

THE SOCIAL BEHAVIOR OF REHABILITATED  
BLACK-HANDED SPIDER MONKEYS (*ATELES GEOFFROYI*)

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by

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## ABSTRACT

### THE SOCIAL BEHAVIOR OF REHABILITATED BLACK-HANDED SPIDER MONKEYS (*ATELES GEOFFROYI*)

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The welfare of captive primates in laboratories, sanctuaries, and zoos is affected by various aspects of their environments. Although space restrictions increase aggression and stress-related behaviors in most captive animals, primates show diverse mechanisms for displacing stress and mitigating conflict. Many primates, including wild spider monkeys (genus *Ateles*), use these mechanisms flexibly to cope with social and environmental stressors. I investigated whether or not captive black-handed spider monkeys (*Ateles geoffroyi*) use behavioral strategies to cope with potential stressors in captivity. In particular, I tested whether an affiliative or avoidant strategy was used in response to changes in available space and enclosure choice and the expected provisioning of food. A trained volunteer assistant and I observed socially-housed black-handed spider monkeys ( $N = 17$ ) at Wildtracks, a wildlife rehabilitation center in Belize. At this site, certain groups have access to a second enclosure on a rotating basis. From June-September, 2016, we collected 337 hr of focal-animal samples, which I aggregated by individual, housing condition, and time relative to expected meals. I found that individual rates of intragroup aggression, stereotypic behavior, and self-directed behavior were significantly lower when space was increased. When I isolated the effect of enclosure choice, the differences in high-severity intragroup aggression and self-directed

behavior remained significant. These trends extended to a pair of solitary-housed adult females who were integrated during the study. Expected meals did not have widespread effects, but there was a significant increase in low-severity intragroup aggression right before meals. Although intragroup aggression varied between conditions, rates of agonism and affiliation were generally low and individuals avoided conflict. Curiously, we did not observe any embraces between individuals despite evidence that these are vital tension-reducing interactions in this taxon. The changes in self-directed and stereotypic behavior suggest that coping strategies exhibited by captive primates, especially those requiring inhibition, may incur individual costs. Overall, increased space and the choice to associate freely appear to positively impact spider monkey welfare; managers of spider monkeys should consider these factors when designing enclosures and planning management strategies.

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## CHAPTER I

### INTRODUCTION

The burgeoning field of animal welfare science is leading to unprecedented changes in the ways that animals are managed and cared for (Broom, 2011; Mason, 2010). In recent years, animals kept in zoos, laboratories and sanctuaries have received unprecedented attention as numerous studies have aimed to accurately assess and effectively improve their welfare (Hill & Broom, 2009). Of these animals, nonhuman primates are some of the most socially, ecologically, and cognitively complex; providing satisfactory living conditions for such animals is a never-ending challenge (Hosey, 2005; McCann et al., 2007). Aspects of captive environments, such as available space and management routines, can have profound effects on their health, social behavior, and psychological well-being (Morgan & Tromborg, 2007). With increasing public support for improved animal welfare, it is critical that behavioral researchers investigate how environmental factors shape the experiences and well-being of nonhuman primates held in captivity (Whitham & Wielebnowski, 2013).

Spider monkeys (genus *Ateles*) exemplify behaviorally-complex species that are not adapted to thrive in captive settings. There are between three and seven species of spider monkey (Morales-Jimenez, Disotell, & Di Fiore, 2015), all of which inhabit Neotropical forests and are in decline due to anthropogenic pressures (Estrada et al., 2017; IUCN, 2015; Ramos-Fernandez & Wallace, 2008). Wild spider monkeys spend most of their time in the forest canopy where they sleep, travel, socialize, and forage on

ripe fruit (Di Fiore, Link, & Dew, 2008; Symington, 1987a; van Roosmalen, 1985). Because of this dependence on scattered and ephemeral resources, spider monkey communities are almost always divided into smaller subgroups that change in composition, cohesion, and size throughout the day (Smith-Aguilar, Ramos-Fernandez, & Getz, 2016; Symington, 1990; Wallace, 2008a). Behavioral differences between the sexes often result in sexually-segregated grouping patterns that are unique among primates (Fedigan & Baxter, 1984; Hartwell, Notman, Bonenfant, & Pavelka, 2014; Shimooka, 2005; Slater, Schaffner, & Aureli, 2009). In such a fluid and complex society, spider monkeys must rely on avoidance, discretion, and tension-reducing behaviors to mitigate conflict in uncertain situations (Aureli & Schaffner, 2008).

