Positional behavior of black-handed spider monkeys (*Ateles geoffroyi*), including a one-armed individual, at El Zota Biological Field Station, Costa Rica

by

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ABSTRACT

Adaptions to arboreal habitats result in species-specific patterns of locomotion and postures in non-human primates. Having a range of positional behaviors enables spider monkeys (*Ateles* spp.) to manage the varying aspects of habitat structure that may hinder their access to preferred food sources, escape predators and myriad of other challenges to an arboreal primate. This study presents new data on the positional behavior and habitat use of black-handed spider monkeys (*A. geoffroyi*) living in lowland tropical rainforest in northeastern Costa Rica, a habitat that is common for the species but where they are not well-studied due to the challenges of this wet environment. The contexts of travel and foraging were compared to observe context-specific postural and locomotor behaviors. Comparisons of locomotor and postural behaviors between contexts approached significance when all individuals were analyzed as a whole. However, results did not reveal significant differences between sexes or age-classes within these contexts. This may be indicative of the value of certain positions when exploiting the environment, regardless of sex or age-class. This study also included data on a one-armed juvenile male spider monkey (JF) to observe his varied use of postural and locomotor modes when compared to the *A. geoffroyi* at the site with all functioning limbs. Overall, his positional behavior appears to mimic that of the other spider monkeys, though results reveal behaviors unique to JF, as well. JF adjusted to accommodate his missing limb in ways to improve his efficiency during daily activities, such as decreasing use of positions involving the forelimbs. Aspects of social behavior were recorded, as well, to assess JF’s social development in comparison to others in his age-class, though the sample size was small. Few encounters yielded social data on JF or other juvenile males, but in interactions with adult males, all of the immature monkeys exhibited similar behavior.

CHAPTER 1

INTRODUCTION

Considered an endangered species (IUCN, 2014), the black-handed spider monkey (*Ateles geoffroyi*) is among the largest of the New World primates and is almost exclusively arboreal (Youlatos, 2002; Mittermeier & Fleagle, 1976; Rowe, 1996). This species is scattered across Central America and along the western coast of South America (Collins, 2008). They typically inhabit tall evergreen and semideciduous tropical forest types (Wallace, 2008; Ramos-Fernández & Ayala-Orozco, 2003; Rowe, 1996) but may reside in dry, deciduous forests and mangrove forests, as well (Chapman, 1990; Wallace, 2008; See Table 1.1 for other *Ateles* spp. studies). As large-bodied, ripe fruit specialists, spider monkeys range relatively widely, in terms of both daily path length and home range size, due to patchy fruit distribution (Di Fiore, Link, & Dew, 2008; Wallace, 2008; Rosenberger, Halenar, Cooke, & Hartwig, 2008). Additionally, they exhibit specialized postural and locomotor behaviors that enable them to exploit these high quality foods.

The subjects of the current study are black-handed spider monkeys living in lowland tropical rainforest in northeastern Costa Rica. In order to efficiently exploit valued fruit resources, spider monkeys enlarge their feeding sphere through their postural and locomotion patterns (Youlatos, 2002). Adaptions to arboreal habitats result in species-specific patterns of locomotion and postures, which serve as coping mechanisms within time and space as primates move and feed within the canopy (Youlatos, 2008). Here, I present new data on the positional behavior and habitat use of *Ateles* spp. in a habitat that is not well studied but common for the species. I will ultimately compare my findings to other positional behavior studies of spider monkeys (Table 1.1). Studying the same species in different habitats allows researchers to make comparisons of how habitat structure influences behavior relative to anatomical design (Youlatos, 2008). Having a range of positional behaviors enables spider monkeys to manage the varying aspects of habitat structure that may hinder access to preferred food sources (Youlatos, 2008). This study addresses the array of positional behaviors used by spider monkeys at El Zota Biological Field Station (EZBFS) in Costa Rica.

Table 1.1: Studies on *Ateles* positional behavior

Study Site	**Habitat Type**	**Study Species**	**References**
Station des Nouragues, French Guiana	Tropical wet forest	*Ateles paniscus*	Youlatos, 2002
Yasuní National Park, Equador	Tropical moist forest	*A. belzebuth*	Cant, Youlatos, & Rose, 2001
Barro Colorado Island, Panama Canal Zone	Tropical moist forest	*A. geoffroyi*	Mittermeier & Fleagle, 1976
Santa Rosa National Park, Costa Rica	Tropical dry forest	*A. geoffroyi*	Bergeson, 1996

Table 1.1 continued

Panama	Tropical moist forest	*A. geoffroyi*	Fontaine, 1990
Guatemala	Tropical dry forest	*A. geoffroyi*	Cant, 1986
Panama; Surinam	Tropical moist forest	*A. geoffroyi*, *A. paniscus*	Mittermeier, 1978

Additionally, I examine specifically how primates cope with physical abnormalities via opportunistic data collection on a disabled individual. In the summer of 2014, an independent (weaned) juvenile male missing his right forearm was identified at EZBFS. While it is unknown how his arm came to be lost, Chapter 2 discusses possibilities. His positional behaviors were observed and recorded in addition to those of able-bodied spider monkeys. Chapter 5 analyzes his behavioral compensations in comparison to individuals with both functioning forelimbs within and outside his age-class. Around the independent juvenile stage, juvenile males tend to increase time associated with older males (Vick, 2008). Moreover, immatures perform play behavior more frequently than do older age-classes, attributable to its function in social learning (Palagi et al., 2006; Rodrigues, 2007). Due to the effects his malformation may impose on his social development, I expected the one-armed juvenile to have higher frequencies of play but less time spent with older males. Observing his positional behavior as well as aspects of social behavior offers insight into how primates adjust to physical deformities. These data also have implications for constructing behavior related to disabilities in the hominin fossil record, where evidence of serious injury or illness has often been explained as evidence for empathy, cooperation and even caregiving (Cuozzo & Sauther, 2006; Gilmore, 2012).

Background

Studies of posture and locomotion in primates

Primates utilize an array of behavioral postures and forms of locomotion. One such locomotor mode is brachiation, a form of below branch, suspensory movement that includes extensive trunk rotation, nearly 180°; however, it has been contested as to which species possess the full capacity to exploit it (Hunt et al., 1996; Mittermeier & Fleagle, 1976). Only hylobatids are considered “true” brachiators, particularly gibbons (*Hylobates* spp.) who brachiate as their primary form of travel (Bertram, 2004; Fan et al., 2013; Rein et al., 2014). However, other species outside the Hominoidea lineage display this type of suspensory behavior, albeit with some modification. These primates are termed “semibrachiators” (Mittermeier & Fleagle, 1976; Morbeck, 1977; Bertram, 2004). Semibrachiation has been coined to describe arboreal quadrupeds who exhibit a variable degree of arm swinging behavior and “leaping with the forelimbs outstretched” (Mittermeier & Fleagle, 1996, p. 248). This term has been applied both to New World primates, like *Ateles* spp., who display high amounts of below branch, bimanual locomotion, as well as to Old World primates, like *Colobus* spp., who do not perform this suspensory activity, but rather display outstretched forelimb leaping behavior (Youlatos, 2002; Mittermeier & Fleagle, 1996; Morbeck, 1977).

The distinction between brachiation and semibrachiation, as well as those included in these categories, has come under contention over the years (Mittermeier & Fleagle, 1976; Morbeck, 1977). Gibbons and siamangs (*Symphalangus*) are the only primates classified as "true" brachiators, which reflects their dependency on the locomotory mode (Bertram, 2004; Fan et al., 2013; Rein et al., 2014). These primates utilize this type of forelimb suspension during approximately 50-80% of locomotion (Rein et al., 2014; Arias-Martorell et al., 2015; Hunt, 1991). Their reliance on this form of locomotion is what seems to distinguish them from other suspensory primates. Suspensory atelines, like *Ateles* and *Brachyteles* species, appear to possess the same brachiating ability but do not engage in this behavior as frequently as the true brachiators (approximately 25% in spider monkeys) (Morbeck, 1977; Youlatos, 2002; Youlatos, 2008). However, there may be ecological or energetic constraints deterring their display of this behavior to the extent observed in the lesser apes.

A study by Mittermeier and Fleagle (1976) questioned the semibrachiator classification, as they did not think it described a true functional group (Bertram, 2004). Their study examined the positional behaviors of New World *Ateles* and Old World *Colobus* due to their inclusion in the semibrachiator category (Mittermeier & Fleagle, 1976; Bertram, 2004). The data yielded greater postural and locomotor variation between these groups than within them, making the semibrachiator classification appear inconsistent. Many do not consider atelines true brachiators due to their possession of a prehensile tail, which assists suspensory movements like brachiation (Youlatos, 2002; Bertram, 2004; Arias-Martorell et al., 2015; Mittermeier & Fleagle, 1976; Turnquist et al., 1999). Prehensile tails are capable of providing full support of the primate's body, acting like a fifth limb (Russo & Young, 2011). Instead, spider monkeys are sometimes referred to as tail-assisted brachiators (Iurck et al., 2013; Arias-Martorell et al., 2015). Moreover, some argue that suspensory atelines should not be considered true brachiators due to their diverse range of locomotory modes (i.e. quadrupedalism, clamber, etc.), while hominoids like gibbons exhibit this behavior as their primary mode of travel (Rowe, 1996; Youlatos, 2002;

Youlatos, 2008). Assistance of their prehensile tail in combination with their decreased use of brachiation when compared to hylobatids extends to *Ateles*' classification as semibrachiators.

Study subjects: *Ateles geoffroyi*

Spider monkey social organization is characterized by a fission-fusion social system in which smaller subgroups are formed as feeding parties, which are influenced by patchy fruit distribution (Aureli & Schaffner, 2008; Di Fiore et al., 2008; Strier, 2011; Rowe, 1996). Fission-fusion social systems are relatively rare in mammals (Aureli & Schaffner, 2008; Di Fiore et al., 2008; Strier, 2011; Rowe, 1996). The frugivorous diet of spider monkeys leads to this social system as a consequence of scramble competition since, as group size increases, so do the costs of competition, as resources become more quickly depleted (Asensio, Korstjens, Schaffner, & Aureli, 2008). Studies report larger subgroups formed during periods of high resource abundance, while smaller groups were formed in less favorable conditions (Asensio, Korstjens, & Aureli, 2009). Such adjustment helps to minimize ranging costs, as well as intragroup feeding competition. *Ateles* spp. home ranges average between 150 and 390 ha in continuous forest, with day ranges varying between 500 and 4500 m (Wallace, 2008). Ranging patterns can shift as a result of spatial variations in fruit abundance.

Spider monkeys are observed to frequently use tail-arm brachiation and arm-swing movements, commonly considered suspensory locomotion (Mittermeier & Fleagle, 1976; Cant, Youlatos, & Rose, 2001; Youlatos, 2002). Suspensory movements encourage increased travel rates and decreased path length within and between tree crowns (Youlatos, 2002; Youlatos, 2008; Strier, 2011). Hominoids, such as *Hylobates* and *Pongo*, exhibit extreme features that allow for such suspensory behavior. The postcranial morphology of *Ateles* spp. converge with that of these extant apes (Turnquist et al., 1999; Cant et al., 2001; Youlatos, 2002). These primates possess comparable shoulder girdle morphology, elongation of the forelimbs, trunk shape, and other features of their skeletal morphology (Turnquist et al., 1999; Youlatos, 2002).

The use of suspensory behaviors by spider monkeys is expected to provide similar benefits in exploiting arboreal food sources. For instance, the use of tail-arm brachiation contributes to faster movement within and across tree crowns and helps these large-bodied primates move more securely on slender, flexible supports (Youlatos, 2008). Their frugivorous diet often drives them to utilize terminal branches of tree crown peripheries; however, the use of below-branch and above-branch postures allows a distribution of body weight that can overcome the risks involved in exploiting such supports. Exploiting fruit, a high-quality food resource, is increased via such suspensory behaviors (Youlatos, 2002). Additionally, their locomotor repertoire includes quadrupedal walking/running, bipedalism, ascent/descent, clambering, and leaping/dropping (Mittermeier & Fleagle, 1976; Cant et al., 2001; Youlatos, 2002). Below branch suspensory activities characterize much of *Ateles'* postural repertoire, or positions maintained while relatively motionless; however, their range also includes sit, squat, lie, and various standing postures (Mittermeier & Fleagle, 1976; Cant et al., 2001; Youlatos, 2002).

Questions & Hypotheses:

The following questions were addressed throughout this study:

(1) Are there differences in the postural and locomotory modes used by spider monkeys during feeding/foraging, travel, and rest?

My null hypothesis states that there will be no differences in postural and locomotory modes used during feeding/foraging, travel, and rest. Certain positional behaviors were expected to be context specific; therefore, differences in the postural and locomotor modes used between these behavioral contexts were anticipated.

(2) Do males and females exhibit differing postural and locomotory behavioral frequencies according to different activities (i.e. feeding/foraging, travel, and rest)?

My null hypothesis states that there will be no difference in the frequency of use of postural and locomotory modes during various activities between males and females. However, I predicted that sex would influence the postural and locomotory behaviors used in each context, as such differences between the sexes have been observed in several primate species (Cant, 1987; Wheeler & Ungar, 2001).

(3) Do independent juveniles exhibit differing postural and locomotory behavioral frequencies according to different activities (i.e. feeding/foraging, travel, and rest) compared to adults/sub-adults?

My null hypothesis states that there will be no difference in the frequency of use of postural and locomotory modes during various activities between independent juveniles and sub-adults/adults. However, I hypothesized a difference would be observed. I predicted that juveniles would display increased clambering during travel and increased suspensory postures when foraging in comparison to adults/sub-adults. Their small size was expected to limit their reach of food items, leading to higher use of suspensory postures; moreover, juveniles tend to move in a clumsier manner when compared to adults, which I anticipated would lead to more clambering behavior (personal observation; Workman & Covert, 2005).

(4) Does the one-armed juvenile (JF) exhibit different postural and locomotory behaviors than *A. geoffroyi* with all functioning limbs?

My null hypothesis states that there will be no difference in postural and locomotory behaviors between JF and monkeys with all functioning limbs. While I predicted high amounts of suspension, I expected JF to exhibit higher amounts of tail-assisted suspension during foraging, as this would enable his available limbs to process food items. Moreover, amplified use of clamber was expected of this one-armed individual.

(5) Does the one-armed juvenile (JF) differ regarding associative social behavior compared to independent juveniles with all functioning limbs?

My null hypothesis states that there will be no difference in associative social behavior between JF and other, independent juveniles. Juvenile males increase time associating with older males around the independent juvenile stage (Vick, 2008). Due to the potential effects imposed by his disability on his social development, I expected JF to spend less time with older males when compared to other male juveniles.

(6) Does the one-armed juvenile (JF) differ in frequencies of play behavior compared to other independent juveniles?

My null hypothesis states that there will be no difference in the frequency of play behavior between JF and two-armed independent juveniles. Play behavior is believed to function in social learning; therefore, immatures typically perform play behavior more frequently than do older age-classes (Vick, 2008). As his disability may impair his social development, I expected JF to exhibit higher frequencies of play to combat its effects.

Significance:

Studies of positional behavior in living primates reveals functional associations with an animal’s postcranial morphology. Locomotor and postural habits of living non-human primates are often used as models to reconstruct similar behaviors in fossil primates (Mittermeier & Fleagle, 1976; Turnquist et al., 1999) since researchers only have the skeletal remains of extinct taxa. Extant species, therefore, are used as a reference point for hypothesizing about the behavior of extinct species (Garber & Pruetz, 1995). Examining their skeletal morphology in relation to locomotory behavior provides insight into the postural repertoire of extinct species (Mittermeier & Fleagle, 1976; Turnquist et al., 1999; Rein et al., 2014). However, these researchers must first have a collection of positional behavioral studies to provide a range of postural and locomotory modes specific to the various primate species. More accurate interpretations of extinct primate behavior can be made by increasing the available dataset. For instance, Rein et al. (2014) drew conclusions about a stem catarrhine, *Pliopithecus vindobonensis*, from the Miocene of central Europe following their analysis of relevant ulnae features in relation to suspensory behavior. They found this ancestral species to be behaviorally linked to the extant brown woolly monkey (*Lagothrix lagotricha*). The evolution of suspensory locomotion has allowed sympatric primates to occupy different niches, leading to increased diversification among species (Cant et al., 2001). This study will assist in examining the adaptive significance of suspensory postures and locomotion of spider monkeys, adding to the available data that better enables us to understand postural and locomotor behavior.

Understanding postural and locomotor behavior has implications for primate conservation as well. The large home ranges associated with suspensory locomotion and frugivory make spider monkeys particularly vulnerable to habitat disturbance. Moreover, the blend of slow life histories and lengthy gestation periods increases their vulnerability. Female spider monkeys are not considered sexually mature until they are about 5 years of age, and they have relatively lengthy gestation periods (7-7.5mo) and interbirth intervals (17-45mo) (Ramos-

Fernández & Wallace, 2008; Campbell & Gibson, 2008; Rowe, 1996). The combination of these factors leads to a low intrinsic rate of population increase for spider monkey species, which may considerably limit their ability to recover from habitat disturbances (Ramos-Fernández & Wallace, 2008). This study will provide insight into habitat use of *A. geoffroyi* through observations of its locomotive behaviors, such as suspensory locomotion. Providing data on the prominence of such behavior in this community, and their implications for the importance of continuous forest, can corroborate conservation initiatives.

Summary:

Primates employ various locomotory and postural behaviors to ensure optimal exploitation of their environment throughout their day-to-day activities (Youlatos, 2002). This study provides new data on the positional behavior of spider monkeys in a typical but not well-studied habitat for the species. The study site, EZBFS in Costa Rica, includes relatively undisturbed lowland, swamp forest but also areas of regenerating forest following anthropogenic disturbance in the form of logging. Results can be used to corroborate existing and future studies on large-bodied, arboreal species in an effort to better understand locomotor behavior in areas where the anthropogenic disturbance likely illustrates the continuing trend in forest disturbance in Latin America and worldwide. In addition, such data can assist conservation initiatives through insight into the importance of continuous forest in the ranging of *A. geoffroyi*, based on observations of the prominence of various types of suspensory locomotion.

The data presented here also include opportunistic recordings of the postural and locomotor behavior of a one-armed juvenile male (JF). Though it remains unknown as to how this deformity occurred, one can speculate its cause as possibly induced by genetic mutation, environmental factors, predation, intraspecies aggression, accident, or disease (Turner, Noburhara, & Matthews, 2008; Rainwater et al., 2009; Valero et al., 2006; Gibson et al., 2008). I systematically examined his postural and locomotor behavior in comparison to his fellow able-bodied community members. Detailing his positional behavior will add insight into how primates adjust to physical deformities, a relatively understudied aspect of primatology. Whether or not his disability influenced aspects of his social behavior was also of interest. Including him in this study expands the range of positional data available on disabled primates in the wild and can inform our understanding of behavioral adjustments to such disabilities. Systematic data collection allows comparison to the able-bodied members of his community. Overall, their postural and locomotory modes provide further insights into the array of positional behaviors utilized in this understudied habitat and can aid future positional behavior studies, as well as studies on extinct taxa.

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CHAPTER 2

PRIMATE DISABILITIES

Spider monkeys (*Ateles* spp.) are characterized by high mobility, suspensory locomotion. Visualizing this hand-over-hand mode of travel, it is difficult to contemplate a spider monkey surviving for long with an injured or atrophied limb, but this is in fact the case regarding a subject in the current study. At El Zota Biological Field Station (EZBFS) in northern Costa Rica, a juvenile male black-handed spider monkey (*A. geoffroyi*) has survived despite missing his right arm. This individual was discovered as an independent (weaned) juvenile male in the summer of 2014 and found again in June 2015. This has sparked the question of how this deformation occurred. The question becomes even more intriguing considering this is not the only case recorded at El Zota. In July 2006, a juvenile female spider monkey at the same site was recorded as missing her left arm (S. Lindshield, personal communication). Were these individuals' lost limbs due to genetic mutation, environmental factors, predator escape, intraspecies conflict, accident, or disease? Some of these possibilities also might be linked to anthropogenic impacts on the environment.

The focus of this chapter is to delve into the potential sources of these deformations as well as the potentially associated impacts on the individuals and their respective communities. First, I will focus on various forms of injury a primate can endure and discuss the probability of such incidents in the case at EZBFS. The prospect of anthropogenic influences through hunting, pesticide use, and habitat destruction will be assessed as well. Understanding the roots of such abnormalities, how they affect species overall, and how individuals adjust to disabilities are important to examine for both evolutionarily and conservation purposes.

