, 2002. Growing Up in a Patrifocal Society: Sex Differences in the Spatial Relations of Immature Muriquis. In *Juvenile Primates: Life History, Development, and Behavior*. Ed. Pereira, ME, and Fairbanks, LA. Chicago: University of Chicago Press. 138-147.
- Symington, MM. 1990. Fission-fusion Social Organization in *Ateles* and *Pan*. *International Journal of Primatology*. 11(1): 47-61.
- Wrangham, RW. 1980. An ecological model of female-bonded primate groups. *Behaviour*. 75: 262-299.
- Wrangham, RW. 2000. Why are Male Chimpanzees more Gregarious than Mothers? A Scramble Competition Hypothesis. In *Primate Males: Causes and Consequences of Variation in Group Composition*. Ed. Kappeler, PM. Cambridge: Cambridge University Press. 248-258.



## CHAPTER 7 CONCLUSION

### Summary

The present study examined whether differences exist in the social behavior, interactions, and proximity patterns of male and female juvenile black-handed spider monkeys. The following questions were addressed:

**1) Is there a difference in the time engaged in social interactions between male and female juveniles?**

Results: Males and females were similar regarding the time spent engaged in social interactions.

**2) Do male and female juveniles differ in the types of social interactions they engage in?**

Results: There were some differences in the types of social interactions males and females engaged in. Males spent more time engaged in play, and less time engaged in vocal behavior, although these differences were insignificant. Only females initiated grooming, and this difference approached significance. No differences were found in the time engaged in agonistic behavior, but the patterns of agonism were different. Females received agonism from other conspecifics, while males received agonism from capuchin monkeys.

**3) Do other group members initiate more interactions with juvenile males than juvenile females?**

Results: The trend observed was the opposite of what was predicted, as females received more social interactions than did males. However, this difference was not significant,

and no conclusions can be drawn due to the large number of interactions for which initiators and recipients could not be assessed.

**4) Do juvenile male initiate interactions with other group members more than juvenile females?**

Results: The trend observed was the opposite of what was predicted, as females initiated more social interactions than did males. However, this difference was not significant, and no conclusions can be drawn due to the large number of interactions for which initiators and recipients could not be assessed.

**5) Do male and female juveniles differ in the time they spend in proximity (within five meters) to other conspecifics (excluding mothers)?**

Results: Males and females did not differ significantly in the time they spent in proximity to other conspecifics.

**6) Do male and female juveniles differ in the distances they maintain from other conspecifics (excluding mothers)?**

Results: Females spent more time at closer distances to nonmother conspecifics than did males, but these differences were not significant.

**7) Do male and female juveniles differ in the age/sex class they spend the most time in proximity to (excluding mothers)?**

Results: Males spent more time in proximity to adult males and juvenile males, and these differences approached significance. In general, females spent more time in proximity to other females and infants, while males spent more time in proximity to other males and other monkey species. However, no other categories showed significant differences.

Some differences were found in variables not specifically addressed by the research questions and hypotheses outlined at the beginning of the study. No significant differences were found in the amount of maternal or nonmaternal care received. Females spent more of their time interacting with their mothers than did males, and this difference approached significance. Males spent more of their time interacting with other juvenile males, and this difference approached significance. Males also played more with other juvenile males, and this difference also approached significance. Males were observed in parties that were significantly larger than parties containing females. Additionally, juvenile males were in parties containing adult males significantly more often than were juvenile females.

The results of this study, specifically the differences found in play, vocalization, and received agonism, suggest that male and female juveniles begin to develop many of the sex-typical behavioral differences observed in adults. These patterns suggest that juvenile spider monkeys are engaging in behavior that will prepare them for their lives as adults, as most of these differences cannot be explained in terms of immediate social or ecological needs. Furthermore, the findings of this study suggest that mothers are caring equally for their offspring. Thus, the differences observed in juvenile behavior cannot be attributed to differential maternal treatment. Rather, these differences may be due to the initiative of the juveniles themselves, or the initiatives of other conspecifics. Finally, the findings of this study contradict Schaffner and Aureli's (2005) assertions that embraces play a more important role than grooming in regulating spider monkey social relationships. For the juveniles of this study, grooming was a common behavior, while embraces were very rare. This indicates that for juveniles, grooming is a valuable indicator of social relationships, and in particular, may be an extremely important component of maternal investment.