Although small groups of spider monkeys are widely kept in zoos (Davis, 2009) and sanctuaries (Trayford & Farmer, 2013), they frequently exhibit atypical and intensified patterns of aggression which likely result from being housed in conditions that are incompatible with their species' social structure (Davis, Schaffner, & Wehnelt, 2009; Schaffner & Aureli, 2005). Given the amount of research that has focused on how other highly flexible species cope with changes in the captive environment (de Waal, 1989; Duncan, Jones, van Lierop, & Pillay, 2013; Judge & de Waal, 1997), it is inconsistent that the abilities of captive spider monkeys to cope with potential stressors have not been thoroughly examined.

From June to September, 2016, a field assistant and I observed the behavior of rehabilitated black-handed spider monkeys (*Ateles geoffroyi*) at a rescue center in Belize. All subjects were presumably orphaned due to the pet trade and most had been integrated

into social groups well before the study. Because three of the four groups had access to a second enclosure on a rotating basis, we were able to observe the behavior of most individuals in housing conditions with different amounts of available space and different degrees of enclosure choice. We also recorded when food was served by caregivers. Thus, I was able to examine the effects of routine changes in housing condition and a predictable feeding schedule on the welfare of these individuals. In this thesis, I have summarized the existing literature on these topics, justified my hypotheses, provided a detailed account of the study, and presented my results. In closing, I have interpreted my findings, discussed their implications, and suggested courses of action that may yield additional insight into spider monkey behavior and lead to improvements in their welfare.

## CHAPTER II

### LITERATURE REVIEW

#### Stress and Animal Welfare

The well-being of captive animals, both wild and domestic, is dependent on effective management practices and provisioning of adequate resources (Broom, 2011; McCann et al., 2007). Quality of life for captive animals is generally referred to as *animal welfare*, but attempts to standardize a universal definition for this term have fallen short (Broom, 2011; Hosey, 2005). In the simplest terms, Broom (1986) defines animal welfare as the ability of an individual animal to cope with the stressors of its environment. The American Association of Zoos and Aquariums (AZA) and the International Primatological Society (IPS) each employ the same expanded description of the measure. According to published IPS guidelines for managing captive primates (McCann et al., 2007), physical fitness, physiological condition, and psychological well-being are all crucial, measureable facets of animal welfare. Psychological health is the most difficult aspect to examine, as it depends on the innate motivations, choices, behavioral adaptations, and cognitive capacities of the individuals and species in question (Broom, 2011; McCann et al., 2007).

The welfare of captive wildlife can be assessed using diverse methodologies, many of which aim to quantify responses to stressors (Broom, 2011). Stressors are environmental conditions or stimuli that challenge homeostasis and are responded to by allostatic changes in physiology, affective state, behavior, and autonomic function

(Honess & Marin, 2006; Morgan & Tromborg, 2007; Novak, Hamel, Kelly, Dettmer, & Meyer, 2013; Sapolsky, 2000). Not all stimuli which stimulate autonomic function are stressors; certain physiological changes promote energy mobilization, including a measurable rise in circulating glucocorticoids, and enable adaptive responses such as avoidance, defense, or evasion. While the natural reaction of most animals is to simply move away from a stressor and return to homeostasis, prolonged failure to avoid or alleviate one or more stressors can result in chronic stress (Morgan & Tromborg, 2007). This condition has widespread consequences for mental, social and physical performance and can dramatically impair individual fitness (Broom, 1986; Morgan & Tromborg, 2007; Sapolsky, 2000).

Although it should not be overlooked that the stress response is a necessary adaptation to the stressors that wild animals face in their natural habitats (Sapolsky, 2000), animals held in captive settings are subjected to stressors that they do not encounter in the wild and are thus incapable of responding to adequately. These stressors include abiotic stimuli, such as anthropogenic sound and artificial lighting (Morgan & Tromborg, 2007), extremely repetitive or unpredictable husbandry routines (Bassett & Buchanan-Smith, 2007), and space restrictions (Hosey, 2005). As coping ability reflects biology, naturally active and social animals are strongly affected by enclosure size and design (Clubb & Mason, 2007; Hosey, 2005; Pomerantz, Meiri, & Terkel, 2013).