Conflict, accident and infection

The missing limbs of these young spider monkeys could be the result of injury through conflict or accident, a common form of injury to wild primates (Jurmain, 1997; Valero et al., 2006; Carter et al., 2008; Gibson et al., 2008; Rimbach et al., 2012; Beamish & O’Riain, 2014). Spider monkeys have few predators, such as jaguars (*Panthera onca*) and boa constrictors (*Boa constrictor*) (Lindshield, 2006), due to their large size, mobility, and arboreal lifestyle, making interspecific conflict a less likely cause of JF’s disability. However, injury as a result of intraspecific conflict or contact with humans may be a more likely scenario. Proximity to humans can play a major role in primate injury, whether through hunting or defense of resources. Beamish and O’Riain (2014) studied groups of chacma baboons (*Papio ursinus*) residing in the Cape Peninsula, South Africa with home ranges overlapping human residential areas. In these troops, 15% of the baboons were disabled in some way, typically due to human-induced injuries. Disabled and uninjured individuals differed in activity budgets in that the former performed higher frequencies of rest and travel but lower frequencies of foraging than the uninjured baboons. Moreover, disabled individuals fed more often on higher quality foods with less handling costs, which the authors noted may necessitate the raiding of high-return food items originating from human activity (Beamish & O’Riain, 2014). The researchers did not find a difference in survival between the able-bodied and disabled individuals. They posit that the lack of predators and access to food sources in the residential areas may offset the constraints placed by disability (Beamish & O’Riain, 2014). Life history data was collected over a 4-year period, so perhaps a longer study would indicate disparity in survival among injured and uninjured individuals. The presence of the researchers may have further inhibited retaliatory attacks by humans raided by the disabled baboons, amplifying raiding behavior and impacting survivability.

Survivability of predominantly terrestrial disabled individuals is likely to contrast with that of disabled, arboreal semibrachiators. Moreover, spider monkeys at EZBFS do not endure the same anthropogenic pressures that led to the injuries of these chacma baboons.

Injuries can be human-induced through other means as well. Human hunting strategies often leave animals wounded. Chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) most often fall injury to snares used by subsistence and bush meat hunters (Beamish & O'Riain, 2014). Often permanent, these injuries can lead to paralysis or partial or complete loss of the affected area (e.g. hand, foot, and/or limb). Behavioral flexibility allows modification of locomotor strategies, but injured individuals are often recorded as moving slower or more awkwardly than those without injury. Foraging efficiency can be inhibited by forelimb or hand injury where manual processing of food is necessary. However, studies of gorillas and chimpanzees reveal moderately novel foraging techniques by injured individuals (Byrne & Stokes, 2002; Beamish & O'Riain, 2014). For instance, the use of dexterous feet during bimanual food processing was infrequent by able-bodied chimpanzees, but apes with injured hands or forelimbs employed this technique significantly more.

While snare injuries are unlikely for arboreal primates, spider monkeys are common targets of subsistence hunters and for the pet trade. They are often considered more palatable than other primate species, and their large size makes them targets in rural areas (Ramos-Fernández & Wallace, 2008). Hunting at EZBFS is uncommon due to the private ownership of the land and frequent occupation by researchers, but station workers and researchers do occasionally come in contact with poachers. While this is infrequent, it gives credence to the possibility that JF's injury was human-induced.

In some cases, injury can lead to infection of the affected area, which can result in natural loss of limb, disease or, in captive situations, amputation. Documented instances of missing limbs have primarily come from captive studies. The Lincoln Park Zoo housed a one-armed, white-cheeked gibbon, Kien Nahn, whose untreatable injury led to amputation at the elbow (Sayer et al., 2007). A study by Sayer et al. (2007) set out to observe behavioral differences between the disabled gibbon and the others in his enclosure. His adjustments are of particular interest due to gibbons' extensive use of suspensory locomotion, predominantly brachiation. These primates utilize this type of forelimb suspension for approximately 50-80% of locomotion (Rein et al., 2015; Arias-Martorell et al., 2015; Hunt, 1991). While it is more energetically expensive to employ one-armed brachiation, modifying such movement may be essential in coping with injury (Sayer et al., 2007). Having this ability to modify would lessen the necessary behavioral adjustments of an injured individual in his natural environment. There is no documentation or acknowledgement of limb amputation at EZBFS, but it is possible that infection after severe injury played a role in this loss. Kien Nahn's reported behavior may be a good model for comparison due to the behavioral similarities between gibbons and spider monkeys. However, one must take the differing pressures placed on wild versus captive primates into consideration when making such comparisons. The limb injury Kien Nahn incurred was an unfortunate and accidental incident that could likely occur in wild gibbons or spider monkeys due to their rapidity of locomotion. Skeletal analyses of wild chimpanzees have indicated the prominence of falls from the canopy as a means of injury and mortality (Carter et al., 2008; Jurmain, 1997). While many of the falls were fatal, the healing patterns of some specimens indicated survival from multiple falls, though fractures were often severe (Carter et al., 2008; Jurmain, 1997; Zihlman, Morbeck, & Goodall, 1990).

Deliberate harm, as opposed to Kien Nahn's unintentional wound, may arise from individuals of the same community. Forced copulations and infanticide have been reported in spider monkeys, although rarely (Gibson et al., 2008; Rimbach et al., 2012). Gibson et al. (2008) documented one observed and two presumed cases of infanticide in *A. geoffroyi* and one observed case in *A. belzebuth*. The victims in each case were young infants whose mothers resumed regular reproductive cycling directly following their deaths. The first observation of infanticide by Gibson et al. (2008) took place in Punta Laguna, Mexico. An adult female black-handed spider monkey and her 3-week-old male infant were attacked by the alpha male, leaving the infant's upper arm with a bite wound. The researchers report intense screams coming from the young male, and describe his arm as "dangling from his body" (Gibson et al., 2008, p. 487). While the infant was left alive the day of the attack, his mother was observed carrying his corpse the following day during travel and social encounters. Two other suspected infanticides occurred at this site during the same field season. Both cases resembled the observed instances of infanticide based on the wounds inflicted. One infant suffered a severe injury to its upper arm, while the other received trauma to one of its legs. Wounds appeared to be the result of a bite. The bodies were never recovered, but death was presumed once the mothers were observed without their infants. *Ateles belzebuth* also exhibited infanticidal behavior at Cocha Cashu Biological Station in Peru (Gibson et al., 2008). Similar to the case at Punta Laguna, the infant killed suffered trauma to the right arm. Its arm was left attached by only a minor piece of tissue, as it was severed through muscle and skin slightly below the shoulder joint. The missing right limb seen at EZBFS may possibly represent a case of a failed infanticide attempt, as all cases described above involve the severed limb of a young male. Surviving such brutality seems unlikely based on the examples above, but it is possible JF is a rare exception. The presence of a second immature *Ateles* with a similar disability at the same site, however, would make the chances of such an explanation slim.

JF was not discovered as a one-armed individual until the summer of 2014, when he was an independent juvenile. It is unknown whether he was born with his disability or whether it is the result of circumstances during his early life. As indicated above, it is possible he sustained this condition from a failed infanticide attempt; however, spider monkeys also display other types of intragroup aggression. Valero et al. (2006) relay a rare, intragroup coalitionary aggressive attack on a weaned male spider monkey. The high relatedness and affiliative nature of male spider monkeys helps explain why this behavior is seldom observed. However, the few times researchers have witnessed adult males direct aggressive attacks toward younger, weaned males, it has led to the death of the latter (Valero et al., 2006). The authors proposed three possible explanations for the agonistic behavior: mate competition, competition over food, or improper behavior of the young male to the higher ranking males. Having been detected in an already healed state, it is impossible to know whether JF sustained injury in this way. I observed two instances of male aggression directed at him, as well as a few cases of male agonism aimed toward both subadult males and females (see Chapter 5). Male spider monkeys at EZBFS regularly traveled together and often enacted the aggressive encounters collectively. Fedigan and Baxter (1984) indicated a higher likelihood of juvenile males receiving aggression from others in their community compared to young females (Fedigan & Baxter, 1984; Shimooka, Campbell, & Di Fiore, 2008). While the agonism I observed was not severe, the possibility of a coalitionary attack seems more probable.

Environmental and genetic factors

The cases of limb deformity observed at EZBFS could be the result of factors prior to birth. *Ateles geoffroyi* live in highly disturbed regions due primarily to agricultural expansion. Fagan et al. (2013) show that though mature forest loss decreased in Costa Rica by approximately 50% with the 1996 deforestation ban, expansion of agriculture increased from 4.5% to 13.3%, with pineapple plantations being the most dominant cropland. The deforestation law's definition of a forest permits re-direction of cropland expansion toward areas of regenerating forest. This places additional stress on these primates by means of habitat destruction and pesticide exposure. Congenital malformations result from numerous circumstances, as evidenced by both pesticide exposure and inbreeding depression. Pesticides have been linked to malformations in humans (Rao & Schwetz, 1982; Kupfer & Bulger, 1982; Multinger et al., 2008) and are suggested as the root for congenital malformations in some primate species as well (Rao & Schwetz, 1982: unspecified genus and species; Turner, 2005; Turner et al., 2008; Turner, 2010: *Macaca fuscata*). Moreover, increased habitat destruction may lead to reduced gene flow between spider monkey populations. Various deformities have been associated with inbreeding, making it a probable cause of the malformations observed at EZBFS (Charpentier et al., 2007). This section will detail the associations and effects of pesticide exposure and inbreeding depression on primate populations.

Spider monkeys are likely vulnerable to the hazards related to pesticides, as non-human primates have been observed showing negative consequences of such exposure. Rainwater et al. (2009) observed the effects of environmental contamination on the health and survival of ring-tailed lemurs (*Lemur catta*) in Madagascar. The researchers were able to collect blood samples from 26 individuals and hair samples from 65 individuals. After performing an organochlorine analysis, 14 OC pesticide compounds were detected in these samples. According to the study, the pesticides p,p’-DDT, heptachlor, aldrin, heptachlor epoxide, endrin aldehyde, and endrin were predominantly detected in the samples (Rainwater et al., 2009), and such compounds have been associated with acute poisoning and impacted fertility. Contamination is attributed here to ingestion and maternal transfer (e.g. breast milk) as the most significant routes of exposure. Pollutants may be ingested if contaminated water or food items are consumed, though this may also occur during grooming if fur is contaminated as a result of aerial deposition (Rainwater et al., 2009). These lemurs’ diet consists mainly of leaves, stalks, flowers, and fruits of various plant species, and pollutants that are air-borne are regularly accumulated on plant surfaces. Though the concentrations of organochlorines in lemur blood was somewhat low, we should not disregard how lemur health may be impacted by contaminants (Rainwater et al., 2009). Perhaps further study can help shed light on the effects on primate health, and improve and enforce regulations on pesticide use.

The ring-tailed lemurs do not appear malformed, but they do represent an example of pesticides impacting a primate species. Perhaps the methods used in the previous study would be beneficial in the cases of congenital malformation seen in Japanese macaques (*Macaca fuscata*). Multiple studies on the free-ranging, provisioned population of Japanese macaques of the Awajishima Monkey Center (AMC) have been carried out (Turner, 2010; Turner et al., 2008; Turner, Gould, & Duffus, 2005). This population has included individuals with congenital limb malformations (CLMs) for nearly 50 years. According to Turner et al. (2008), 16.1% of AMC infants were born with CLMs, which can vary from minor differences in the structure and mobility of digits to the lack of whole limbs. Though the cause of the deformities in these monkeys is unclear, CLM can be caused by genetic or environmental factors or can result from a combination of both. These malformations have largely been attributed to anthropogenic effects, as early primate studies did not report any such congenital or hereditary anomalies. Reports of the high prevalence of CLMs began appearing within the last 50 years.

Though the etiology of Japanese macaque limb malformation has yet to be established, researchers have indicated organochlorine pesticides as a possible source (Turner et al., 2008). Examination of bodies of deceased monkeys with CLMs, as well as mothers of infants with CLMS, revealed significantly higher amounts of organochlorine pesticide residue than observed in morphologically normal monkeys (Turner, 2010). Habitat reduction, fragmentation and degradation due to human action may also play a role in its prevalence, as this may increase population isolation and inbreeding (Turner et al., 2005). More data need to be collected regarding the consequences of such physical impairment. Turner's dissertation research (2010) showed behavioral flexibility and innovation by CLM macaques, such as including higher frequencies of rest but lower frequencies of social activity, as well as developing unique locomotor and grooming behaviors. Moreover, able-bodied monkeys in the group were tolerant of disabled individuals, and appeared indifferent to their condition.

Turner et al. (2005) examined the survival of deformed infants, and found that mothers altered their behavior to aid infants incapable of ventral clinging during locomotion. Due to the lack of predators and constant availability of food at AMC, mothers were flexible in their ability to increase their investment in offspring. With the importance of suspensory travel in spider monkey communities, this type of adjustment does not seem to be as reasonable of an assumption to make of mothers. Japanese macaques are semi-terrestrial primates, making this type of aid appear more feasible than would be in the fast paced, arboreal lifestyle of *Ateles* spp. Moreover, the Japanese macaques in Turner's study are largely provisioned and have relatively low predation levels (Turner et al., 2005; Turner et al., 2008). This is not the case in wild *A. geoffroyi*, whose ranging behavior is dependent upon resource availability (Wallace, 2008). Adult females may not have the excess energy required of increased maternal investment, especially if combined with the additional stress due to habitat loss. JF and his mother may represent an atypical circumstance in this regard. Should JF's malformation be found as products of pesticide exposure, then such exposure may critically alter his survivability, as well as that of future offspring in the community. Analysis of blood or fecal samples of the spider monkeys at El Zota may allow us to determine the effects of pesticide contamination on this community (L. Knapp, personal communication).

A look into how other non-human primates are influenced by external contaminants allows us to make assumptions about additional primate species. Black-handed spider monkeys are scattered across Central America and along the western coast of South America (Collins, 2008). Tropical locations are ideal for banana cultivation and other plantations due to their nutrient rich soils, placing *A. geoffroyi* in proximity to plantations using excessive amounts of pesticides (Henriques et al., 1997). Banana bunches are bagged with pesticide-lined bags for protection against various pests, like insects (Henriques et al., 1997; Castillo, Ruepert, & Solis, 2000). To improve banana cultivation, there are drainage systems created to allow runoff into local river systems (Henriques et al., 1997). Though the drainage systems enhance crop growth, the pesticide-lined bags occasionally fall from the bunches and into the drainage ditches. The chemicals then are transferred from the lining to the ditches, eventually flowing into the nearby river systems (Castillo et al., 2000). High rainfall in these areas increases contamination risk (Henriques et al., 1997). Castillo et al. (2000) found that the pesticide residues in surface waters and sediments of the La Suerte River Basin drain into the Tortuguero conservation area, which is approximately 20 km from El Zota Biological Field Station (Lindshield, 2006)

Application techniques can also increase spider monkey exposure to potentially harmful chemicals. Aerial application, for instance, can quickly deliver pesticides to large regions, but may also reach unintended targets. This may increase wildlife risk of hazardous ingestion. Mantled howling monkeys (*Alouatta palliata*) sympatric with black-handed spider monkeys at EZBFS may have experienced this form of contamination, as is evidenced from the frequency of individuals exhibiting patches of skin and hair lacking melanin, though more research needs completed before further confirmation (J. D. Pruetz, personal communication; R. Gómez, personal communication). Though all howlers observed to date retain functioning limbs, many individuals have displayed such pigmentation abnormalities (Figure 2.1).

Figure 2.1: Mantled Howling Monkey (*Alouatta palliata*) displays depigmentation on tip of tail.
Photo credit: N. Black

This pattern is not unique to EZBFS. In the summer of 2013, I witnessed this trait at a field site (La Suerte Biological Field Station) located in the same region of Costa Rica. Due to large numbers of banana plantations in this region, pesticide exposure has been suggested as a potential cause for the discoloration, though research has yet to be published on the subject (J. D. Pruetz, personal communication).

Spider monkeys are highly vulnerable to disturbances as a factor of their slow life histories, frugivorous diet, and long ranging patterns. Reduction of population sizes and geographic distribution result from both habitat loss and degradation (Ramos-Fernández & Wallace, 2008). Loss driven by agricultural expansion and land clearance contribute significantly to deforestation rates in Latin America. The clearing of forest for plantation sites is a direct disturbance placed on these, and many other, primates, and such disruptions critically threaten the survival of most primate populations (Cowlishaw & Dunbar, 2000; Strier, 2011). Highly fragmented forested areas cause populations to decrease in size and become isolated (Cowlishaw & Dunbar, 2000; Strier, 2011; Ramos-Fernández & Wallace, 2008). As a result of habitat isolation, spider monkey females are unable to disperse due to a lack of connectivity to other populations. This leads to a higher likelihood of inbreeding and lower genetic variation within the population (Cowlishaw & Dunbar, 2000).

Low levels of genetic variation typically have negative implications for population viability, as populations with little diversity become virtually unable to cope with disturbances. Congenital malformations as well as disease susceptibility have been associated with inbreeding depression. Charpentier et al. (2007) outlines cases of congenital malformations related to inbreeding depression cited in studies of captive-bred primates conducted from the 1980s to the early 2000s. They include limb malformations in rhesus and Japanese macaques; polydactylism, syndactylism and dwarfism similar to achondroplasia in neonatal tamarins; blind males and females that anencephalic and acranial in rhesus macaques; and functionally infertile, fused labia in common marmosets (Charpentier et al., 2007). While inbreeding depression was cited as the likely source of these deformities, inbreeding was not quantified by the researchers. Intensification of inbreeding leads to higher levels of infant mortality, as well (Cowlishaw & Dunbar, 2000; Charpentier et al., 2008; Hagell, Whipple, & Chambers, 2013). The blend of slow life histories and lengthy gestation periods and interbirth intervals of spider monkeys in conjunction with low infant survivorship will increase vulnerability to extinction by demographic disturbance.

Aside from physical deformities, highly inbred primates have shown increased susceptibility to parasitism than populations with more genetic diversity (Charpentier et al., 2008). Studies of ring-tailed lemurs housed in semi-natural conditions found that more heterozygous adults were less inclined to infection by *Cuterebra* larvae than the more homozygous adults (Charpentier et al., 2008). Moreover, reduced fitness of inbred individuals was reflected in their higher mortality rates. These factors jointly have implications for conservation efforts.

A case study by Hagell, Whipple and Chambers (2013) analyzing the impacts of habitat loss on genetic diversity examined a wild population of *A. geoffroyi* in Nicaragua. The study consisted of 185 individuals across 15 study sites on the River Isthmus (50,000 ha area). By extracting DNA from collected fecal samples, they were able to conclude that forest-dependent spider monkey populations undergo genetic consequences from increased human pressures on their habitat (Hagel et al., 2013). The researchers found lower levels of heterozygosity than random mating would suggest and lower than what is found in other populations of spider monkeys. Results suggest the occurrence of intense localized mating that is negatively impacting overall genetic diversity. A relatively recent decrease in gene flow and risk from inbreeding are likely revealed by this trend. The long history of anthropogenic disturbance in these areas is thought to have accelerated this decline. This species is facing habitat isolation and population declines, which is leading to decreased genetic diversity and increased variation among social groups. Therefore, it is crucial to maintain gene flow between populations. Species viability may be enhanced by increasing connectivity with other populations in the area.

The primates at EZBFS are at an increasing risk of facing habitat isolation. Native and planted trees on the property are being cut for carbon offset management schemes (personal observation). The station owner has teamed up with a carbon dioxide offset program, Reforest the Tropics (RTT), designed to mitigate climate change. Businesses partner with RTT to help reach sustainability goals by offsetting their CO2 output with the planting of RTT forests. Local partners receive benefits when it comes time to thin the RTT forests, as they are given the opportunity to sell the lumber. While this program gives a positive impression, making room for the RTT trees has led to the decimation of patches of regenerating native forest at El Zota. There are currently large, empty patches of land where native and planted trees once stood and where non-native, RTT trees are in the beginning stages of growth. It is unknown whether these new trees will be used by wildlife as corridors, but currently they are faced with recently vacant areas disrupting their habitat.

Conclusion

Various processes can leave primates physically altered. This chapter examined some of the mechanisms leading to primate disabilities, both before birth and during early life, in order to speculate about sources of the deformities witnessed at El Zota. Spider monkeys maintain slow life histories and are highly vulnerable to outside disturbances, making recover from external threats improbable (Ramos-Fernández & Wallace, 2008; Rowe, 1996; Cowlishaw & Dunbar, 2000). Therefore, it is important to analyze primates' ability to adjust to disabilities in the wild, particularly with increasing anthropogenic impacts on wildlife.

Genetic studies have the potential to further indicate probable cause of the malformations observed at EZBFS. These studies could provide data on relatedness, revealing possible inbreeding. Blood samples, while difficult to obtain, can expose lingering toxins should they be present. Pesticides have been connected to reproductive complications in both human and non-human primates (Rao & Schwetz, 1982; Kupfer & Bulger, 1982; Multinger et al., 2008; Henriques et al., 1997; Turner et al., 2005). These cases reveal that limb malformation is a possible side effect to intense pesticide exposure and could possibly be linked to the missing limbs of the EZBFS spider monkeys. Other reproductive and health implications from exposure may lower infant survivorship, reducing probability of species persistence. These data are imperative when devising conservation plans.

We cannot definitively know the exact cause of the missing limbs in *Ateles* at EZBFS, but additional studies can bolster certain speculations. Injury may be deduced as the likely cause if evidence suggests a low probability of inbreeding or absence of toxin contamination. Moreover, low incidence of hunting in the area and the arboreal nature of spider monkeys makes hunter traps less probable. Infanticide and lethal aggression have both been recorded in wild *Ateles geoffroyi* populations (Gibson et al., 2008; Valero et al., 2006). The reported targets of such aggression have not survived, but perhaps rare circumstances permit survival. Indication of additional cases of male-directed aggression may offer information about *A. geoffroyi* population dynamics. The examples provided throughout this chapter help illustrate various processes that could have led to the disabilities found at El Zota.