Furthermore, the sex differences in the amount of grooming initiated suggest that grooming may be a more important social behavior for females than for males.

### **Implications**

The results of this study support the hypothesis that the extended juvenile period evolved within primates in order to provide the necessary time for immature primates to acquire the social skills necessary for adult life. The differences observed cannot be accounted for by ecological hypotheses, as ecological pressures would affect each sex equivalently during the juvenile period. Furthermore, if the extended juvenile period in *Ateles* related to the differential foraging needs that each sex will have in adulthood, one would expect juveniles to exhibit sex differences in time engaged in feeding/foraging. The finding that males and females exhibited very different patterns in the age/sex classes with which they interacted and associated suggests that the juvenile period evolved in order for juveniles to learn the social skills needed for adulthood as well as to begin developing long-lasting relationships.

These findings also indicate that the behavioral convergence of spider monkeys and chimpanzees begins at an early age. Like chimpanzees, male and female juveniles did exhibit differences in social behavior and association patterns related to the different pressures that each sex faces in adulthood. Female chimpanzees and spider monkeys concentrate more of their social interactions around their mothers and close female conspecifics, as many of the skills they need for adulthood can be acquired through associating with these individuals (Pusey, 1990). Conversely, juvenile male spider monkeys and chimpanzees demonstrate an interest in their male peers and adult males, who will continue to be important social partners throughout life. Additionally, juvenile male spider

monkeys and chimpanzees interact more with conspecifics of all age/sex classes, as many of these individuals will continue to be social partners for the duration of their lives.

Some differences between juvenile spider monkeys and chimpanzees were observed, however. The differences observed in spider monkey whinnies and chimpanzee pant-hoots indicate that the while juveniles of both species exhibit the typical patterns of adults in these vocal behaviors, these vocal behaviors cannot be considered functional equivalents, as Ramos-Fernandez (2005) suggested. Additionally, the patterns of sex-segregation apparent in social interactions, social play, and proximity patterns suggest that like the eastern chimpanzee subspecies, black-handed spider monkeys are male-bonded. However, determining whether there are species differences in the social relationships of juvenile and adult spider monkeys requires further study.

Differences observed in the sex ratios and patterns of agonism in this study and those reported elsewhere suggest that, like chimpanzees, the patterns of spider monkey social behavior are variable between different sites. Such differences may be due to species differences, ecological differences, or both. The lack of agonism toward juvenile males and the equivalency of the juvenile sex ratio suggest that in the productive habitat of El Zota, post-weaning resource competition is not as severe as has been reported at other sites, such as the dry forest of Santa Rosa. Weghorst (2007) reports that in the wet lowland forest of Corcovado, Costa Rica, juveniles exhibited a male-biased sex ratio while adults had a female-biased sex ratio. However, she notes that the skew in adult sex ratio is less severe than has been reported for other sites. These results suggest that, in a productive habitat, the adult sex ratio is a reflection of differential mortality during the subadult period. However, this hypothesis needs to be tested through investigations specifically focused on the social

and ecological pressures that face subadult males. Overall, the different patterns in juvenile sex ratio and aggression suggest that, among different habitats, spider monkeys are under different pressures. Examining how these pressures affect adult and juvenile social behavior are both topics that need further investigation.