Nonhuman primates are especially susceptible to the stressors of captivity, which Hosey (2005) groups into three general dimensions: presence of unfamiliar humans, active management practices, and limited space. The relationships between human



presence, human activity, and stress are exceedingly complex. The presence of visitors has been identified as a key stressor for primates housed in zoos (Amrein, Heistermann, & Weingrill, 2014; Chamove, Hosey, & Schaetzel, 1988; Davis, Schaffner, & Smith, 2005; Hosey & Skyner, 2007) despite evidence that some interactions with visitors can be enriching (e.g., Cook & Hosey, 1995). Likewise, presence of and interaction with personnel may also be stressful for primates if the procedures are painful, invasive, unpredictable, or cause uncertainty (Chelluri, Ross, & Wagner, 2013; Coleman et al., 2008; Gottlieb, Coleman, & McCowan, 2013; Rimpley & Buchanan-Smith, 2013). While capture, restraint, immobilization, and venipuncture typically induce a stress response (Novak et al., 2013), even noninvasive husbandry procedures, such as distributing food, may have unintended consequences varying from stressful (e.g., Rimpley & Buchanan-Smith, 2013) to enriching (Bassett, Buchanan-Smith, McKinley, & Smith, 2003; Coleman & Maier, 2010; Jensvold, 2008; Jensvold, Zager, & Bismanovsky, 2013).

Similarly, seemingly benign procedures, such as serving food and cleaning enclosures, have been shown to affect primates differently depending on the context and manner in which they are conducted (Bassett & Buchanan-Smith, 2007). Because enclosed primates do not exert much control over their environment, predictability has been recommended as a way to alleviate any stress caused by husbandry routines (Bassett & Buchanan-Smith, 2007; Bloomsmith & Lambeth, 1995; Gottlieb et al., 2013). Conversely, a strict, invariable feeding regiment can also result in boredom and atypical behavior (Bloomsmith & Lambeth, 1995). Bassett and Buchanan-Smith (2007) suggest

that managers of captive primates are responsible for finding the balance of variation and predictability that best suits the needs of their individual animals.

### The Coping Model

Space restrictions are especially detrimental to animal welfare as they constrain movements, force proximity to humans, and limit individual choice in social partners and associates (Hosey, 2005; Morgan & Tromborg, 2007). Ethologists once assumed that housing in social groups directly led to stress and subsequent aggression (Archer, 1970; Calhoun, 1962; Lorenz, 1967). Laboratory experiments led to the acceptance of the density-aggression model, which posits that aggression among captive animals is a direct function of social density (Calhoun, 1962). Like the relationship between human activity and stress in captive primates, however, the relationship between available space and stress is equally intricate and variable. Early studies that aimed to assess how space influences aggression in primates suffered from experimental design flaws and a misunderstanding of primate social behavior (de Waal, 1989). Observational studies of captive primates, such as laboratory-housed pigtail macaques (*Macaca nemestrina*, Erwin & Erwin, 1976), revealed that social instability increases aggression rates much more dramatically than changes in available space.

Subsequent studies of nonhuman primates continued to yield counterintuitive results. For example, short-term spatial crowding resulted in decreased physical aggression in pigtail macaques (Anderson, Erwin, Flynn, Lewis, & Erwin, 1977), chimpanzees (*Pan troglodytes*, Nieuwenhuijsen & de Waal, 1982), and stump-tailed

macaques (*Macaca arctoides*, Demaria & Thierry, 1989). The latter studies were especially powerful; Nieuwenhuijsen & de Waal (1982) avoided confounding variables by comparing a stable group of captive chimpanzees in two familiar settings, and Demaria and Thierry (1989) found that aggression rates remained constant despite a 50-fold increase in the amount of available space.

These findings, among others, led de Waal (1989) to develop the coping model. This simple perspective on captive primate behavior proposed that “spatial crowding results in an increased risk of aggression and that the animals respond with calming gestures that serve to reduce this risk” (p. 144). In the aforementioned study of captive chimpanzees, for example, crowding was responded to by increased rates of allogrooming and submissive gestures (Nieuwenhuijsen & de Waal, 1982). Given that allogrooming is a vital tension-reducing behavior in social primates (Aureli & van Schaik, 1991; Fraser, Stahl, & Aureli, 2008; Schino, Scucchi, Maestripieri, & Turillazzi, 1988; Terry, 1970), the increased grooming engaged in by crowded chimpanzees was almost certainly a countermeasure to alleviate tension and inhibit aggression in a risky socioecological context.

In addition to a general lack of support for Calhoun's (1962) density-aggression model (de Waal, 1989; Judge & de Waal, 1997), successive testing of the coping model in a variety of contexts and species has resulted in the proposal of three strategies by which nonhuman primates mitigate aggression in confined spaces. The long-term rise in affiliative and pro-social behavior exhibited by some captive groups has been called a “tension reduction” strategy (Judge, Griffaton, & Fincke, 2006) and is accordant with de

Waal's coping model. By increasing affiliation, nonhuman primates can moderate social tension, and ease the corresponding increase in conflict. In addition to chimpanzees (Nieuwenhuijsen & de Waal, 1982), this effect has been found in rhesus macaques (*Macaca mulatta*, Judge & de Waal, 1993), bonobos (*Pan paniscus*, Sannen, van Elsacker, & Eens, 2004), and lowland gorillas (*Gorilla gorilla*, Cordoni & Palagi, 2007).