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CHAPTER 3

RESEARCH METHODOLOGY

This chapter will detail the methodology used to complete this research. Data on black-handed spider monkeys (*A. geoffroyi*) were collected at El Zota Biological Field Station, Costa Rica, from May 28 to August 4, 2015 to test hypotheses related to posture and locomotion. Monkeys were observed using standardized methods of observational data collection (Altmann, 1974). Instantaneous focal animal sampling was used to collect systematic data samples with which I compared to previous studies of posture and locomotion on this genus. I considered variables such as sex, age-class, substrate size and inclination, crown zone, and locomotor and postural modes during travel, rest and feeding. Furthermore, data on a one-armed spider monkey at the site were recorded using the same methods as those used on the individuals with all functioning limbs to examine the effects that such a disability might have on this individual.

Study Site

This study was conducted at El Zota Biological Field Station (EZBFS; 10° 33.437’, -83° 44.177’) in Northeastern Costa Rica (Figure 3.1). Formed in 2001, the station was the product of the cooperation of landowner Hiner Ramirez of Guapiles, Costa Rica, Dr. Jill Pruetz of Iowa State University, and Dr. Thomas LaDuke of East Stroudsburg University (Pruetz & LaDuke, 2001; Luckett, Danforth, Linsenbardt, Pruetz, 2004). The site contains about 700 ha of natural forest, comprised of lowland rainforest and lowland swamp forest, as well as regenerated forest areas (Lindshield, 2006). Swamp forest is characterized as a low-lying, poorly-drained habitat, while the better-drained areas are considered wet forest (Lindshield, 2006; Senf, 2009).

Approximately 8.5 km of trails have been established throughout the field station, spanning areas of primary and secondary forest, gallery forest, and plantations (Rodrigues, 2007; Lindshield, 2006). Rainfall averages about 4000 mm annually (Fernandes & Sanford, 1995).

The station is comprised of approximately 1000 ha, with roughly 270 ha consisting of planted native and non-native trees at the time the station was established (Luckett et al., 2004). As discussed in the previous chapter, a carbon offset program, Reforest the Tropics (RTT), has partnered with the station owner, which has led to the destruction of patches of regenerating natural forest for the planting of non-native, RTT trees. The cut areas consisted of both planted forest and regenerating natural vegetation. The planted trees were once a part of a sustainable tree harvesting initiative, consisting primarily of *Gmelina arborea*, a fast-growing Asian tree used for the production of paper pulp (Luckett et al., 2004). Natural forest has since regenerated, interspersing the areas of planted *Gmelina*, and primates utilized these trees as travel pathways (Luckett et al., 2004). The offset program was initiated to replace the non-native *Gmelina*, but regenerating native trees were cut, as well. While the non-native RTT trees have been planted, the cut areas are currently awaiting their growth (personal observation). These large, patches devoid of mature trees and canopy growth may influence ranging habits and food availability for the primates at this site especially.

Three sympatric primate species occupy the forest at EZBFS: black-handed spider monkeys (*Ateles geoffroyi*), mantled howling monkeys (*Alouatta paliatta*), and white-faced capuchins (*Cebus capucinus*). Densities of the different species have been estimated as 6.0 capuchins/km^2, 8.4 howling monkeys/km^2, and 12.2 spider monkeys/km^2 (Lindshield, 2006; Rodrigues, 2007). Two spider monkey communities and an estimated two capuchin groups are present at El Zota, though there is not currently an updated estimate of howling monkey groups at the site (Rodrigues, Wittwer, & Kitchen, 2015). Sympatry of these three closely related primate species is possible because of their varied diets and subsequent ecological niche differentiation. In particular, the species vary as to their choice of fallback foods during times of resource scarcity (Hanya & Chapman, 2013). Mantled howling monkeys rely primarily on folivorous vegetation but can include fruit in their diet depending on availability (Milton, Casey, & Casey, 1979; Rowe, 1996; Luckett et al., 2004). Conversely, while black-handed spider monkeys consume leaves, they are highly frugivorous, and typically occupy the higher canopy, as a result, in addition to having long daily path lengths and large home ranges (Rowe, 1996; Luckett et al., 2004; Di Fiore, Link, & Dew, 2008). White-faced capuchins are known omnivores, and maintain a highly varied diet, comprised of, but not limited to, fruits, leaves, vertebrate prey, and insects (Rowe, 1996; Luckett et al., 2004; Mosdossy, Melin, & Fedigan, 2015). Interspecific associations and interactions have occasionally been observed between the three species (Rose et al., 2003; Rodrigues, 2007; Senf, 2009; personal observation). For instance, several times I observed an individual spider monkey traveling with a capuchin group. Moreover, there were numerous times when all three species fed in the same *Ficus* tree (personal observation). The nearby banana plantations are also periodic hosts to spider monkeys and capuchins, particularly when the forest trees lacked adequate fruit (Lindshield, 2006; personal observation).

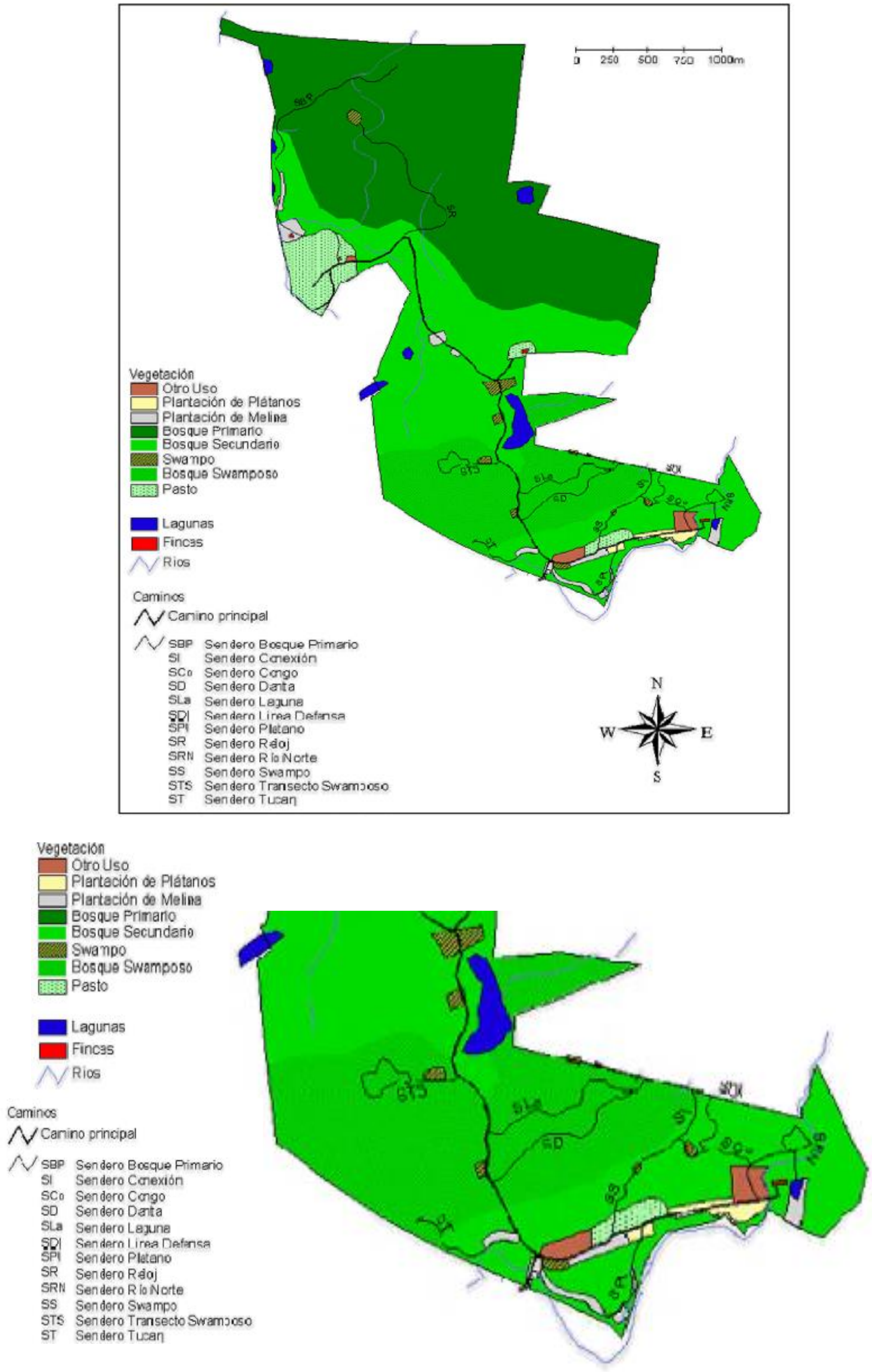

Figure 3.1: Map of El Zota Biological Field Station

Courtesy of Fiebelkom and Busse (unpublished data). The southern portion of the station is given in the lower map, as this is where the Pilón community ranges. Line transects' English interpretation are as follows: Sendero Bosque Primario (SBP) = Primary Forest Transect (PFT); Sendero Reloj (SR) = Watch Trail (WT); Sendero Transecto Swamposo (STS) = Swamp Forest Transect (SFT); Sendero Linea Defensa (SDI) = Fence Line Transect (FLT); Sendero Platano (SPI) = (SP)

Study Community and Individuals

It is estimated that two *Ateles* communities occupy the forests within and directly adjacent to the station (Pruetz & LaDuke, 2001; Lindshield, 2006; Rodrigues et al., 2015). This study focused on the well-habituated Pilón community, whose range includes the southern secondary forest area and neighboring properties, as well as the northwest and southeast portions of EZBFS (Pruetz & LaDuke, 2001; Lindshield, 2006; Rodrigues, 2007; Rodrigues et al., 2015). As of 2011, this community consisted of approximately 39-41 individuals: 17 adult or sub-adult females, 15 infants and juveniles, and 7–9 adult or sub-adult males (Rodrigues et al., 2015; Table 3.1). My data from the summer of 2015 indicate a similar community size: approximately 39-45 individuals, with 23-27 adult and sub-adult females, 8 adult and sub-adult males, and 8-10 infant and juvenile offspring. Significantly, this community contains a male juvenile-3 (JF) that is missing his right forearm.

Data Collection

Data were collected using instantaneous focal sampling from May 28 – August 4, 2015. The first eight days were used for preliminary data collection and identifying individuals. This allowed me to make any necessary methodological adjustments before actual data collection began. Official data collection occurred June 5 – August 4, 2015 (N=53.5 days). All spider monkeys (N=42) were individually identified by sex, size, pelage, and facial patterns.

Table 3.1: Breakdown of spider monkey age-classes

Class	Age range (mo.)	Pelage	Facial pigment	Travel	Feed	Social
Juvenile-1	15-24	Buffy reddish-brow; black hindlimbs & forelimbs	Decreasing pinkish areas replaced with black pigmentation	Mainly independent; bridging behavior & some dorsum travel	Nurse	N/A
Juvenile-2	24-36	Buffy reddish-brow; black hindlimbs & forelimbs	Decreasing pinkish areas replaced with black pigmentation	Independent; bridge behavior rare	Weaning	Males engage in embracing pectoral sniffling & scrotum sniffing among other males
Juvenile-3	36-50	Buffy reddish-brow; black hindlimbs & forelimbs	Decreasing pinkish areas replaced with black pigmentation	Independent	Weaned/ Independent	Mostly stay with mother; Males long-

						call; male sexual behavior
Subadult	50-65	Buffy reddish-brow; black hindlimbs & forelimbs; hair denser than adults	Decreasing pinkish areas replaced with black pigmentation	Independent	Independent	Frequently play with juveniles; females mostly stay with mother; males range independently of mother; male sexual behavior
Adult	65+	Buffy reddish-brow; black hindlimbs & forelimbs	Black face	Independent	Independent	Females mostly with other females & offspring or alone; all-male subgroups

Note: *Ateles* age-class characteristics adapted from van Roosmalen and Klein (1988) and Lindshield (2006).

Photographs and videos were taken of most individuals to assist in this process (See Appendix B for list of subjects). Certain individuals could be recognized based on an identification file provided by a field researcher who previously studied this community (M. Rodrigues, personal communication). To avoid researcher fatigue, approximately one day each week was reserved for rest and data summary; this summed to about 6.5 total rest days, not including delays due to heavy rainfall and lack of visibility.

A typical field day began around 4:30 AM, allowing me to enter the forest between 5:15-5:30AM. Extreme weather conditions occasionally led to unexpected delays in this onset. I intended to locate subgroups at their sleeping sites each morning; however, I more frequently encountered the monkeys once they began their morning movement. I originally proposed to stay with a subgroup for half a day, then find and follow a new subgroup for the remainder of the field day, but various factors often prevented this plan (e.g. swamps, weather, spider monkey travel patterns and speed). Due to the difficulty of locating individuals, the first subgroup discovered that day was followed until lost or until another appropriate subgroup/individual (i.e., one with individuals in need of more samples) was encountered. To maintain consistency between sample sizes for individuals, I tallied daily the number of samples per identified individual to prevent an abundance of data on a single subject. The uncertainty of finding a new subject created a dilemma regarding when to abandon a frequently sampled valuable subject. Higher encounter rates unavoidably fuel greater individual sample sizes of certain monkeys. Moreover, I had intended to put the monkeys “to bed” each night, yet the location of sleeping sites, as well as other factors, often prevented me from fulfilling this intent, resulting in field days ending between 3:30-6:00 PM.

Instantaneous focal animal sampling was employed throughout the study. All adult, sub-adult and independent juveniles in each party were sampled for 10 minutes, with data recorded at 30-second intervals. I also collected opportunistic data on the handicapped juvenile, JF, whenever he was encountered so as to compare his repertoire of positional behaviors to other members in his community, both within and outside his age-class. Individual subjects were cycled through relatively evenly during the time spent with each subgroup. Initial focal animals were chosen by selecting the nearest available individual to the right of the first sighted animal (following Lindshield, 2006). Nearest available individual to the left of the first sighted was selected if the former method proved spatiotemporally impossible. The first sighted subject was only selected if discovered alone, was the only available monkey in the subgroup (e.g. in a subgroup of an adult female and her infant; I could not collect samples on the latter), or was under sampled relative to others in its subgroup. Paterson (2001) states that only one third of sample time should consist of out-of-sight data. Therefore, if the focal animal becomes lost from view for six or more intervals, the sample should be discarded. However, I adjusted this value to my particular study to include up to eight out-of-sight data points due to the poor visibility offered by the emergent feeding trees at EZBFS, especially. The quick travel behavior of spider monkeys also influenced this decision, as it became difficult to obtain travel data with a threshold of only six out-of-sight instances. The amount of time between each interval was adequate to record each variable, as other positional behavior studies have used 20-second intervals (Cant, Youlatos, & Rose, 2001; Youlatos, 2002). I extended the interval time to 30-seconds to maintain intraobserver reliability (Paterson, 2001) under the conditions at EZBFS.

Measures

Data recorded comprised variables such as sex, age-class, substrate size and inclination, crown zone, and locomotor and postural modes during travel, rest and feeding. The recorded positional modes were consistent with those described by Hunt et al. (1996) to maintain uniformity with other positional behavior studies (See Appendix A for behavioral catalog). Behaviors were distinguished by context and positional categories. This allows analyses of postural repertoire employed during travel vs. during foraging. Contexts included were (1) foraging: seeking, obtaining and processing food items within single or contiguous feeding trees; (2) travel: moving to and from sleeping sites or between feeding sites; (3) rest: body relaxed and relatively motionless; and (4) play: solitary or social interaction through grappling, wrestling, lunging, or chase games (Youlatos, 2002; Rodrigues, 2007). An “other” category was included for behaviors that could not be classified into these select contexts, and “out of sight” was recorded if the individual was not visible at the sample interval. Positional behaviors were described within the context during which they occurred, and were distinguished by postural and locomotor modes for analysis. Locomotor modes were defined as the positional behaviors employed during movement, while postural behaviors were relatively motionless positions. Brachiation, clamber and quadrupedal walk/run are but a few behaviors that comprise the modes of locomotion (Table 3.2; Figure 3.2). Postural modes involved positions such as sit, squat and tail-only suspend (Table 3.3; Figure 3.3). For full inventory of these positions and associated descriptions, see the behavioral catalog in Appendix A.

Table 3.2: Definitions of main locomotor modes exhibited by *A. geoffroyi*

Locomotor Behavior	Definition
Brachiation	Below & along or across one or multiple supports via orthograde suspensory locomotion involving an alternate gait of the abducted & extended forelimbs & tail with extensive trunk rotation approaching 180◦
Clamber	Body displacement in various directions on & across multiple, diversely oriented supports with no particular gait; all appendages attach to substrates in different ways
Forelimb Swing	Below & along or across one or multiple supports via orthograde suspensory locomotion involving an alternate gait of the forelimbs & occasionally the tail with little trunk rotation
Quadrupedal Walk	Locomotion on top of supports angled at <45°; typically all the four limbs contact the support in a particular sequence.
Bridging	Gap-crossing mode involving secure retention of the initial supports by both hind limbs and tail, & cautiously pulling the body on the terminal supports across the gap
Leap	Gap crossing mode involving an extended period of free flight with propulsion provided by a simultaneous extension of the hindlimbs
Drop	Gap crossing mode involving a period of free flight with takeoff initiated usually by falling instead of active propulsion

Table 3.2 continued

Vertical Climb	**Continuous quadrupedal upward or downward movement along a single vertical support, typically angled at ≥45°**

Note: Definitions are taken from Hunt et al. (1996) and Youlatos (2002) with modifications by N.W.

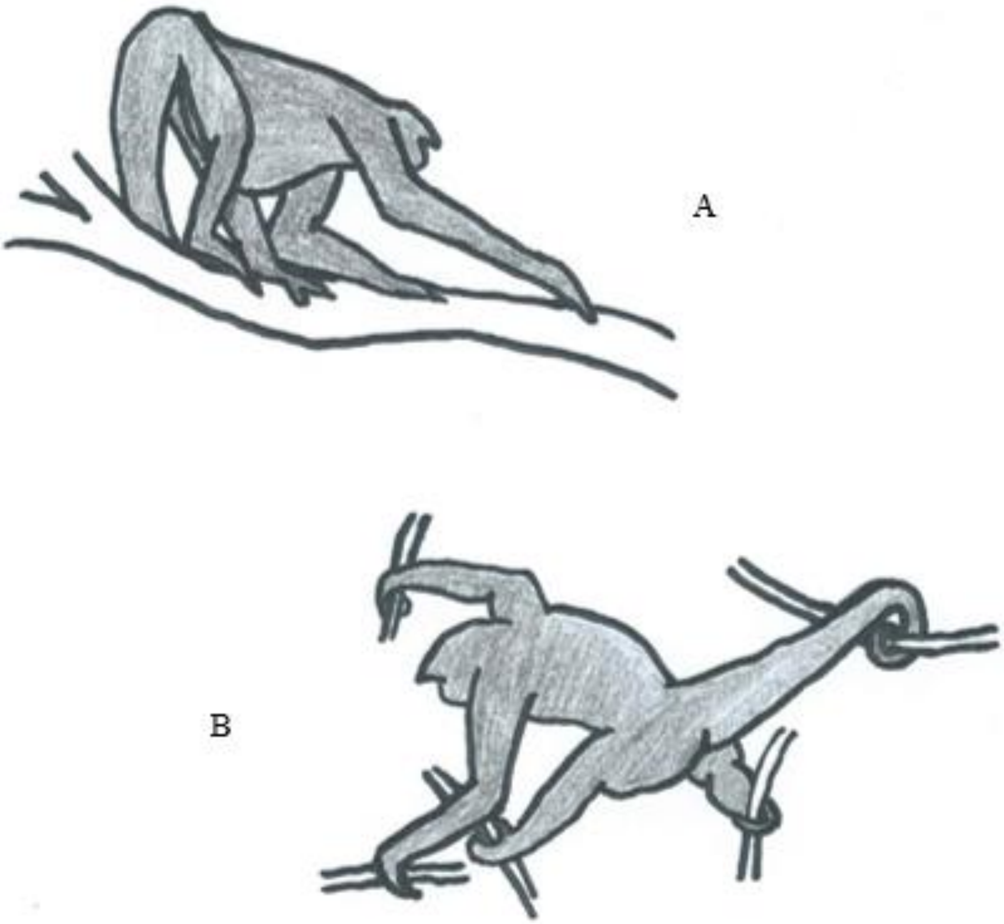

Figure 3.2: Frequent locomotor modes of *Ateles geoffroyi*

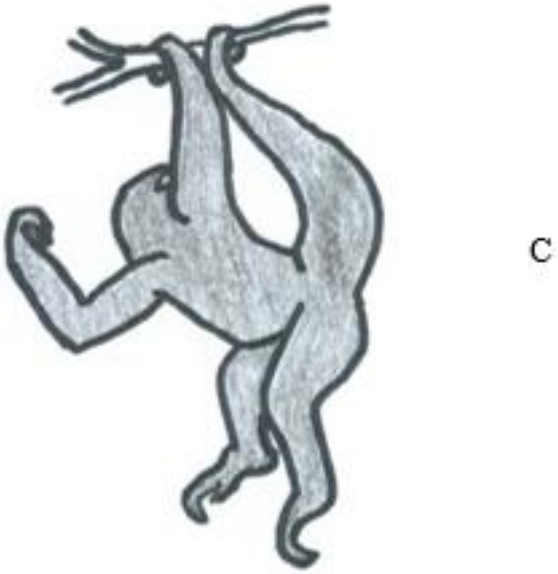

Figure 3.2 continued
Note: Modified based on Youlatos (2002). (A) quadrupedal walk; (B) clamber; (C) tail-arm brachiation