The results of this study have practical implications for the management of captive spider monkeys. This study indicates that for juvenile males, the opportunity to interact with a wide variety of conspecifics, especially other juvenile and adult males, is a vital part of juvenile socialization. However, for females, interaction with the mother and a few other conspecifics may be sufficient for providing sufficient social opportunities. Thus, for captive groups, it is important to ensure that there are other adult, subadult, or juvenile males for immature males to interact with. Furthermore, in determining group composition for confiscated animals, where well-socialized, adult conspecifics may not be present, effort should be made to ensure that juveniles have access to conspecifics of their own sex. In determining ideal group composition for animals destined for reintroduction, it may be valuable to compose a group with a female-biased sex ratio similar to those reported for wild spider monkeys, with at least two males. Finally, the patterns of social behavior exhibited by the juveniles of this study may be valuable in evaluating whether captive juveniles display age- and sex-typical social behavior, as a measure of their social competency.

### **Future Directions**

The results of this study open up a variety of new questions that may be fruitful avenues for further research. First, while this study presents some interesting results, it was constrained by the short duration of the study, the habituation level of the focal population, and the small sample size of juveniles. Further study of these questions for a longer duration

of time on juveniles of multiple communities may be necessary to conclusively answer many of the questions investigated. Additionally, cross-site comparisons may be valuable in assessing how juvenile social behavior varies across habitats. The conflicting patterns observed in juvenile sex ratios, agonism, and maternal investment suggest that these are areas that require extensive cross-site comparison. It is clear that one of the key areas that remains understudied in spider monkeys is the transition between the juvenile and adult period. While the process of emigration to a new community is assumed to be stressful, no studies have specifically examined this process in female spider monkeys. Likewise, data from other sites suggests that the process of integration into the adult male hierarchy may be a very challenging time for subadult males, but this is another area that requires further investigation. One particularly fruitful avenue for study may be an investigation of the social interactions and cortisol levels of male and female subadults. Additionally the patterns of social interaction observed in this study suggest that an assessment of genetic relatedness, particularly paternity, may be valuable in understanding the interactions between adult and juvenile males. An assessment of genetic relationships amongst all community members might also shed light on whether the subadult and adult females who interacted most frequently with juveniles were related or unrelated individuals.

Direct investigations of the ecological factors affecting juvenile spider monkeys may be another productive avenue of research. In order to address the hypothesis that there are underlying ecological reasons for sex differences in juvenile behavior, the foraging and feeding behavior of juvenile males and females should be investigated. Additionally, investigation of the relationship between party size, composition, and fruit abundance may help illuminate factors that may contribute to the differences observed within this study.

One challenge in understanding how the patterns found in this study relate to adult behavior is the paucity of information available on adult behavior in similar environments. Thus, additional data on the social behavior of adult spider monkeys at El Zota could provide the data necessary for direct comparisons between adult and juvenile behavior. Finally, observations of tool use (Rodrigues & Lindshield, 2007) during this study and a concurrent study (Lindshield, 2006) are the first conclusive observations of tool use in this genus. Thus, additional study of the communities at El Zota may yield further observations and insight into this rare behavior.

### References

- Lindshield, SM. 2006. The Density and Distribution of *Ateles geoffroyi* in a Mosaic Landscape at El Zota Biological Field Station, Costa Rica. Masters Thesis. Iowa State University, Ames.
- Pusey, AE. 1990. Behavioural Changes at Adolescence in Chimpanzees. *Behaviour*. 115: 203-246.
- Ramos-Fernandez, G. 2005. Vocal Communication in a Fission-Fusion Society: Do Spider Monkeys Stay in Touch with Close Associates? *International Journal of Primatology*. 26(5): 1077-1090.
- Rodrigues, MA, Lindshield, SM. 2007. Scratching the Surface: Observations of Tool Use among Wild Spider Monkeys (*Ateles geoffroyi*). *American Journal of Physical Anthropology*. 132(S44): 201-202.
- Schaffner, CM, Aureli, F. 2005. Embraces and Grooming in Captive Spider Monkeys. *International Journal of Primatology*. 26(5): 1093-1106.
- Weghorst, JA. 2007. High Population Density of Black-handed Spider Monkeys (*Ateles geoffroyi*) in Costa Rican Lowland Wet Forest. *Primates*. 48: 108-116.