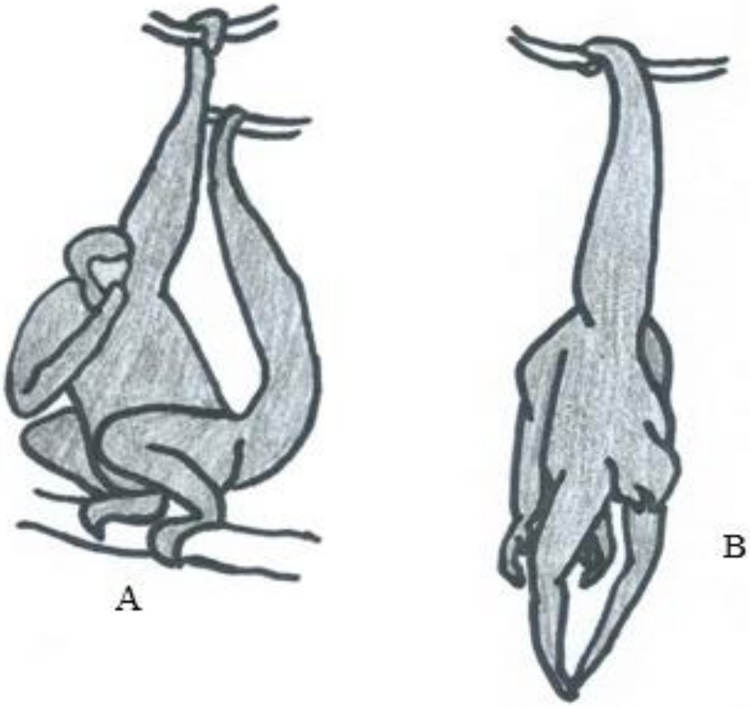

Figure 3.3: Frequent postural modes of *Ateles geoffroyi*

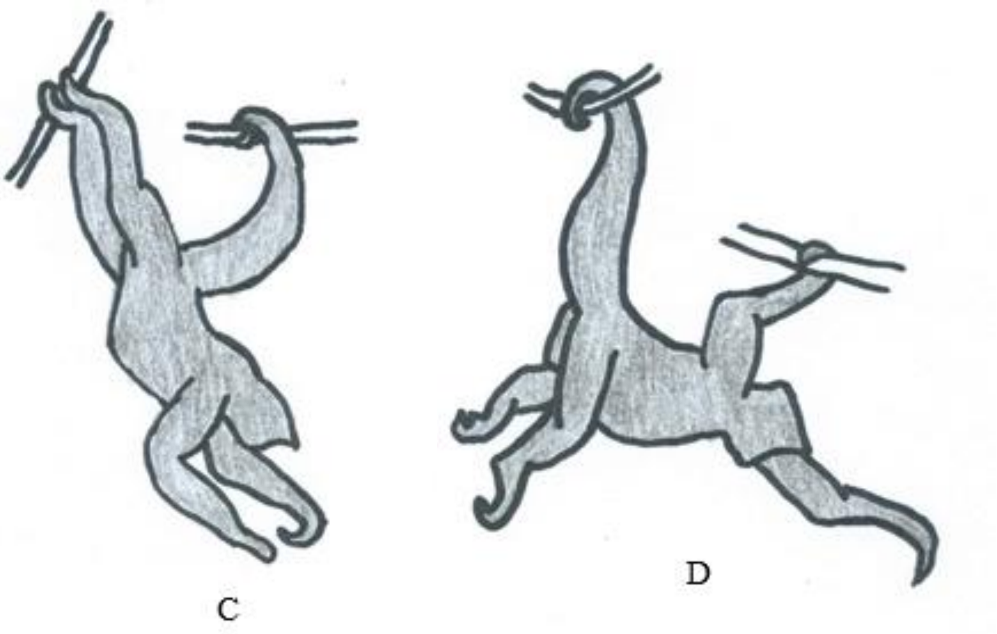

Figure 3.3 continued
Note: Modified based on Youlatos (2002); (A) squat; (B) tail-only hang; (C) tail-hindlimb hang; (D) tail-forelimb hang

Table 3.3: Definitions of main postural modes exhibited by *A. geoffroyi*

Postural Behavior	Definition
Sit	Ischia bear a substantial portion of body weight & torso is relatively orthograde
Squat	Body weight is borne solely by the feet, both hip & knee are strongly flexed. Substantial body weight not borne by forelimbs or ischia.
Lie	Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso

Table 3.3 continued

Stand	**Three or four-limbed standing on horizontal or subhorizontal supports; elbow & knee are (relatively) extended & trunk is near horizontal**
Bipedal Stand	Standing on the hindlimbs with no significant support from any other body part; hips & knees may be flexed or extended
Tail-Only Suspend	Suspension from the tail with little or no support from the limbs
Tail-Forelimb Suspend	At least an half the body weight is borne by the tail with significant weight borne by the forelimb(s).
Tail-Hindlimb Suspend	Suspension with substantial support from the extended hindlimb(s) and the tail
Vertical Cling	Adhering to a vertical support via strongly flexed forelimbs and hindlimbs

Note: Definitions are taken from Hunt et al. (1996) and Youlatos (2002) with modifications by N.W.

Select habitat variables were assessed during data collection. Support size was visually estimated through these four classes: small (≤2 cm), medium (>2 cm, ≤10 cm), large (>10 cm, ≤20 cm) and very large (>20 cm; Youlatos, 2002); however, due to concerns over intraobserver reliability, these data were not analyzed. Additionally, support inclination consistent with Youlatos (2002) was indicated: horizontal (0◦–10◦), moderate (10◦–45◦), steep (45◦–80◦), and vertical (80◦–90◦). Two tree crown zones were considered: the periphery and the center. The periphery includes the terminal branch zone, while the remainder of the crown and major branches are considered the central part (Youlatos, 2002). These definitions allow cross-study consistency with other *Ateles* spp. studies (Youlatos, 2002). Basic food type was noted, as well (i.e. fruit, leaves, flowers, epiphytes).

Around the juvenile stage, young males begin to associate with the older males of the community (Vick, 2008). I addressed whether the social behavior of the one-armed juvenile differed from that of the able-bodied juveniles. Therefore, I also noted my focal subject’s proximity to other individuals during feeding and resting. Spider monkeys travel in subgroups within their community, so I recorded travel companions accordingly. I specifically indicated the presence of nearest neighbors within a 1m and 2m radius. Frequency of general play activity was recorded, as well, due to its importance in the socialization process of young primates (Vick, 2008).

One-armed individual

I opportunistically sampled the one-armed juvenile male (JF) of the Pilón spider monkey community using the same systematic data collection measures described above (Figure 3.4). Upon encounter, the same recording methods were utilized to maintain uniformity throughout for comparison during analysis. His behavior required some modification of definitions, however, such as tripedal walk/run rather than quadrupedal walk/run. While JF did not have the physical ability to brachiate as others in his community, he created his own form of suspensory locomotion. These instances were scored the same as instances of brachiating by able-bodied individuals, yet the differences in form were descriptively noted. For example, JF attempted brachiation by employing his prehensile tail in place of the right arm. The first two weeks of the study were set aside for preliminary data collection, as I hoped to locate JF and note potential behaviors not anticipated in the established behavioral catalog during this time. However, JF was not located during this period, but this did not affect data collection.

Figure 3.4: One-armed juvenile individual (JF) foraging

JF proved somewhat elusive; thus I maintained my initial protocol and began following him even if recording focal data in a separate party. I decided to abandon a focal party's subjects based on JF's travel patterns (i.e., if he was soon to leave the area or if he looked to stay), and on the amount of time remaining in my current focal subject sample. If JF's travel activity appeared to subside, and less than three minutes remained in the sample, I completed the focal sample and next moved to sample JF. However, if JF continued highly active travel – not appearing to remain near my current focal party – and more than three minutes remained in my sample, I chose to abandon that sample and follow JF. To ensure I did not divert excessive observational time toward JF, when following his subgroup I alternated samples between him and other individuals. Subjects were chosen so as to equalize the amount of data collected for each individual.

Data Analysis

To analyze these data, multiple categorical variables and a lack of independence within samples had to be considered. Therefore, models were chosen to address these items. Monte Carlo inference about behavioral distribution across groups (i.e., sex, age-class or context) was used initially to account for multiple levels of dependence during the study. Within Monte Carlo inference, data were analyzed through Fisher's exact tests once independence was established. These analyses allowed me to examine my questions of whether positional behavior is associated with sex, age-class, or context. Behaviors were categorized as locomotor or postural and were subsequently considered separately. The established test statistic of group data was compared to the computed null data to determine significance of the distributions. Individuals were pooled, as not all individuals were identifiable (N=4 unidentified; N=37 identified). Samples occasionally stemmed from brief engagements, where the encounter with the monkey was long enough for a sample but not for reliable individual identification. Therefore, not every sample contained an identified individual. The model considered correlations within viewings to help account for outliers.

The behavioral distributions between the contexts of foraging and travel differed significantly, indicating that postural and locomotor modes are associated with the context in which they are used. Thus logistic regression was further employed to compare individual behaviors across these contexts to demonstrate which behaviors are most linked to activity (i.e., foraging or traveling). The behaviors were first categorized as locomotor or postural. To assess behavioral differences, generalized liner mixed effects models (GLMM) were applied, as the data were binary. The mixed model considers fixed (i.e., context) and random (i.e., viewing) effects and allows correlations to be assessed within each variable. This ensures that the results are not skewed by the contents of a single viewing. Rstudio was used in making these inferences.

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CHAPTER 4

RESULTS & DISCUSSION

This chapter will summarize and discuss the results of my analyses. The overall activity budget as well as sex-specific activity budgets of the spider monkeys in the Pilón community were analyzed to indicate where time is allocated throughout the day and if it differs between the sexes. Distributions of postural and locomotor behaviors were examined across groups (i.e. contexts, sexes, age-classes) for differences. Only the distributions across the contexts of foraging and travel differed significantly; thus these data were analyzed further to distinguish which specific behaviors led to this variation. These data revealed context specific behaviors in this species.

Results

A total of 123 h of instantaneous focal animal sampling (738 interval samples; 14,760 data points) were collected over the course of this study (males = 291 samples; females = 477 samples). After removing out-of-sight sample points and those of the one-armed individual (JF), 106.5 h of data (639 samples; 12,780 data points) were in the final analysis. The discrepancies between the sample number for male and females can be attributed to the higher number of females in the community. Approximately 27 adult/sub-adult females and 8 adult/sub-adult males comprise the study community. Three juvenile females and three juvenile males were also included in this data set. While the total amount of samples on both sexes varied, individual samples within sexes were relatively even. Data on individuals were pooled, as not all monkeys were identifiable to the level of the individual.

Activity budget

A high prevalence of foraging (40%) and resting (40%) characterizes the overall activity budget of individuals in the community (Figure 4.1). Travel accounted for approximately 19% of all activity. The difficulty in collecting travel samples during this relatively short study and in the challenging wet forest and swampy habitat may explain in part why travel was less than in some other spider monkey studies (Cant et al., 2001: *A. belzebuth*, Yasuní National Park; Graham et al., 2013: *A. geoffroyi*, Caño Palma Biological Station).

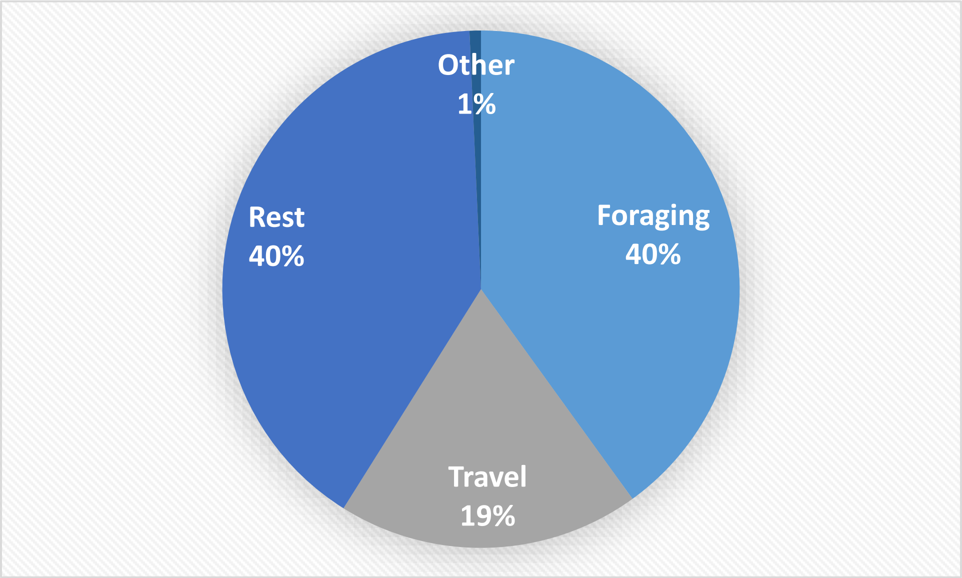

Figure 4.1: Overall activity budget for *A. geoffroyi* at El Zota Biological Field Station

Overall activity budgets of males and females were examined using chi-square tests with a significance level of 0.05 (Figure 4.2). The chi-square test indicates a significant difference in the activity budgets between the sexes ($p<0.05$), with males resting more than expected and females resting less (males=53%; females=33%). Females appear to forage more than males (males=29%; females=46%). However, with the low male sample size, these data could theoretically be skewed by individual male outliers, which pooling of individuals masks. Other abiotic factors during data collection, such as weather or time of day, may have also impacted these values. However, travel is similar between males and females (males=17%; females=20%).

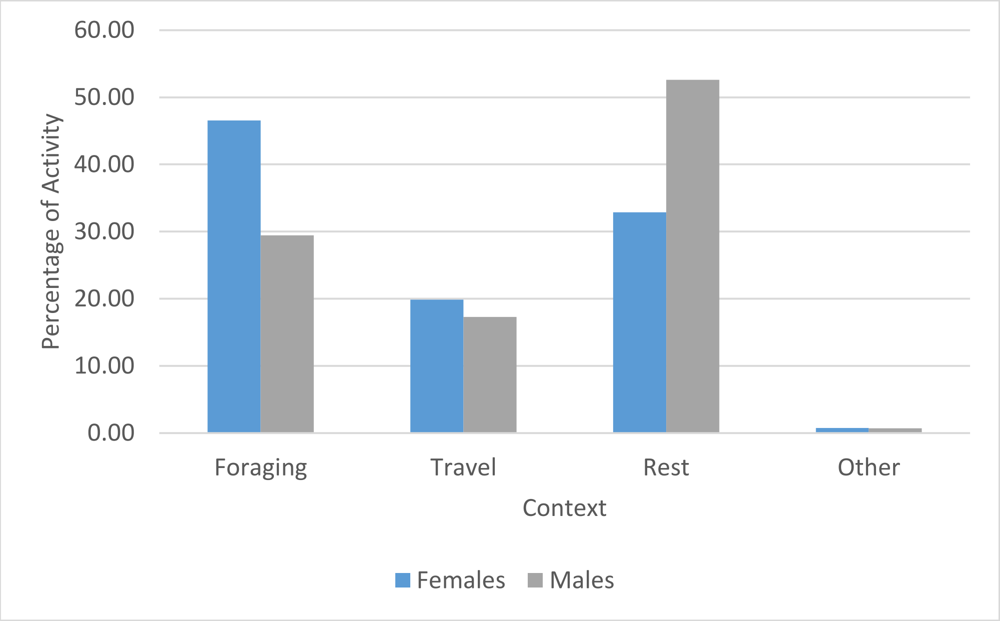

Figure 4.2: Male vs. female *A. geoffroyi* activity budgets at El Zota Biological Field Station

Locomotor behaviors

Instantaneous focal animal sampling was used to record the various locomotory modes used by subjects during travel and foraging. Probability of each locomotor mode was calculated in relation to the other locomotor behaviors, separate from postural modes. Distributions of modes of locomotion during travel and foraging were analyzed as a whole (Figure 4.3), as well as between the sexes (Figure 4.4) and age-classes (Figure 4.5) using Monte Carlo based inference across groups. No significant differences were found between the distributions of the sexes nor between age-classes. However, when all individuals were analyzed as a whole, the distribution of locomotory modes between the contexts were significantly different ($p<0.05$). Because of this divergence, logistic regression using a generalized linear mixed effects model (GLMM) was performed on these overall data (i.e. not distinguished by sex or age-class) to decipher differences between individual modes of locomotion rather than general distribution based on context. These data are summarized in Table 4.1. A significance level of 0.05 was used in this analysis. Logistic regression was not applied to the data separated by sex or age-class, as there were no significant differences between these distributions based on Monte Carlo analyses ($p>0.05$).

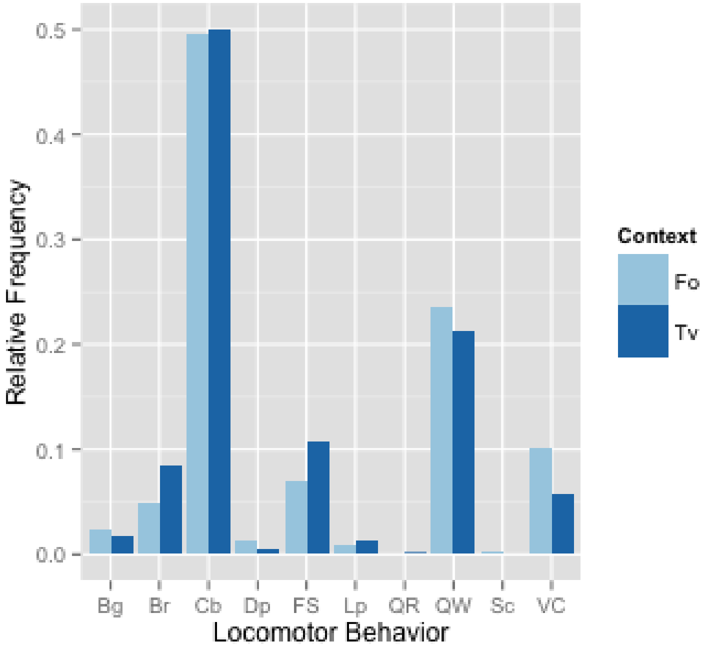

Figure 4.3: Distributions of locomotor behaviors between contexts of travel (Tv) and foraging (Fo)
Key: bridging (Bg), brachiation (Br), clamber (Cb), drop (Dp), forelimb swing (FS), leap (Lp), quadrupedal run (QR), quadrupedal walk (QW), scoot (Sc), vertical climb (VC)

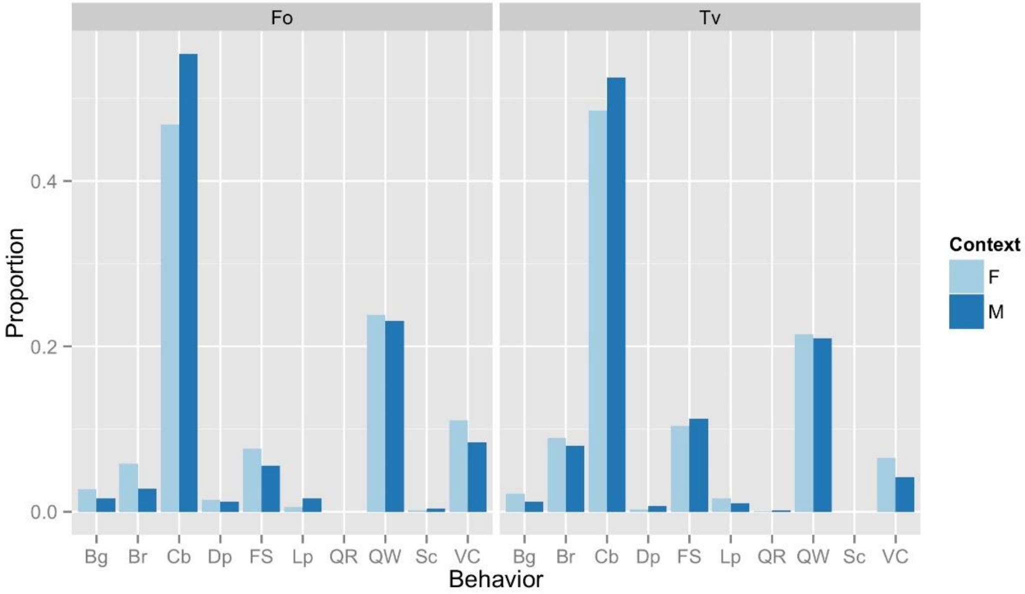

Figure 4.4: Distributions of locomotor behaviors between the sexes within the contexts of travel (Tv) and foraging (Fo)
Key: bridging (Bg), brachiation (Br), clamber (Cb), drop (Dp), forelimb swing (FS), leap (Lp), quadrupedal run (QR), quadrupedal walk (QW), scoot (Sc), vertical climb (VC)

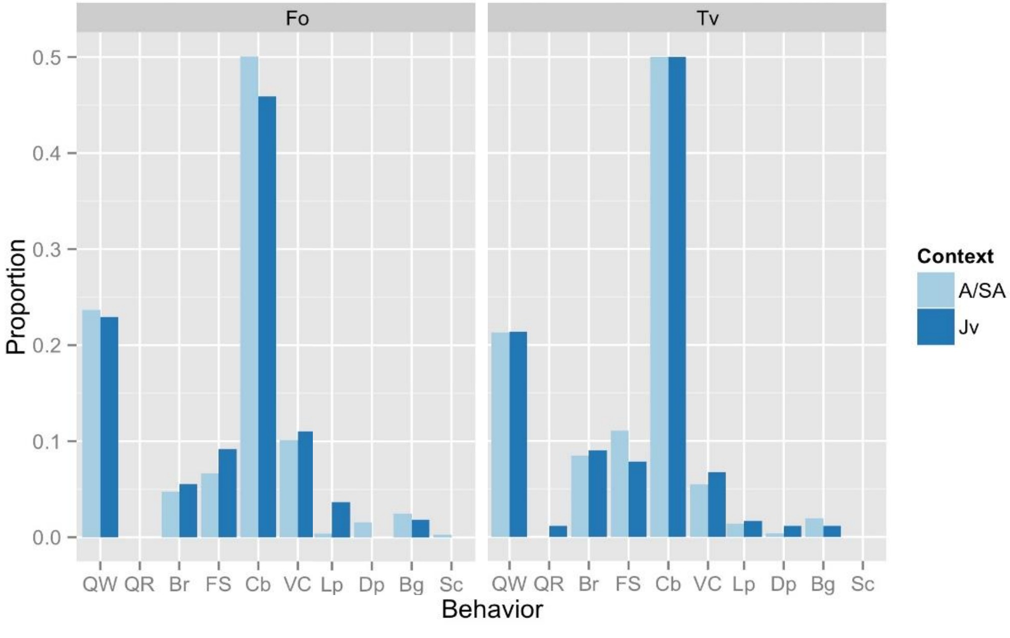

Figure 4.5: Distributions of locomotor behaviors between age-classes within the contexts of travel and foraging
Key: quadrupedal walk (QW), quadrupedal run (QR), brachiation (Br), forelimb swing (FS), clamber (Cb), vertical climb (VC), leap (Lp), drop (Dp), bridging (Bg), scoot (Sc)

Of the different types of locomotion recorded, clamber was the most frequent during both foraging (49.53%) and travel (50.0%). Quadrupedal walk occurred at a relatively high frequency in both travel (22%) and foraging (23.57%). The differences in the use of these locomotor modes between contexts is not significant ($p>0.05$). Brachiation (Br) and forelimb swing (FS) movements were used significantly more frequently during travel (Br=8.49%; FS=10.49%) than in foraging (Br=4.82%; FS=6.77%). Vertical climb/descent differed significantly between contexts based on GLMM analyses, as well, with 10.1% during foraging (Fo) and 5.58% during travel (Tv) (Table 4.1; $p<0.001$). Leaping yielded similar results between contexts (Fo=0.72%; Tv=1.14%), while dropping yielded a slightly significant difference in favor of foraging (Fo=1.33%; Tv=0.43%). Bridging was observed in both contexts less than expected, and did not generate significant contrast among foraging and travel (Fo=2.21%; Tv=1.72%).

Table 4.1: Probabilities of locomotor behaviors during travel and foraging based on GLMM analyses

	Forage %	**Travel %**	**p-value, significance**	**Forage 95% CI**	**Travel 95% CI**
Brachiation	4.82	8.49	0.00074, ***	[3.50, 6.59]	[7.11, 10.11]
Clamber	49.53	50.0	0.83, n.s.	[46.01, 53.07]	[47.44, 52.56]
Forelimb Swing	6.77	10.49	0.0023, **	[5.13, 8.89]	[8.82, 12.44]
Quadrupedal Walk	23.57	21.29	0.21, n.s.	[20.76, 26.63]	[19.34, 23.38]
Bridging	2.21	1.72	0.41, n.s.	[2.20, 2.22]	[1.71, 1.74]
Leap	0.72	1.14	0.28, n.s.	[0.31, 1.68]	[0.63, 2.05]
Drop	1.33	0.43	0.017, *	[0.58, 3.01]	[0.17, 1.09]

Table 4.1 continued

Vertical Climb	**10.1**	**5.58**	**7.3e-05, *****	**[8.06, 12.59]**	**[4.49, 6.92]**

Note: the center column provides the p-value and represents significance of differences between probabilities of locomotor behaviors in travel and foraging (n.s.: not significant, *p<0.05, **p<0.01, ***p<0.001)

Postural behaviors

Analysis of postural behaviors was executed using the same procedures as the analysis of locomotory modes. There were no significant differences in the distribution of postural modes between the sexes or between age-classes (Figures 4.6 and 4.7, respectively). When analyzing the distributions of postural behaviors according to the contexts of foraging and travel, differences were significant (Figure 4.8). Therefore, logistic regression was used to evaluate individual postural modes when comparing contexts (Table 4.2).

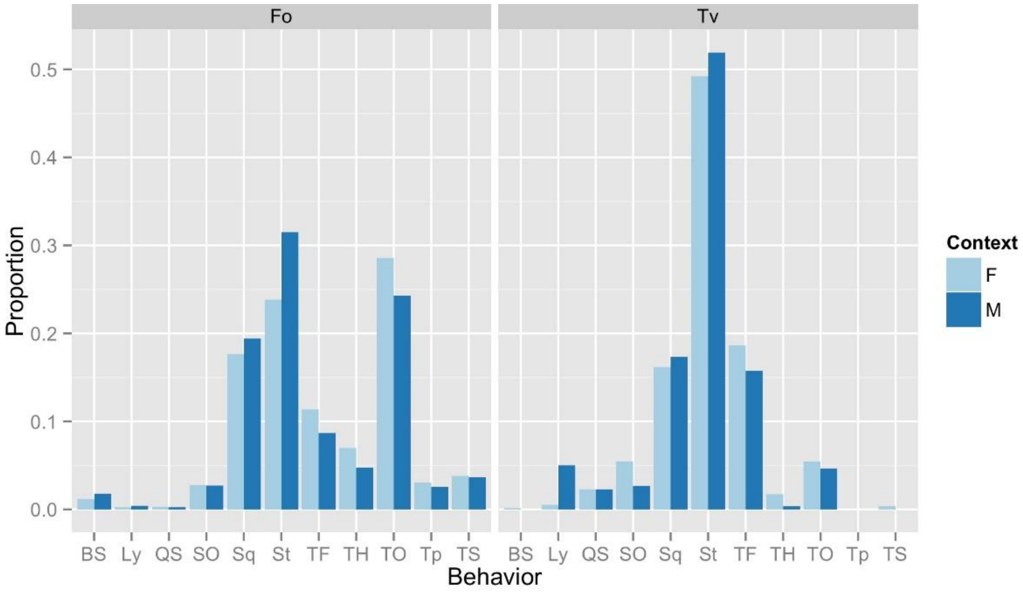

Figure 4.6: Distributions of postural behaviors between sexes within the contexts of travel (Tv) and foraging (Fo)
Key: bipedal stand (BS), lie (Ly), quadrupedal stand (QS), other suspensory (OS), squat (Sq), sit (St), tail-forelimb hang (TF), tail-hindlimb hang (TH), tail-only hang (TO), tripod (Tp), tripedal stand (TS)

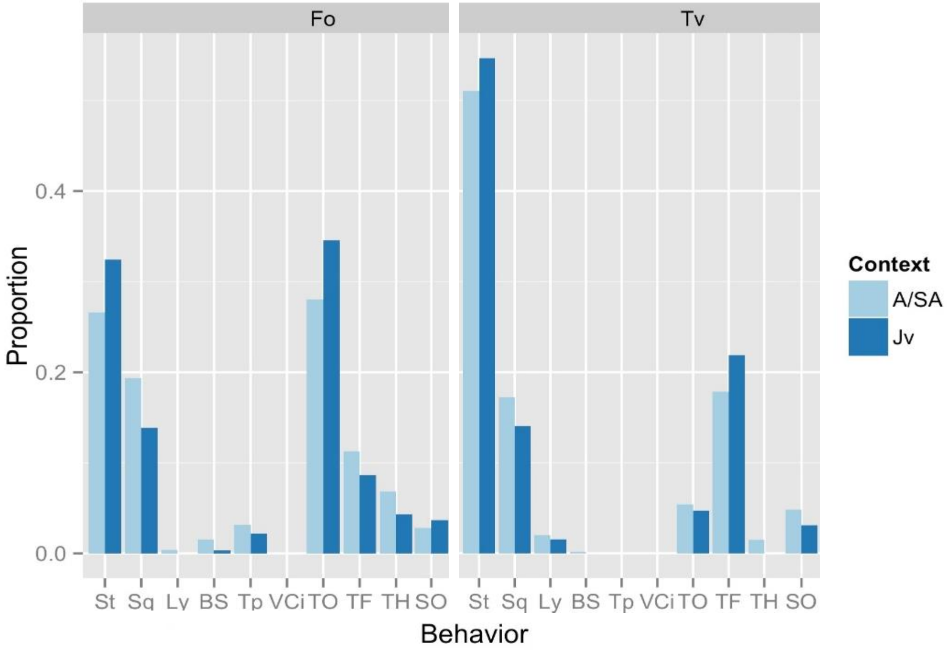

Figure 4.7: Distributions of postural behaviors between age-classes within the contexts of travel (Tv) and foraging (Fo)
Key: sit (St), squat (Sq), lie (Ly), bipedal stand (BS), tripod (Tp), vertical cling (VCi), tail-only hang (TO), tail-forelimb hang (TF), tail-hindlimb hang (TH), other suspensory (SO)

The most frequently used posture during foraging was tail-only hang (TO) (TO=27.12%); however, this behavior was observed significantly less during travel (Table 4.2; TO=5.10%; p<0.001). Sit (St) was also frequently used during foraging (St=25.07%) and was the most frequently used immobile position during travel (St=49.48%). Traveling individuals performed tail-forelimb hang (TF=18.21%) and squat (Sq=15.89%) relatively frequently, but did not regularly employ tail-hindlimb hang (TH) during travel (TH=1.29%). This posture was used significantly more during foraging (Table 4.2; TH=6.09%; p<0.001). Vertical cling was not frequently observed in either context (Fo=0.19%; Tv=0.29%). Moreover, monkeys were not often seen standing while foraging nor when traveling based on GLMM analyses. Tripedal stand and quadrupedal stand combined produced 3.53% of foraging and 2.19% of travel, while bipedal stand contributed to 1.30% of foraging and 0.11% of travel (Table 4.2).

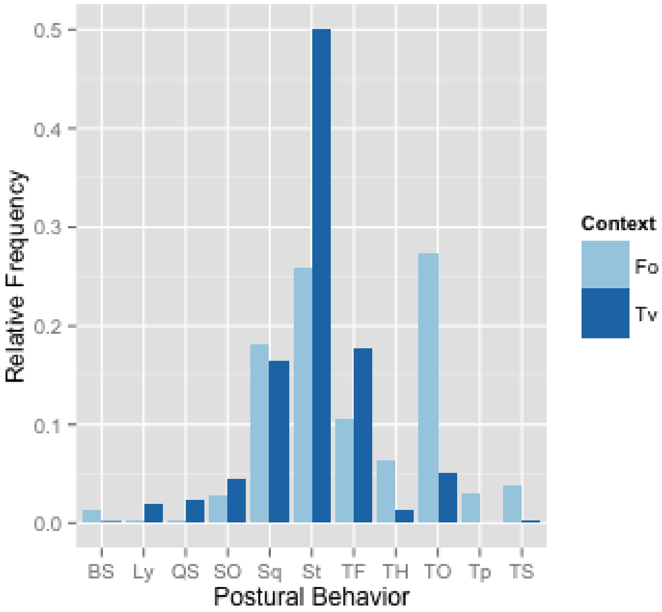

Figure 4.8: Distributions of postural behaviors between contexts of travel (Tv) and foraging (Fo)
Key: bipedal stand (BS), lie (Ly), quadrupedal stand (QS), other suspensory (OS), squat (Sq), sit (St), tail-forelimb hang (TF), tail-hindlimb hang (TH), tail-only hang (TO), tripod (Tp), tripedal stand (TS)

Table 4.2: Probabilities of postural behaviors during travel and foraging based on GLMM analyses

	Forage %	**Travel %**	**p-value, significance**	**Forage 95% CI**	**Travel 95% CI**
Sit	25.07	49.48	<2e-16, ***	[22.12, 28.28]	[44.48, 54.49]
Squat	18.21	15.89	0.11, n.s.	[16.09, 20.54]	[13.12, 19.11]
Lie	0.32	1.92	2.8e-06, ***	[0.19, 0.55]	[1.18, 3.11]
Quadrupedal/ Tripedal Stand	3.53	2.19	0.027, *	[2.76, 4.51]	[1.38, 3.48]
Bipedal Stand	1.30	0.11	0.00015. ***	[0.92, 1.85]	[0.02, 0.81]

Table 4.2 continued

Tail-Forelimb Hang	**10.76**	**18.21**	**1.7e-08, *****	**[9.50, 12.17]**	**[15.36, 21.44]**
Tail-Hindlimb Hang	6.09	1.29	3.4e-11, ***	[5.21, 7.11]	[0.71, 2.32]
Tail-Only Hang	27.12	5.10	<2e-16, ***	[25.4, 28.92]	[3.78, 6.84]
Other Suspensory	2.76	4.56	0.0088, **	[2.31, 3.29]	[3.33, 6.20]
Vertical Cling	0.19	0.29	0.44, n.s.	[0.07, 0.56]	[0.08, 1.08]

Note: the center column provides the p-value and represents significance of differences between probabilities of postural behaviors in travel and foraging (n.s.: not significant, *p<0.05, **p<0.01, ***p<0.001)

Discussion

I investigated whether spider monkey postural and locomotor modes were context specific, and whether they differed according to sex and age-class. There were no significant differences between sex and age-classes when comparing the distributions of foraging and traveling positions. This may indicate the importance of certain postural and locomotory behaviors within each context regardless of age and sex.

Differences in positional behavior between the sexes have been observed in several primate species. Such differences are often associated with variation in body size (Cant, 1987; Wheeler & Ungar, 2001). Suspensory postural and locomotor behaviors are thought to aid larger bodied, arboreal primate species' exploitation of their habitat. It is easier for larger bodied primates to suspend below branches than balance above them (Wheeler & Ungar, 2001). Therefore, it is often hypothesized that heavier males will engage in more suspensory behaviors than females. For the most sexually dimorphic primate species, it was somewhat surprising to learn that positional studies of male and female orangutans (*Pongo pygmaeus*) did not follow this trend (Cant, 1987; Zhu et al., 2015). Females employed higher frequencies of below-branch suspensory postures than males, who are roughly double the size of females. Doran's (1989) study on chimpanzees and bonobos also did not follow this expected trend, as males did not increase their use of suspensory behaviors when compared to females.

In this study, I examined whether variation in locomotor and postural modes would hold true in a species experiencing little to no sexual dimorphism. Male and female spider monkeys are considered monomorphic, with insignificant body size differences according to sex in this genus (Rosenberger et al., 2008). One species of spider monkey (*A. paniscus*), in fact, displays negative dimorphism, in which adult females are reported to outweigh males (dimorphic index = 0.853) (Ford & Davis, 1992; Rosenberger et al., 2008). *Ateles geoffroyi*, however, have a 1.101 dimorphic ratio, signifying a marginal difference in male and female body size, with males weighing slightly more than females. I therefore anticipated some differences in positional behaviors between the sexes. However, my results did not yield significant sex differences in the distributions of postural and locomotor behaviors within the contexts of foraging and travel (Figures 4.4 and 4.6). Certain postures and locomotor modes slightly diverged, but these discrepancies were not significant. If use of certain postural and locomotor modes is correlated with body size, one would expect minimal variation in a monomorphic species as was observed in this study. Following this assumption, expected differences would occur between individuals of different ages, however.

Suspending below branches rather than operating above facilitates the foraging behavior of large bodied primates (Wheeler & Ungar, 2001). It is often hypothesized that older individuals will use suspensory behaviors more than their younger counterparts, as such behaviors help to distribute weight across several arboreal supports (Bezanson, 2012). However, Bezanson's (2012) study on the ontogeny of prehensile tail use in mantled howling monkeys and white-faced capuchins shows an opposite trend. Younger individuals tended to employ their tails more often in mass-bearing modes than did adults. Workman and Covert's (2005) study on red-shanked douc langurs (*Pygathrix nemaeus*) also illustrates increased suspensory behavior in younger individuals when compared to adults. Therefore, I predicted juveniles would employ increased suspensory postures when foraging, as this has been the case in other positional behavior studies focused on ontogenetic differences (Workman & Covert, 2005; Prates & Bicca-Marques, 2008; Bezanson, 2012). Prehensile tails not only facilitate balance and mass distribution, but may also enhance a primate's ability to reach resources (Prates & Bicca-Marques, 2008; Bezanson, 2012). Juveniles' smaller body size may limit their reach of food items, enhancing the benefit of suspensory postures. Moreover, their lower body weight would allow them to employ smaller substrates in the peripheries to gain food items unavailable to heavier adults.

My results did not match my predictions, as I found no significant differences between the distributions of postural modes used during foraging and travel. Perhaps the larger body size of spider monkeys limited the effect of ontogenetic differences observed in capuchins and howling monkeys. Given that capuchins and howling monkeys are arboreal quadrupeds, their differing body types compared to suspensory spider monkeys may also necessitate differing behaviors (Duren, 2001; Isler, 2004; Wright et al., 2015). *Ateles* species have a high intermembral index (IM=101-105) (Isler, 2004) indicative of longer forelimbs for suspension. Arboreal quadrupeds like howling monkeys, however, have relatively even limb lengths

(Fleagle, 1988; Duren, 2001), though *Cebus capucinus* forelimbs are slightly shorter than their hindlimbs, according to their IM (IM=81) (Wright et al., 2015). However, considering the ontogenetic variation observed in other species that employ suspensory postures via prehensile tail (Workman & Covert, 2005; Prates & Bicca-Marques, 2008; Bezanson, 2012), my results may be influenced by the small sample size of juveniles (n=51) when compared to the number of samples of adults/subadults (n=588) in this study, as a single juvenile's behavior would more likely to impact results. The few juveniles (n=6) available proved difficult to find and follow, limiting my sample size of postural and locomotory behavior in these young spider monkeys. A longer study focused more specifically on ontogeny may further elucidate differences. Variation in locomotor behaviors between juveniles and older individuals was examined, as well. Young primates are limited by their small stature, strength, motor control and skills, and lack of experience (Workman & Covert, 2005). Moreover, spider monkeys exhibit slow life histories with relatively long gestation periods (7-7.5mo) and interbirth intervals (17-45mo) (Ramos-Fernández & Wallace, 2008; Campbell & Gibson, 2008; Rowe, 1996). The extended juvenile period assists not only in social augmentation, but also in locomotor growth and development (Workman & Covert, 2005).

Juveniles are experimental in learning their surroundings and their own capabilities. They tend to move in a clumsier manner when compared to adults (personal observation; Workman & Covert, 2005). Other studies indicate increased suspensory behavior exhibited by younger individuals (Workman & Covert, 2005; Prates & Bicca-Marques, 2008; Bezanson, 2012). Therefore, I predicted juveniles would display higher amounts of clamber than older monkeys (adults/subadults). Clamber is a form of below- and above-branch locomotion in which all appendages attach to several, diversely oriented supports in various ways (Hunt et al., 1996).

However, my results did not indicate a significant difference in the distributions of locomotor behaviors of older subjects and juveniles within the contexts of travel and foraging. In fact, adults/subadults and juveniles utilized clamber in relatively even amounts during travel (Figure 4.5). What is more, older individuals appeared to use clamber slightly more than juveniles during foraging. Perhaps the prevalence of discontinuous canopy in swamp forest at El Zota presents distinct challenges in relation to this type of movement, increasing the amount of clamber observed.

Variation in locomotor behaviors between contexts

Various modes of locomotion are used during both travel and foraging. Here I examine differences in the frequency of use between these contexts and compare the results to what has been observed in other studies on this genus. However, it must be noted that differences between studies may be attributed to interspecific variation in morphology and ecology, as well as methodological discrepancies between studies. Youlatos (2002) (*A. paniscus*) and Cant et al. (2001) (*A. belzebuth*) performed instantaneous focal animal sampling using 20-sec intervals, rather than the 30-sec employed in this study. The shorter intervals used in past studies likely allowed the researchers to record various, transient locomotor modes, such as leaping and dropping, that may be lost with longer intervals. Moreover, the lengths of each sample varies between studies. While I executed 10-min samples, Youlatos (2002) performed 15-min samples. Cant et al. (2001) followed his subjects for as long as possible with simultaneous 5-min and 20-sec intervals, collecting differing variables at each interval. Moreover, the statistical analyses differed slightly, which may elicit varying results. Both studies followed behavioral definitions and methods similar to my own, allowing for a more reliable comparison than would be possible with other positional studies on this genus. Both Cant et al. (2001) and Youlatos (2002) use definitions generally following Hunt et al. (1996), as I used in this study. This standardized paper was not yet available to early researchers (i.e. Mittermeier, 1978; Cant, 1986; Fontaine, 1990) on spider monkey positional behavior, limiting the amount of crossover between studies for comparison. Some of the early research, for instance, included clamber as a form of quadrupedalism, whereas others included clamber in their definition of climb. More recent studies recognize clamber as its own locomotive behavioral category. Therefore, I focused my comparison on the more recent spider monkey studies, though will still make reference to the older research.

When examining the use of locomotor modes in both foraging and travel contexts, my results reveal clamber as the most frequently used behavior in each context (50% in both travel and foraging). While this is consistent with both Youlatos (2002) and Cant et al. (2001) in foraging samples, the latter studies recorded this behavior to a much lesser degree during travel (25.8% and 25.3%, respectively). Use of this mode is thought to be enhanced during foraging, as it provides a more deliberate climbing motion useful in locating and gathering food items (Youlatos, 2002). It is also considered less rapid than brachiation, suggesting such fast-paced movement is not as essential during foraging. In the present study, the relatively even use of clamber in both contexts does not match these expectations. Each of these studies take place in tropical, wet forests, but there may be structural differences lending to variation in use of clamber (Youlatos, 2002). Mittermeier and Fleagle (1976) do not provide direct reference to clambering behavior, but their definition of climbing includes descriptions similar to clamber. They did not quantify use of “climbing,” but it was described as “very common” in *A. geoffroyi* (Mittermeier & Fleagle, 1976, p. 247). While more precise definitions and quantifiable results are needed to make a more accurate comparison, these data may indicate interspecific variation in use of clamber between *A. geoffroyi*, *A. paniscus*, and *A. belzebuth*.

Following clamber, quadrupedal walk was observed at a relatively high frequency in both travel (21%) and foraging (24%) contexts. This finding is similar to what is observed in other positional behavior studies for this genus (Table 4.3). However, while clamber and quadrupedal walk were observed in the highest frequencies in the population at El Zota, other populations exhibited higher amounts of brachiating and suspensory behavior. For instance, brachiation was the most common type of locomotion during travel in Youlatos' (2002) study on *A. paniscus* (32.0%), and this value increased when combined with forelimb swing (35.2%). Cant et al. (2001) combined *A. belzebuth* behaviors that kinematically resembled each other, counting brachiation and forelimb swing together generally as suspensory locomotion. Suspensory locomotion of *A. belzebuth* was observed during travel to a lesser extent (23.3%) than *A. paniscus*; however, these findings are more in line with what was observed in the El Zota population (20.0%).

Suspensory locomotion at El Zota was observed at higher frequencies during travel (20%) than during foraging (12.0%). This is consistent with the expectation that such rapid locomotion is not as necessary during foraging than as in travel. *Ateles paniscus* and *A. belzebuth* exhibit suspensory locomotion more frequently during foraging when compared to the El Zota population (24.1% and 22.0%, respectively). This is likely related to the high use of clamber observed in *A. geoffroyi*, but other factors, such as interval length or length of study, may also be influential.

Table 4.3: Summary of data from other *Ateles* spp. studies for comparison

	Travel			Foraging		
	A. geoffroyi (this study)	*A. paniscus (1)*	*A. belzebuth (2)*	*A. geoffroyi* (this study)	*A. paniscus (1)*	*A. belzebuth (2)*
Site	Costa Rica	Fr. Guiana	Ecuador	Costa Rica	Fr. Guiana	Ecuador
Rain forest type	Wet	Wet	Wet	Wet	Wet	Wet
Instantaneous sampling interval	30-sec	20-sec	20-sec	30-sec	20-sec	20-sec
Quadrupedal	21.0	19.3	21.2	24.0	18.7	18.6
Clamber	50.0	25.8	25.3	50.0	44.3	43.6
Suspensory (forelimb swing & brachiation)	Br: 9.0 FS: 11.0 Total: 20.0	Br: 32 FS: 3.2 Total: 35.2	23.3[a]	Br: 5.0 FS: 7.0 Total: 12.0	Br: 19.2 FS: 4.9 Total: 24.1	22.0[a]
Vertical climb	6.0	2.3	12.5	10.0	1.9	12.4
Bridging	2.0	8.8	12.2	2.0	3.0	2.9

Table 4.3 continued

Leap/drop	**1.0**	**Lp: 2.6** **Dp: 0.4** **Total: 3.0**	**2.7**	**2.0**	**Lp: 1.5** **Dp: 0.4** **Total: 1.9**	**0.0**

Note: 1. Youlatos (2002), 2. Cant et al. (2001)
[a.] Combined forelimb swing and brachiation generally as suspensory locomotion (Cant et al., 2001)

Bridging and leaping/dropping remained relatively consistent across contexts. However, vertical climb was significantly higher during foraging, likely related to the acquisition of food items (Hunt et al., 1996; Youlatos, 2002). *Ateles belzebuth* employed this behavior roughly twice as much as *A. geoffroyi* during travel (12.5%), but its use was similar during foraging (12.4%). It was striking how infrequently *A. paniscus* exhibited this behavior (Tv=2.3%; Fo=1.9%). I thought perhaps there were differences in the definition of vertical climb between the studies, but this was not the case here. This may be an instance of ecological variation between species if relatively few feeding trees require this form of locomotion. Amounts of bridging during travel also appeared to vary across species. Both *A. paniscus* and *A. belzebuth* maintained similar frequencies of bridging, whereas *A. geoffroyi* was seldom recorded utilizing this mode (2.0%). While results indicate low use of bridging, I partially attribute this to my data collection methods, as this is a quick mode often witnessed between my slightly longer intervals. Differences in forest canopy structure could also contribute to such differences, but these were not measured in my study.

Bipedal walk was rarely observed, and was therefore not included in this analysis. Bipedal posture was occasionally employed during feeding, but bipedal walk was scarcely recorded in the trees. Bipedalism on the ground, however, was qualitatively observed by myself and another primate field researcher (M. Buehler, personal communication) on multiple accounts throughout my study period (Figure 4.9). As spider monkeys are known for their arboreal lifestyle, it is startling to observe them terrestrially (Campbell et al., 2005). Their elongated forelimbs and adapted shoulder joints make quadrupedalism on the ground more difficult compared to sympatric capuchins; therefore, bipedalism is a common form of locomotion for spider monkeys when terrestrial.

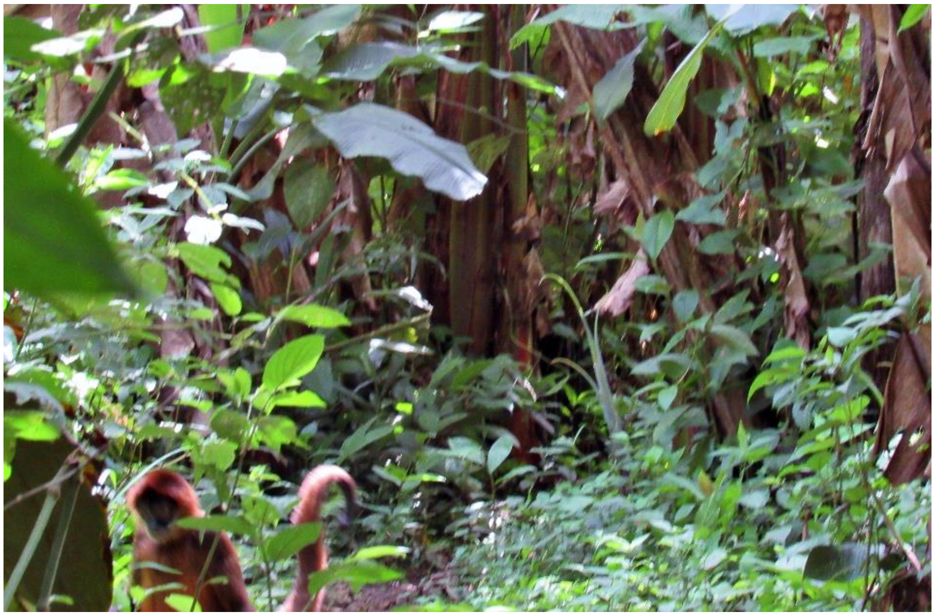

Figure 4.9: Adult Male *Ateles geoffroyi* (foreground, left) on the ground walking bipedally (EZBFS)
Photo credit: M. Buehler

Campbell et al. (2005) suggests *Ateles* spp. venture to the ground for specific food sources (i.e. soil, rotten wood or nutrients in salt licks), to consume water during the dry season (i.e. in puddles or streams), crossing gaps without proper forest cover, intraspecific aggression (i.e. males attacking or females escaping attacks), or in play contexts (i.e. chase game). At El

Zota, *A. geoffroyi* were terrestrial when crossing the road in an area lacking canopy connection, as well as when foraging for fallen banana bunches on a forest trail (Figure 4.9). In each of these instances, bipedalism was qualitatively recorded as the primary locomotor mode.

Postural behaviors

The significant differences observed of the distribution of postural modes between the contexts of travel and foraging suggests that foraging maintains a more complex postural repertoire than is used in travel. Most positional behavior studies neglect examination of postures used during travel. While various modes of locomotion are expected during travel, relatively stationary postures are also purposefully used during this activity. Neglecting the use of certain postures in their repertoire during this context may be indicative of an energy saving strategy. Moreover, one is able to examine which postures are used most frequently overall when considering multiple contexts. Probability of use differs between foraging and travel, but within each context, a similar pattern of use is observed. The four most commonly used postures were the same in both contexts, though there was variation in the ordering of these behaviors (i.e., which behaviors are more vs less frequent).

Travel yields a high probability of sit as opposed to the other postures considered in the behavioral catalog. When moving throughout the tree canopies, spider monkeys sit to wait for travel companions, contemplate their next move, or momentarily rest (personal observation). As this position was brief and locomotion quickly resumed, these short instances of sit were considered a part of travel rather than as a separate resting bout. While foraging also employed a high probability of sit, other postures were frequently used, as well. Spider monkeys utilize a number of suspensory postures to assist foraging efficiency, as below-branch postures expand their feeding sphere (Youlatos, 2002). Tail-only suspend was the most frequent foraging posture but was hardly used during travel. This may demonstrate that certain postures are more context specific than others.

When examining the most common postures in both contexts, the results are strikingly similar. Though probability of use differs greatly, the four most frequently used postures in each context are the same, but in varying order (i.e., TO, St, Sq, and TF). Squat is the third most frequently used in each context, without significant differences in amount used. Sit and tail-forelimb hang are employed more during travel (St=49.48%; TF=18.21%), though are still often used while feeding (St=25.07; TF=10.76%). Again, immobile postures are engaged primarily when the monkey briefly rests, waits for conspecifics, or in route determination during travel (personal observation). For instance, tail-forelimb hang was often observed as an extended pause during brachiation or clamber. Tail-forelimb hang in this context often splays a single substrate, though sometimes more than one, utilizing one or both forelimbs with the prehensile tail. Figure 4.10 illustrates a young, adult male (Nv) displaying this position with both forelimbs in use. During foraging, this posture was used to a lesser extent, perhaps because free hands were needed to handle food items. Instead, foraging was accompanied more frequently by tail-only suspend, during which the hindlimbs and forelimbs were not assisting suspension, typically falling below the trunk of the monkey. Forelimbs were used most in handling food, while hindlimbs often assisted grasping substrates on which food items are found, holding them in place for more efficient foraging (Figure 4.11).

Figure 4.10: Young Adult Male (Nv) engaging tail-forelimb posture (EZBFS)

Figure 4.11: Adult Female (Fey) engaging tail-only posture while foraging on leaves (EZBFS)

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CHAPTER 5

ONE-ARMED JUVENILE (JF) RESULTS & DISCUSSION

Results

A total of 4.33 h of instantaneous focal animal sampling (26 samples; 520 sample points) were collected on the one-armed juvenile (JF) over the course of this study. After removing out-of-sight sample points, 3.57 h of data (21.4 samples; 427 sample points) were then analyzed through logistic regression using a generalized linear mixed effects model (GLMM) to compare differences in his locomotor and postural behaviors between the contexts of travel and foraging. Methods of data collection between JF and individuals with all functioning limbs were standardized to allow a more reliable means of comparison. Having only one individual with a missing limb does not allow robust statistical comparison with other individuals in the community, but visual comparison of the separate inferences can allow some assessment, which is discussed later in the chapter. Moreover, the limited number of samples obtained on JF restricts what these data can tell us.

Activity Budget

Foraging accounted for the highest percentage of JF's overall activity budget (42%) (Figure 5.1). Travel and rest comprised 28% and 22% of all observed behaviors, respectively. The remaining 8% consisted of contexts such as play or other distinctly social behaviors. Data samples represent all times of day relatively evenly, thus his data should not be influenced by a particular hour of the day.

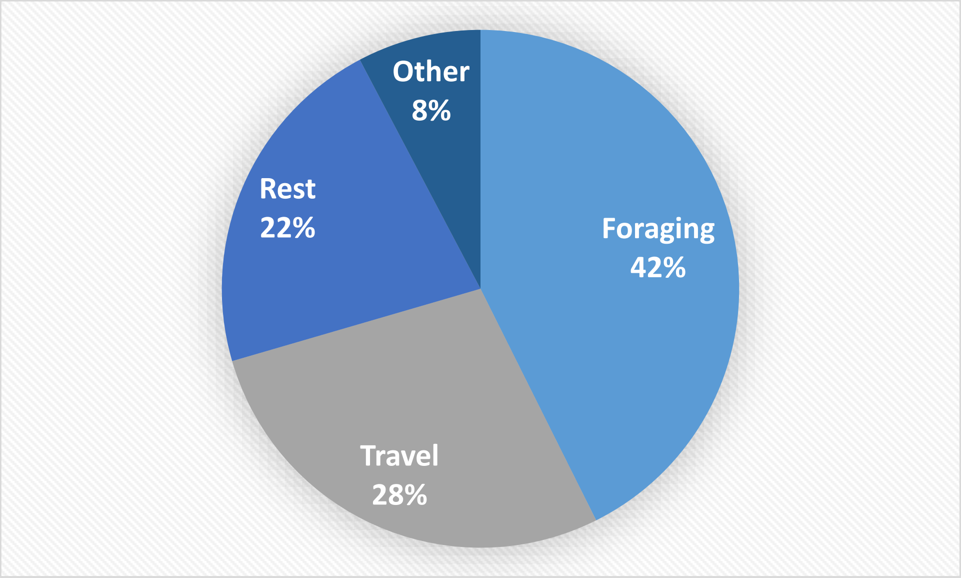

Figure 5.1: Overall activity budget for JF during the study period

Locomotor behaviors

The various locomotory modes used during travel and foraging were recorded using instantaneous focal animal sampling. The relative frequencies of the different locomotor behaviors were examined separately from the postural modes. Inference on the differences between individual modes of locomotion was made using logistic regression through a generalized linear mixed effects model (glmm). These data are summarized in Table 5.1. A significance level of $p \leq 0.05$ was used in this analysis. Figure 5.2 illustrates the frequencies of each behavior based on the probabilities given in logistic regression. Using the model data rather than raw proportions provides a more accurate visual representation of these data to the reader, as the model takes into account repeated measures within a 10-minute sample.

Table 5.1: Probabilities of locomotor behaviors during travel and foraging based on GLMM analyses

	Forage %	Travel %	p-value, significance	Forage 95% CI	Travel 95% CI
Brachiation	1.784e-05	8.277e-03	0.23, n.s.	[1.33e-12, 7.05]	[8.98e-06, 7.09]
Forelimb Swing	4.54	5.06	0.9, n.s.	[1.14, 16.44]	[1.91, 12.73]
Clamber	49.29	52.55	0.75, n.s.	[35.59, 65.12]	[39.92, 64.86]
Tripedal Walk	20.83	21.69	0.93, n.s.	[9.61, 39.43]	[12.03, 35.66]
Bridging	2.27	2.53	0.93, n.s.	[0.32, 14.45]	[0.63, 9.56]
Leap	8.55e-14	3.80	0.1, n.s.	n.a.	[1.23, 11.12]
Drop	n.a.	n.a.	n.a., n.a.	n.a.	n.a.
Vertical Climb	8.26	1.87	0.1, n.s.	[1.23, 39.48]	[0.13, 21.89]

Note: the center column provides the p-value and represents significance of differences between probabilities of locomotor behaviors in travel and foraging (n.s.: not significant, *$p<0.05$, **$p<0.01$, ***$p<0.001$, n.a.: not applicable)

Following logistic regression, none of the locomotor behaviors exhibited by JF differed significantly between the contexts of foraging and travel. JF demonstrates a high frequency of clamber during both foraging and travel (Fo=49.29%; Tv=52.55%), similar to what is observed in other individuals in the community. Tripedal walk occupies much of JF’s locomotor behavior, with 20.83% used during foraging and 21.69% in travel. Behaviors such as bridging, leaping/dropping and vertical climb were used to a lesser extent. Vertical climb was more prevalent during foraging (8.26%) than in travel (1.87%), though these differences were not significant. While leaping comprised 3.80% of travel and less than 1% of foraging, no dropping behavior was recorded.

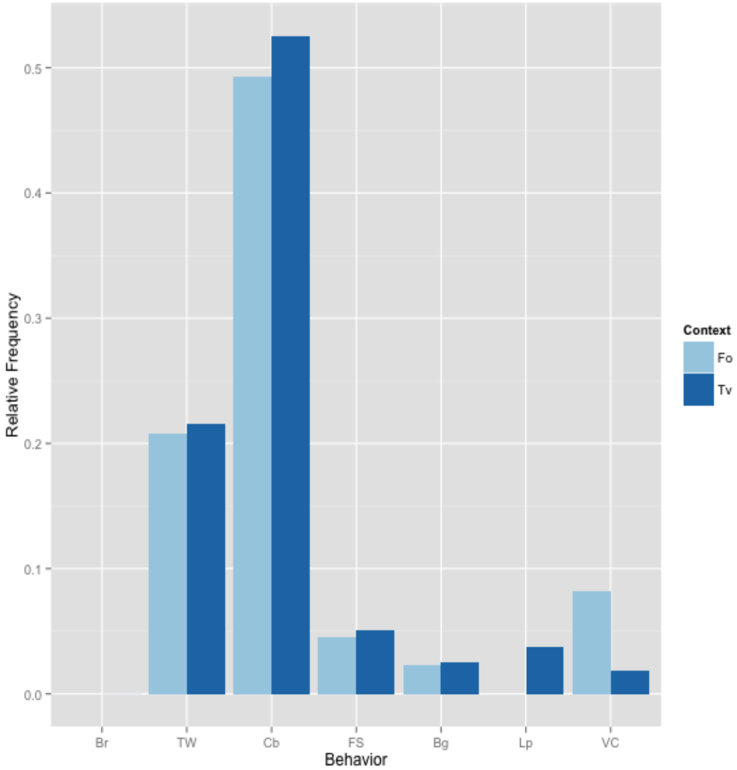

Figure 5.2: Distributions of JF locomotor behaviors between contexts of travel (Tv) and foraging (Fo) based on linear regression model
Key: brachiation (Br); tripedal walk (TW); clamber (Cb); forelimb swing (FS); bridging (Bg); leap/drop (Lp); vertical climb (VC)

The data indicate the presence of modified brachiation, though minimal, in JF's locomotor repertoire. JF revealed alternate forms of tail-arm brachiation by making use of his prehensile tail, which will be detailed later in the discussion. These instances were scored the same as brachiation observed by individuals with all functioning limbs for comparison. While use of tail-arm brachiation was expectedly low, JF made use of forelimb swing in each context fairly regularly (Fo=4.54%; Tv=5.06%).

Postural behaviors

Postural behaviors were analyzed using the same logistic regression as applied to locomotory modes. Postures utilized in the contexts of foraging and travel appeared to vary more than was observed with locomotory modes (Table 5.2). Sit was the primary postural mode employed during travel (69.44%), but this was not the case for foraging (21.01%). JF exploited his prehensile tail through tail-only hang most often while feeding (35.29%), showing significant differences ($p<0.001$) from use of this posture during travel (2.51%). Squat was also a frequently used posture in both contexts (Fo=24.41%; Tv=11.55%), and differences between use in travel and foraging were not significant.

Limb assisted suspensory postures, such as tail-hindlimb or tail-forelimb suspend, were limited in use in both contexts. Tail-hindlimb suspend was observed in 4.35% of foraging modes but was never recorded during travel. Moreover, tail-forelimb suspend, as expected, was scarcely observed, with less than 1% recorded in each context. Vertical cling was not seen at all during foraging and in less than 1% of travel. Standing postures were used relatively infrequently, with bipedal stand employed somewhat more during foraging (1.15%) and tripedal stand during travel (2.78%). Figure 5.3 depicts the frequencies of each postural mode based on the probabilities given in logistic regression, as the model provides a more transparent visual representation of these data than do the raw proportions.

Table 5.2: Probabilities of postural behaviors during travel and foraging based on GLMM analyses

	Forage %	Travel %	p-value, significance	Forage 95% CI	Travel 95% CI
Sit	21.01	69.44	3.6e-06, ***	[15.01, 28.61]	[52.79, 82.20]
Squat	24.41	11.55	0.12, n.s.	[14.65, 37.78]	[3.99, 29.04]
Lie	0.72	1.19e-14	0.49, n.s.	n.a.	n.a.
Tripedal Stand	9.10e-15	2.78	0.26, n.s.	n.a.	[0.39, 17.3]
Tail-Hindlimb Hang	4.35	n.a.	0.092, n.a.	n.a.	n.a.
Tail-Forelimb Hang	3.63e-10	0.018	0.52, n.s.	[3.54e-10, 3.72e-10]	[0.017, 0.019]
Tail-Only Hang	35.29	2.51	6.2e-05, ***	[24.56, 47.75]	[0.34, 16.42]
Bipedal Stand	1.15	5.20e-15	0.33, n.s.	n.a.	n.a.
Vertical Cling	n.a.	4.347e-05	0.77, n.a.	n.a.	[4.29e-05, 4.4e-05]
Other Suspensory	1.22	1.89	0.71, n.s.	[1.21, 1.222]	[1.87, 1.90]

Note: the center column provides the p-value and represents significance of differences between probabilities of postural behaviors in travel and foraging (n.s.: not significant, $*p<0.05$, $**p<0.01$, $***p<0.001$, n.a.: not applicable)

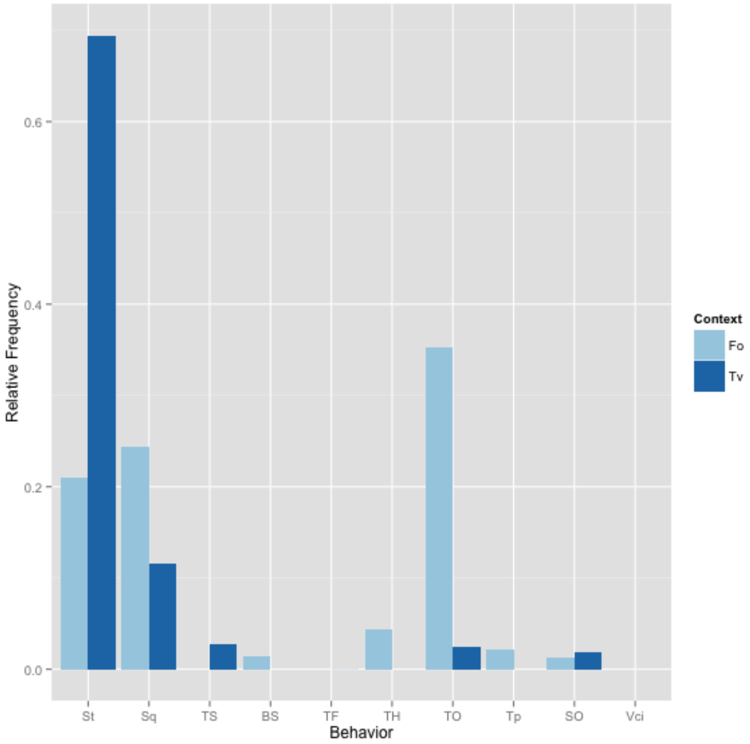

Figure 5.3: Distributions of JF postural behaviors between the contexts of travel (Tv) and foraging (Fo) based on linear regression model
Key: sit (St); squat (Sq); tripedal stand (TS); bipedal stand (BS); tail-forelimb hang (TF); tail-hindlimb hang (TH); tail-only hang (TO); tripod (Tp); other suspensory (SO); vertical cling (VCi)

Discussion

Activity Budget

JF's activity budget differed slightly from that of the other spider monkeys in his community. While the amount of foraging was similar (42% in JF, 40% others), JF demonstrated a higher frequency of travel (28%) than did the able-bodied individuals (19%). This could indicate the necessity of an increased daily path length to compensate for his missing limb. Perhaps he is compelled to take longer routes as an adjustment to his disability, as he may be unable to clear certain gaps. Chapman and Chapman (1987) recorded the behavior of a recently injured juvenile male *A. geoffroyi* in Santa Rosa National Park, Costa Rica, who lost a large portion of his prehensile tail. This individual was described as having greater difficulty in making crossings than his peers, leading to increased bridging or carrying behavior by his mother or finding alternate routes. I witnessed some of JF's failed attempts at crossing gaps in the canopy, after which he altered his desired path by finding a simpler route. Conversely, he may move at a slower pace, increasing the amount of travel time observed, as it would take him longer to arrive at his destination. Injured individuals in other studies have been described as moving awkwardly and reducing their speed when compared to those lacking injuries (Beamish & O'Riain, 2014: *Papio ursinus*; Munn, 2006: *Pan troglodytes*; Quaitt, 1996: *Pan troglodytes*; Kano, 1984: *Pan paniscus*). In JF's case, it is more likely a combination of both scenarios, and perhaps the limited sample size, leading to the variation observed.

JF also appeared to rest less than others in his community, but it is likely because he is a juvenile and that is already a general primate trend observed in younger individuals (Vick, 2008; Bezanson, 2012). For comparison, I examined the activity budget of the other juveniles in the community, and found similar results (Figure 4). The other juveniles also rested less than their older counterparts (29% versus 40%, respectively). The able-bodied juveniles appeared to invest more in travel than older individuals, which may be related to their small body size and inexperience in the trees. Like JF, they are likely limited in which paths they can take by size constraints. Their clumsiness when compared to adults/subadults may also lengthen travel time. Still, JF exhibited a slightly higher frequency of travel (27.87%in JF, 23.80% in other juveniles) when matched against other juveniles further indicating behavioral adjustment in relation to his disability.

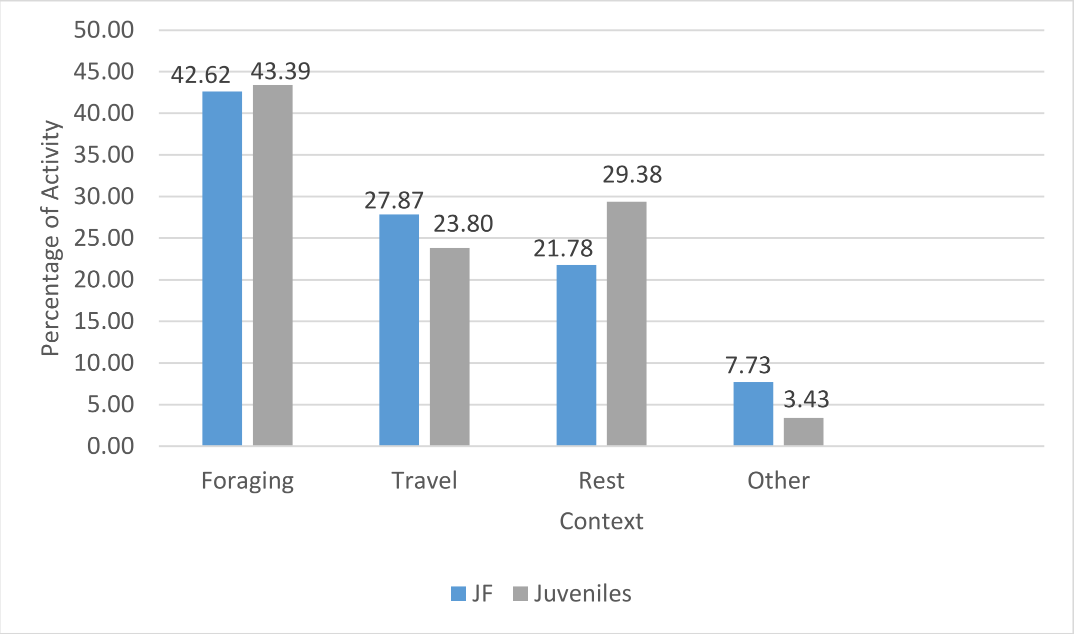

Figure 5.4: JF vs. other juvenile *A. geoffroyi* activity budgets at El Zota Biological Field Station

Locomotor behaviors

Spider monkeys are expected to employ a relatively high frequency of tail-arm brachiating behavior (Morbeck, 1977; Youlatos, 2002; Youlatos, 2008). The use of this locomotory mode helps these large-bodied primates move more securely on flexible, slender supports and promotes faster movement within and across tree crowns (Youlatos, 2008). Brachiation is defined as a hand over hand suspensory motion with extensive trunk rotation (Hunt et al., 1996), so the use of this behavior is impossible in an individual possessing only a single forearm. However, spider monkeys possess a prehensile tail that assists brachiating behavior (Mittermeier & Fleagle, 1976; Cant et al., 2001; Youlatos, 2002; Iurck et al., 2013); therefore, a form of semibrachiation could still exist for an individual missing a forelimb.

Initially, I expected minimal use of this behavior. I had briefly observed JF the previous summer (2014), and witnessed his innovative approach to tail-arm brachiation. Rather than avoiding its use all together, JF used his prehensile tail in place of his missing arm. Figure 5.5

displays JF in action following the release of his tail during this form of locomotion. During my study, I witnessed this version of tail-arm brachiation, for lack of a better term, on several accounts, but only three times during actual data collection. His infrequent use of this behavior, according to my results, matches expectations, but utilizing a unique form by means of prehensile tail use is a remarkable adjustment.

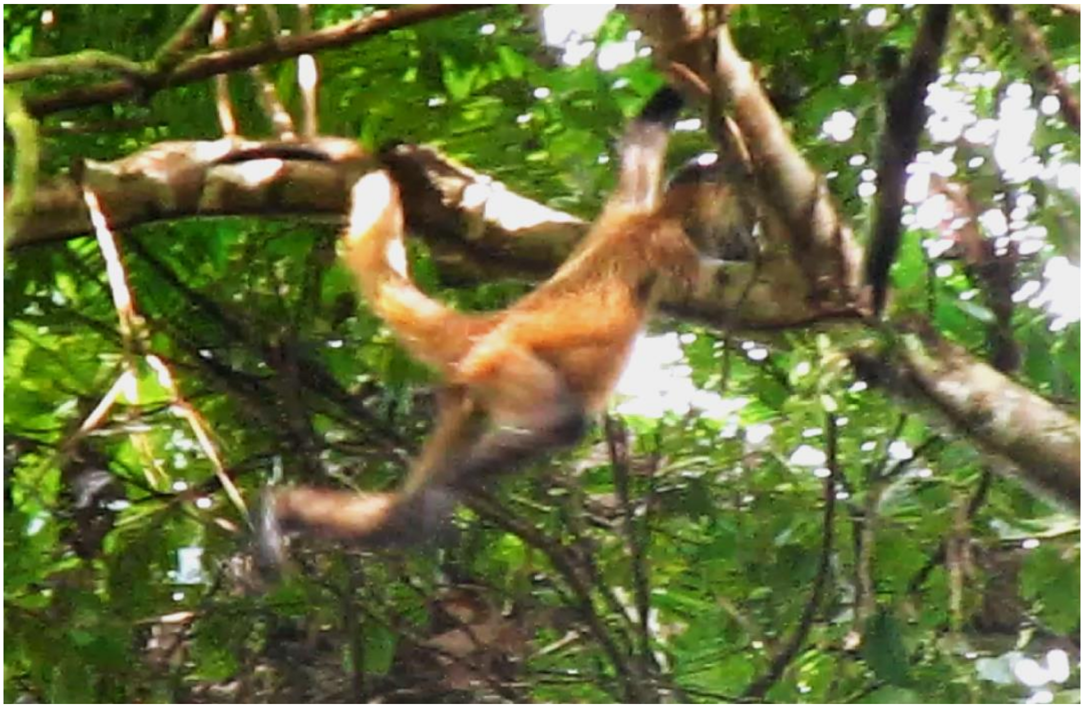

Figure 5.5: One-armed *Ateles geoffroyi* exhibiting adjusted form of tail-arm brachiation (EZBFS)

I witnessed another form of below-branch suspensory behavior that also appeared to be a substitute for brachiation, during which JF used his left arm to swing forward then caught himself on the same substrate by grasping with his feet. It was as though he replaced his right arm with his feet in a semibrachiating movement. I only observed this motion a single time, but another field researcher provided an additional account of this behavior (J. D. Pruetz, personal communication). To attempt to quantify these "semibrachiating" behaviors, I defined both of these behaviors as "brachiation" during data collection, as they most resembled this locomotor mode. However, I qualitatively described each instance while collecting data samples. This allowed me to distinguish the amount of each type of modification observed, even though they were categorically considered as one. Results indicate a probability of less than one percent of locomotor instances consisting of modified tail-arm brachiation. *Ateles geoffroyi* at EZBFS already seem to exhibit less brachiating activity than is observed at other sites, but JF, as expected, is far more limited in his use even with such modifications. Limited samples collected (N=26) on the one-armed individual may lend part to why this relative frequency is so low, but it is more likely to do with his disability and accompanying behavioral adjustments.

It is quite apparent that JF differs in use of brachiating behavior when compared to his able-bodied counterparts; however, when comparing remaining locomotor modes between these monkeys, JF appears to be adjusting fairly well (Table 5.3). His use of clamber and tripedal walk (the tripedal equivalent to quadrupedal walk) mimic what was observed in the other spider monkeys at the site. I anticipated increased clamber behavior by JF, due to both his age-class and missing limb. Brachiation was expected to be infrequent considering his disability, as was tripedal walk expected to pose challenges, especially in relation to balance; therefore, use of clamber was predicted to increase. Moreover, I predicted that juveniles' small size and clumsy manner of moving in the canopy would reflect an increased relative frequency of engaging various, diversely oriented substrates, above- and below-branch (i.e. clamber). However, my data indicate JF used similar amounts of clamber to the others in his community.

Table 5.3: Summary of locomotor data of able-bodied *Ateles geoffroyi* at EZBFS for comparison to JF

	Travel			Foraging		
	JF	Juveniles [a]	All but JF	JF	Juveniles [a]	All but JF
Brachiation	8.277e-03	7.85	8.49	1.784e-05	4.40	4.82
Clamber	52.55	48.96	50.0	49.29	44.59	49.53
Forelimb Swing	5.06	7.87	10.49	4.54	9.17	6.77
Quadrupedal Walk/ Tripedal Walk	21.69	21.35	21.99	20.83	22.94	23.57
Bridging	2.53	1.12	1.72	2.27	1.84	2.21
Leap	3.80	1.69	1.14	8.55e-14	3.64	0.72
Drop	n.a.[b]	1.12	0.43	n.a.[b]	3.41e-16	1.33
Vertical Climb	1.87	6.74	5.58	8.26	11.0	10.1

Note: [a.] Juveniles with all functioning limbs at EZBFS
[b] n.a.: not applicable; zero instances of this behavior were observed in this context

Qualitative assessment of observations implied amplified use of leaping during locomotor behavior. Short leaps along and across substrates characterize much of this behavior. His short distance leaps along substrates resembled small hops, during which he typically landed on his feet. From that point, he often emerged into tripedal walk/run or, depending on angle of substrate, may scoot momentarily to descend. Scoot is employed when a monkey descends a substrate by sliding with its body weight primarily supported by the ischia (Hunt et al., 1996). This mode was only recorded once in my data set, so was not included in the model, but *ad libitum* notes indicate additional instances of this behavior. The data also do not reflect excessive amounts of leaping, but this mode of locomotion is very brief and instances were likely missed between intervals. The absence of drop in my data set is also likely due to the longer intervals, as my notes indicate multiple instances of drop throughout my observations of JF. Instead of swinging to a branch below as done by many of his conspecifics, JF was spotted dropping to the desired substrate.

The use of vertical climb was somewhat unexpected given JF's condition. While he appears to exercise this locomotor mode less than others, the models display only slight differences. JF was able to adjust his movements to vertical climb relatively efficiently despite missing a forearm. When doing so, he shifted his body weight left to right giving a wobble-like impression.

Postural behaviors

Like the able-bodied spider monkeys at El Zota, JF also used tail-only suspension as his main posture during feeding, but to an even greater extent (35.29%) (Table 5.4). This is likely a trade-off from the other postures used in typical spider monkey repertoire. The monkeys with all functioning limbs have a greater capacity to utilize postures like tail-forelimb hang during foraging, but JF's missing limb prevents this use. As the forelimbs are most used in processing food items, it would be unlikely for JF to employ tail-forelimb hang while feeding, as his hand would be supporting his body weight and unavailable for handling food. Use of his functional arm was needed more to assist his feeding efforts (e.g. to bring food to his mouth) rather than to maintain his body posture. Individuals with functioning limbs hold and manipulate food items with their forelimbs, while their hindlimbs dangle or bring substrates closer for more efficient foraging. JF, however, typically employed his right hindlimb as if it were his missing right arm (Figure 5.6). His adjustments here resemble what was found in studies on chimpanzees with snare injuries on their hands (Byrne & Stokes, 2002; Beamish & O'Riain, 2014). When compared to able-bodied chimpanzees, those with injuries increased use of dexterous feet during bimanual food processing (Byrne & Stokes, 2002; Beamish & O'Riain, 2014). Yet again, JF displays means of adjusting to accommodate his missing limb in ways to improve his efficiency during daily activities.

Table 5.4: Summary of postural data of able-bodied *Ateles geoffroyi* at EZBFS for comparison to JF

	Travel			**Foraging**		
	JF	Juveniles [a]	All but JF	JF	Juveniles [a]	All but JF
Sit	69.44	57.29	49.48	21.01	32.81	25.07
Squat	11.55	9.82	15.89	24.41	12.06	18.21
Lie	1.19e-14	1.54	1.92	0.72	8.22e-10	0.32
Quadrupedal/ Tripedal Stand	2.78	n.a.[b]	2.19	9.10e-15	n.a.[b]	3.53
Tail-Hindlimb Hang	n.a.	2.84e-11	1.29	4.35	2.57	6.09
Tail-Forelimb Hang	0.02	21.52	18.21	3.63e-10	8.38	10.76

Table 5.3 continued

Tail-Only Hang	2.51	4.27	5.10	35.29	31.35	27.12
Bipedal Stand	5.20e-15	n.a.	0.11	1.15	n.a.	1.30
Vertical Cling	4.347e-07	1.35	0.29	n.a.	1.39	0.19
Other Suspensory	1.89	3.08	4.56	1.22	3.59	2.76

Note: [a.] Juveniles with all functioning limbs at EZBFS
[b]n.a.: not applicable; zero instances of this behavior were observed in this context

Figure 5.6: One-armed *Ateles geoffroyi* employing right hindlimb in place of missing arm (EZBFS)

Instead of exploiting suspensory postures during travel, JF utilized sit as his preferred travel posture. This is similar to what is observed in his community members, but they also apply tail-forelimb hang to a relatively high degree in this context. JF also considerably reduced use of tail-forelimb suspend during travel. Spider monkeys occasionally hold immobile postures throughout travel periods when resting briefly, waiting for conspecifics, or in route determination (personal observation). JF looked to decrease use of this travel posture likely because of the difficulty faced in maneuvering into and out of the position with a missing forelimb. Shifting back into a mode of locomotion following use of this posture would provide additional challenges, such as grasping a new substrate with available limbs when his only forelimb is engaged in this position.

When beginning this study, I was concerned about JF's ability to survive considering the prominence of suspensory behaviors in spider monkey repertoire. It seems his prehensile tail has enabled him to perform daily activities with competence even if some behavioral adjustments are necessary. As discussed in Chapter 2, the fact that spider monkeys do not undergo many threats from predators likely also plays a role in his survival thus far, as his slower pace and limited path choice would make him an easier target prey item. Injured individuals at other sites are also often recorded as moving slower or in an awkward manner than those without injury, though behavioral flexibility allows modification of postural and locomotor strategies (Beamish & O'Riain, 2014). Additionally, the fission-fusion social dynamic maintained in spider monkey communities probably allowed his mother to alter her pace where necessary, as she was not obliged to keep pace with a large group of monkeys. Compensatory care has been observed in a case of injured *Ateles geoffroyi* in the past, providing credence to this assumption (Chapman & Chapman, 1987).

Social behavior

Survival of a disabled individual like JF is concerning when returning to a field site after a year's absence, as one cannot be sure how the individual will be affected by his abnormality. I did not reconnect with JF until about two weeks into my time back at El Zota. I happened upon him on June 19th, 2015. I had wandered through a pasture to reach a part of the forest where I hoped to find adult males. I found JF and his mother, as well as two adult males and another adult female. Here I was able to observe some of his interaction with adult males.

Male spider monkeys remain in their natal communities, allowing for enhanced social bonds to form between them (Vick, 2008). Adult and subadult males tend to form travel parties, so young males around JF's age begin strengthening bonds with older males with whom they will most likely become travel companions when they grow older. The Chapman and Chapman (1987) study of an injured juvenile male *A. geoffroyi* showed signs of inhibited socialization as a result of the juvenile's disability. While the "normal" juvenile male was reported as ranging with all-male subgroups, the injured individual remained with his mother. I too hoped to compare JF to other juvenile males to see if his social growth has been impacted by his abnormality. However, I could not gather enough data in my three months of data collection for reliable comparison.

JF was only recorded associating with males in three cases, while other juvenile males were observed in this context only once. I witnessed JF attempt to connect with the adult males during these incidents. The first day I found him, he warily approached and retreated from the two adult males present. He made chirp-like vocalizations upon approach and received agonistic reactions from the males in the form of lunges and harsh vocalizations. JF responded by returning to his mother and attempting his advances again later. During this period, he managed to briefly rest-in-contact with an adult male.

On a separate occasion, I again witnessed JF receive brief agonism from an adult male in the form of a branch shake and vocalization. JF retreated from the male and made contact with his mother with whom he then rested-in-contact. A later encounter left me questioning whether he was on the receiving end of aggression, as I could not see the actors and could only hear the harsh vocalizations. JF was in the vicinity of the adult male actors, and he then fled from their location following the incident, appearing tense. He proceeded to make chirp-like noises for the remainder of my time with him (about 15 minutes), vigilantly keeping his distance from the adult males.

It is difficult to compare JF's associations with males to those of other juvenile males, because I did not often come into contact with such associations. The single encounter observed between an adult male and an able-bodied juvenile male yielded similar results. While no agonism was recorded, the juvenile behaved in a similar manner as JF. He exhibited the approach and retreat technique utilized by JF. A longer study focused more heavily on social behavior may lend information on any discrepancies observed between JF and able-bodied members of his age-class. It would be interesting to discover whether his disability impacts not only his movements but also his long-term social behavior. This can provide insight into how primates adjust to having such limitations and how other individuals in the community respond to disabilities.

Juvenile play behavior was also of interest when comparing JF to individuals in his age-class. Play has been considered a means of juvenile development, both physically and cognitively (Palagi et al., 2006; Rodrigues, 2007). It is thought to aid development of social and motor skills, as it often includes another group member and involves exploratory behavior. I predicted JF would exhibit a higher frequency of play to compensate for his disability. Chapman and Chapman's (1987) study indicated increased solitary play behavior exhibited by the injured juvenile male when compared to his uninjured peers. I expected JF's missing arm would impact his motor development, thus more play behavior would advance his hampered physical abilities.

While instances of play were observed, samples of JF did not contain social play activity. Lack of play data inhibits proper comparison with other juveniles, but it is still significant to note anecdotally. There were a few instances of solitary locomotor play recorded, as he employed various postural and locomotor behaviors while neither foraging nor traveling. While solitary play behaviors were observed in other juveniles, none were reflected in the data. These individuals were more often observed engaging in social play, as their mothers often formed subgroups together. JF and his mother often fissioned into their own subgroup, occasionally including a third individual. This may explain why observations of JF social play behavior were scarce. In only one encounter did I observe JF playing with another juvenile male. This was the only instance I saw him engaging with an individual of his age-class. No data samples were collected here, however, due to the extensive palm coverage preventing a proper visual on the study subjects. Based on *ad libitum* data, the two engaged in chase and grappling behavior, while older individuals rested nearby.

Juveniles with all functioning limbs were observed playing together to a higher degree, though not many samples contained play data. Play data are difficult to record in areas where visibility is poor, so these samples were often discarded because of excess out-of-sight sample points. The mothers of a juvenile male (CH) and juvenile female (McK) regularly formed a subgroup, allowing their offspring to play rather frequently. Their play actions resembled the modes exemplified by JF and the juvenile male (i.e. chase, grapple). Aside from CH and McK, I witnessed one other juvenile female engaging a subadult female in play. Together, only two samples of play were recorded, negating the use of statistical testing.

Social play behavior is limited in a fission-fusion social system by the number of individuals in a subgroup. Perhaps JF is hindered by the size of his subgroup, as he typically traveled with only his mother and another adult female. When small fusions occurred between subgroupings, JF engaged in social behaviors expected of males his age. However, the size of his subgroup may be restricted by his disability. As noted early in the chapter, JF's travel speed is influenced by his missing limb, as he often must redirect to find a suitable path. Fissioning into a small subgroup likely permitted a slower travel pace (Pontzer & Wrangham, 2006), given that JF and his mother would not be compelled to keep pace with a larger group of monkeys. If JF's subgroup size is limited by his disability, there is greater likelihood that he will later be affected socially.

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CHAPTER 6

CONCLUSION

Summary

The *Ateles* genus is characterized as frequently employing below-branch suspensory behaviors (Mittermeier & Fleagle, 1996; Youlatos, 2002). As frugivores, spider monkeys expand their feeding sphere through their postural and locomotor patterns to efficiently exploit these valued resources (Youlatos, 2002). Such positional behaviors develop through constant interaction with the surrounding habitat, serving as a coping mechanism within time and space as primates move and feed within the canopy (Youlatos, 2008). Having a range of positional behaviors enables spider monkeys to manage the varying aspects of habitat structure that may hinder access to preferred food sources. Moreover, suspensory locomotion encourages increased travel rates and decreased path length within and between tree crowns (Youlatos, 2002). Most *Ateles* spp. studies on positional behavior are conducted in dry, deciduous forests, with relatively little data collected on those residing in tropical, wet forested areas even though most spider monkeys populations are found in such environments (See Table 1.1).

The present study examined the locomotor and postural behaviors of the black-handed spider monkey (*A. geoffroyi*) in a typical, but not well-studied, habitat for the species, a lowland wet forest. Questions and hypotheses relating to differences in postural and locomotor modes used during the contexts of foraging and travel were addressed and tested, respectively and compared to previous studies on this genus. I examined overall differences in use of locomotor and positional behaviors, as well as those related to sex and age-class differences. Results indicate significant differences in the locomotor and postural modes used between foraging and travel contexts when all individuals were analyzed as a whole (See Tables 4.1 and 4.2). During foraging, clamber was the most frequent locomotor mode, while tail-only suspend was the most used postural mode. Similarly, clamber had the highest relative frequency during travel, though sit was the most used postural mode. When separately examining the distributions of the sex and age-classes, however, no significant differences were found between groups in each context. This may be indicative of the value of certain positions when exploiting the environment, regardless of sex or age-class.

My study also considered the potential behavioral adjustments of a one-armed individual (JF) discovered at the site the previous year (2014). Though it remains unknown as to how this deformity occurred, one can speculate its cause as possibly induced by genetic mutation, environmental factors (Turner et al., 2008; Rainwater et al., 2009), predation, intraspecies aggression (Valero et al., 2006; Gibson et al., 2008), accident (Carter et al., 2008; Jurmain, 1997), or disease. Spider monkeys have few predators due to their large size and arboreal lifestyle, making interspecific conflict a less likely cause of JF's disability. Infanticide and coalitionary attacks have been exhibited by black-handed spider monkeys, and are typically geared toward young males (Valero et al., 2006; Gibson et al., 2008). The missing right limb seen at EZBFS may possibly represent a case of a failed infanticide attempt, as severed limbs are often presented as a consequence of these attacks. Surviving such brutality seems unlikely given the fatal outcomes of documented encounters; moreover, given that JF is the second immature *Ateles* with a similar disability at EZBFS makes this explanation seem improbable. Additionally, *A. geoffroyi* live in highly disturbed regions due primarily to agricultural expansion, which places additional stress on these primates by means of habitat destruction and pesticide exposure. Congenital malformations can result from both pesticide exposure and inbreeding depression

(Turner, 2005: *Macaca fuscata*; Isachenko et al., 2002: *Callithrix jacchus*; Nakamichi et al., 1997: *Macaca fuscata*; Rawlins & Kessler, 1983: *Macaca mulatta*; Rao & Schwetz, 1982: unspecified genus and species). As multiple individuals at EZBFS have been observed with this condition, this may indicate congenital anomalies at the site. The rapidity of spider monkey locomotion, however, heightens the probability of an accidental fall leading to an atrophied limb. Skeletal analyses of wild chimpanzees have indicated the prominence of falls from the canopy as a means of injury and mortality (Carter et al., 2008; Jurmain, 1997). While many of the falls were fatal, the healing patterns of some specimens indicated survival from multiple falls, though fractures were often severe (Carter et al., 2008; Jurmain, 1997; Zihlman, Morbeck, & Goodall, 1990). Spider monkeys are often found in the high canopy, making survival from falls questionable, though this scenario could be likely if the fall was from lower in the tree.

JF's positional behaviors were observed and recorded in addition to those of able-bodied spider monkeys to address questions regarding his varied use of postural and locomotor modes when compared to the *A. geoffroyi* at the site with all functioning limbs. I was also interested in aspects of his social behavior in relation to the able-bodied juveniles in his community. Qualitatively, JF's behavioral adjustments appeared to be most prominent regarding a reduction in postural and locomotor behaviors that involved use of the forelimbs, as expected (See Tables 5.3 and 5.4). Other behaviors showed parallels to the able-bodied individuals, implying that even with his abnormality, JF is able to adjust and physically behave in a manner similar to unaffected conspecifics.

Due to the effects his malformation may impose on his social development, I expected JF to have higher frequencies of play, but less time spent with older males. There was greater difficulty in testing my questions regarding his social behavior due to limited sample size on both JF and the other juveniles. Few encounters yielded social data on JF or other juvenile males, but in interactions with adult males, all of the immature monkeys exhibited similar behavior. The adult males seemed less tolerant of JF, but this is a qualitative assessment. It will be interesting in the future to address whether JF's association with the older males in ranging behavior is delayed compared to his peers.

JF was not observed participating in social play as frequently as those in his age-class, though he was recorded engaging in solitary play. However, insufficient data on play behavior prevents statistical testing between these groups. Juvenile play data help support the idea that play is an important aspect of primate development (Palagi et al., 2006; Rodrigues, 2007). These data imply limitations of social play in regards to both physical abnormalities and social structure. Perhaps JF would be observed playing with his peers more frequently if spider monkeys did not form subgroups through their fission-fusion social system, as he and his mother were often seen alone. What is more, JF's small subgroup may be a factor of his disability, namely his seemingly slower pace. Fissioning into a smaller subgroup eliminates the need to keep pace with other monkeys.

Implications

When pooled data on the EZBFS spider monkeys were compared to prior positional behavior studies, the differences observed were slight (See Table 4.3). Clamber differed the greatest between studies, as the spider monkeys at EZBFS displayed this locomotor mode to the highest degree in both foraging and travel. However, methodological differences, such as interval length, may produce the variation observed (Cant et al., 2001; Youlatos, 2002). This does not preclude the possibility that ecological factors necessitate its increased use at EZBFS though. Varying forest structure at different field sites can influence the locomotor and postural repertoire of primate species (Youlatos, 2002). Moreover, these data have implications for researchers examining the fossil record to determine postural and locomotor modes of early primate species.

Living non-human primates are often used as models in studies of fossil primates (Garber & Pruetz, 1995), as researchers can make inferences about their locomotor and positional behaviors relative to data recorded by primatologists (Mittermeier & Fleagle, 1976; Turnquist et al., 1999; Rein et al., 2014). The spider monkeys compared here were of different species, so differences may be a factor of interspecies variation, while similarities may further characterize the genus. However, ecological variables at the different field sites may also play a role in the use of certain positional behaviors (e.g. forest type, native flora, canopy cover).

Observations of JF have implications for constructing behavior related to disabilities in the hominin fossil record, as well, where evidence of serious injury or illness has often been explained as evidence for empathy, cooperation and even caregiving (Cuozzo & Sauther, 2006). Antemortem tooth loss in the hominin fossil record has created questions regarding social care, as it is suggested that surviving with such a handicap would require assistance from conspecifics (Cuozzo & Sauther, 2006; Gilmore, 2012). Spider monkeys exhibit relatively high degrees of below-branch, suspensory behavior (Mittermeier & Fleagle, 1996; Youlatos, 2002). JF's missing limb was expected to impact his ability to maintain locomotor and postural behaviors similar to the able-bodied monkeys in his community. However, after examination of his positional behaviors, he appears to have adjusted favorably. His mother's behavior may have influence over his ability to adjust efficiently. JF's activity budget implied increased travel time, suggesting a potentially slower travel pace. This would imply waiting on the part of his mother, who was typically his only travel companion. It is fascinating that a juvenile missing an arm has survived with such limited indirect care. Chapman and Chapman (1987) observed similar compensatory care by a mother *A. geoffroyi* toward her injured, and consequently disabled, son. Though this juvenile had been already weaned and traveled independently, his mother resumed nursing and carrying him following his incident. Observing such care behavior in non-human primates provides a basis for such behavior in early hominins, especially for those whose relative brain size far exceed that of spider monkeys. For instance, traumatic lesions have been reported in Neandertal specimens, such as Shanidar 1's atrophied arm (Berger & Trinkaus, 1995). Observing a form of indirect, compensatory care in a living non-human primate enhances hypotheses of similar care exhibited by extinct hominins.

Future research

Though JF's behavioral adjustments were remarkable, results do not suggest that his survivability or that of other disabled primates is of no concern. Looking further into JF's condition may reveal hidden threats to the primate populations at the field site. Further studies should examine how the primates at EZBFS are impacted by human-induced ecological factors, such as habitat loss and proximity to pesticides used in nearby banana plantations. Fecal analyses may give insights into potential contamination due to pesticide exposure. Additionally, genetically testing fecal material can indicate relatedness among individuals, revealing the threat of inbreeding at the site. Studies on connectivity to other forest patches can provide further insights into the risk of isolation and inbreeding for these primates, as well.

Observations of JF should be maintained to better understand the survivability of injured or malformed arboreal, suspensory primates. Moreover, further research on JF's social development in contrast to his peers would further elucidate the impacts of disabilities on primate populations. These data would also expand our knowledge of the ontogenetic patterns in social affiliation of philopatric male *A. geoffroyi*. Should it be found that his malformation was likely caused by anthropogenic factors, these data can be influential in conservation initiatives. They may indicate serious repercussions to socialization and longevity of populations facing similar anthropogenic effects.

EZBFS is currently experiencing relatively small patches of habitat loss, as native and planted trees on the property are being cut for carbon offset management schemes (personal observation). However, placement of these plots may severely hinder travel by primate species for some years. Examining potential shifts in positional behavior could indicate a tighter link between the environment and the locomotor and postural modes used. Additionally, forest corridors should be monitored to determine the need for intervention to maintain connectivity between patches (Luckett et al., 2004).

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APPENDIX A

BEHAVIORAL CATALOG

Behavioral Catalog is taken from Hunt et al. (1996) and Youlatos (2002) with modifications by N.W.

Type of Pattern	Code	Description
Mutually Exclusive Behaviors		
Foraging	Fo	Grasping food source and placing in mouth followed by masticating and ingesting substance; face relaxed and eyes open; bout includes stationary position or movement within a food patch, such as a tree crown
Traveling	Tv	Any combination of hindlimb, forelimb or prehensile tail use to propel body in a swinging or forward motion between tree crowns; face relaxed; subject usually in the middle to upper canopy for passage between food resources and to or from sleeping sites
Resting	RE	Body relatively motionless, but can include small movements, such as tail movement and shifting body weight; face relaxed and eyes open or closed; breathing regular with or without the presence of yawning
Play	Pl	May include grappling and wrestling (involving pulling, pushing, and mock-biting); hitting (swing hand forward, touch

		other animal); chase (following retreating individual); Panting (basic noisy, one syllable sound that may be repeated continuously for several minutes, often teeth exposed with lateral shaking of head)
Other	O	Any activity functionally discrete from Tv, Fo or RE (see patterns below)
Out of Sight	OS	Focal animal is obstructed from view; unable to discern behavior
Type of Pattern	Code	Description
Postural Behavior		
Sit	St	Ischia bear a substantial portion of body weight and torso is relatively orthograde
Squat	Sq	Body weight is borne solely by the feet, both hip and knee are strongly flexed. Substantial body weight not borne by forelimbs or ischia. The trunk is orthograde or suborthograde and the back is typically flexed
Lie	Ly	Torso orthograde posture on a relatively horizontal supporting stratum, body weight borne principally by the torso
Vertical Cling	Vci	Adhering to a vertical support via strongly flexed forelimbs and hindlimbs

Quadrupedal Stand	QS	Four-limbed standing on horizontal or subhorizontal supports; elbow and knee are (relatively) extended and trunk is near horizontal
Tripedal Stand	TS	Three-limbed standing on horizontal or subhorizontal supports; elbow and knee are (relatively) extended and trunk is near horizontal
Bipedal Stand	BS	Standing on the hindlimbs with no significant support from any other body part; hips and knees may be flexed or extended
Tripod	Tp	Below branch posture that is a combination of tail-hang and bipedal standing, in which the animal is anchored to a support above the base of the tail, and the hindlimbs press the vertical or steeply inclined substrate; body is pronograde or quasipronograde
Tail-Only Suspend	TO	Suspension from the tail with little or no support from the limbs
Tail-Forearm Suspend	TF1; TF2	At least an half the body weight is borne by the tail with significant weight borne by the forelimb (TF1) or forelimbs (TF2). Abducted humerus, and extended elbow; the trunk is likely never fully orthograde
Tail-Hindlimb Suspend	TH1; TH2	Suspension with substantial support from the extended hindlimb (TH1) or hindlimbs (TH2) and the tail
Quadrumanous Suspend	QA	Suspension with all limbs providing approximately equal support; torso is pronograde

Other suspensory	SO	Miscellaneous suspensory modes involving pendular movement of the tail that propels the body forward (tail swing) and quadrupedal suspensory bodily progression below and along or across supports with regular or irregular gaits
Locomotor behavior		
Tail-arm brachiation	Br	Below and along or across one or multiple supports via orthograde suspensory locomotion involving an alternate gait of the abducted and extended forelimbs and tail with extensive trunk rotation approaching 180◦
Forelimb swing	FS	Below and along or across one or multiple supports via orthograde suspensory locomotion involving an alternate gait of the forelimbs and occasionally the tail with little trunk rotation
Clamber	Cb	Body displacement in various directions on and across multiple, diversely oriented supports with no particular gait; all appendages attach to substrates in different ways; maintaining the body either pronograde or orthograde
Quadrupedal Walk	QW	Locomotion on top of supports angled at <45°; typically all the four limbs contact the support in a particular sequence. Torso is pronograde or roughly parallel to the support; slow-medium paced movement.

Tripedal Walk	TW	Locomotion on top of supports angled at <45°; only three limbs contact the support in a particular sequence. Torso is pronograde or roughly parallel to the support
Bipedal Walk	BW	The hindlimbs provide support and propulsion, with only insignificant contributions from other body parts. The hip and knee may be flexed or extended
Quadrupedal Run	QR	Fast locomotion using asymmetrical or irregular gaits and with a period of free flight
Tripedal Run	TR	Gallop with only three limbs contacting the support
Scoot	Sc	The body is propelled by sliding while substantial proportion of the body weight is supported by ischia; flexed knee and thigh during motion
Vertical Climb	VC	Continuous quadrupedal upward or downward movement along a single vertical support, typically angled at $\geq$45°
Leap	Lp	Gap crossing mode involving an extended period of free flight with propulsion provided by a simultaneous extension of the hind limbs; the horizontal bodily displacement component is always longer than the vertical one
Drop	Dp	Gap crossing mode involving a period of free flight with takeoff initiated usually by falling instead of active propulsion, and with mainly vertical bodily displacement, though some possible horizontal displacement

Bridge	Bg	Gap-crossing mode involving secure retention of the initial supports by both hind limbs and tail, and cautiously pulling the body by the abducted forelimbs on the terminal supports across the gap with variable bodily orientation permitting closing of the gap; never involving an airborne phase

APPENDIX B

LIST OF STUDY SUBJECTS

Age-Class	**Sex**	**Name**	**Notes**
Adult	Female		
		Gellar	McKenna's mom; Possibly Strawberry based on M. Rodrigues, personal communication
		Redd	Charlie's mom
		Rita	Infant: Skeeter
		Gallagher	Mary-Katherine's mom
		Tonks	
		Fey	Infant: Tina
		Poehler	Infant: Amy
		Fake Fanta	Fake Frito's mom; Possibly Fanta based on M. R., personal communication)
		Rhea	Hailey's mom; Zelda on M. R., personal communication

		Jill (JF's mom)	Juan Franco's mom; matches description of Jill based on M. R., personal communication
		Noah's mom	Noah's mom
		Mellie	Young adult female (YAF)
		Fake Gal	YAF
		Maya	YAF
		Willow	YAF
		Jill's friend	Unidentified
		Spondias	Unidentified
		SCO	Unidentified
Adult	Male		
		Fallon	Likely Romeo based on M. R., personal communication
		Moony	
		Warrior	Likely Colonel Sanders based on M. R., personal communication

		Prongs	Young adult male (YAM); Likely Dylan based on M. R., personal communication
		Neville	YAM
Sub-adult	Female		
		Frankie	
		Eunice	
		Mindi	
		Luna	
		Mini Paige	
		Paige	
		Katie	
		Buffy	
Sub-adult	Male		
		Seth	
		Meyers	Light wisps around face – likely Aaron based on M. R., personal communication

		Padfoot	Likely Zander based on M. R., personal communication
Juvenile-3	Female		
		McKenna	Possibly Shortcake based on M. R., personal communication
		Mary-Katherine	
		Hailey	Possible J-2
Juvenile-3	Male		
		Charlie	
		Fake Frito	Possibly Frito based on M. R., personal communication
		Noah	Missing right eye
		Juan Franco	JF – one-armed individual; Jordan based on M. R., personal communication