However, tension reduction is not the only strategy by which nonhuman primates maintain social stability. Using an alternative "conflict avoidance" strategy, increased spacing between individuals and the inhibition of risky social behaviors diminish the increased risk of aggression (Aureli, van Panthaleon van Eck, & Veenema, 1995).

Captive primates which have adopted this strategy include olive baboons (*Papio anubis*, Elton & Anderson, 1977), long-tailed (*Macaca fascicularis*) and rhesus macaques (Aureli et al., 1995; Judge & de Waal, 1993; Judge & de Waal, 1997), and chimpanzees (Aureli & de Waal, 1997). Recent studies have suggested that the tension reduction and conflict avoidance strategies may be complementary, not contradictory, and the degree to which individual primates adopt each is flexibly dependent on factors such as personality, sex, age, rank, degree of crowding, duration of crowding, and familiarity with group members (Cordoni & Palagi, 2007; Duncan et al., 2013; Judge & de Waal, 1997; Videan & Fritz, 2007).

The ways in which primates manage risks are not limited to allogrooming, and risk is not a direct function of space. For example, bonobos subjected to temporary crowding use more play signals and choose play partners more selectively to reduce the chance of rough play escalating into conflict (Tacconi & Palagi, 2009), and the number of

available spaces appears to be more important than the total amount of available space for mitigating conflict during chimpanzee introductions (Herrelko, Buchanan-Smith, & Vick, 2015). As evidenced and explained by Ross, Wagner, Schapiro, and Hau (2010), many of these aforementioned studies are complicated by confounding variables such as structural and climatic differences between housing conditions. In fact, Ross et al. (2010) found that aggression among captive chimpanzees was significantly higher during crowding and that aggression among gorillas also followed that general trend. Therefore, the ability of nonhuman primates to cope with space restrictions through social mechanisms may be highly dependent on context. Furthermore, researchers who study coping strategies must not only consider social interactions but also take non-social behaviors, such as self-directed and stereotypic behaviors, into consideration (Baker & Aureli, 1997; Duncan et al., 2013).

### The Coping Hypothesis

Rushen's (1993) "coping hypothesis," which focuses on non-social behaviors, is regarded as a third strategy by which primates may mitigate potential increases in stress (Duncan et al., 2013). According to this hypothesis, individual primates cope with stressors by increasing rates of self-directed displacement activities (Tinbergen, 1952), stereotypic behaviors (Mason, 1991), and other abnormal behaviors (e.g., Baker & Easley, 1996), which may moderate the stress response.

Many displacement activities are behaviors that are functional in certain contexts; although they appear irrelevant in other contexts, they may still serve an important

adaptive function by inhibiting potentially costly responses (Tinbergen, 1952). In nonhuman primates, self-directed behaviors (SDBs), such as scratching and yawning, appear to be the most common displacement activities in both captivity and the wild (Baker & Aureli, 1997; Maestripieri, Schino, Aureli, & Troisi, 1992; Troisi et al., 1991). Scratching, in particular, has been pharmacologically validated as a reliable indicator of anxiety and frustration and can therefore be a useful tool for animal welfare scientists (Schino, Perretta, Taglioni, Monaco, & Troisi, 1996; Schino, Troisi, Perretta, & Monaco, 1991; Troisi, 2002).

Stereotypic behaviors (STBs) are repetitive, habitual behaviors which show little variation in form across time and do not typically occur in wild animal populations (Mason, 1991). In primates, including humans, STBs are performed by individuals who have been diagnosed with psychological disorders, raised in abnormal conditions, given stimulating drugs, or kept in captivity for extended periods of time (Mason, 1991, 2006, 2010). In captive nonhuman primates, common STBs include repetitive locomotion patterns, such as pacing (Coleman & Maier, 2010; Pomerantz et al., 2013) and head rolling (Reamer, Tooze, Coulson, & Semple, 2010), and self-injurious behaviors such as rough hair-pulling (Hosey & Skyner, 2007; Pomerantz et al., 2013) and self-biting (Hosey & Skyner, 2007; Reinhardt & Rossell, 2001). Although seemingly maladaptive, these behaviors seem to buffer individuals from psychological trauma and chronic stress, thus contributing to homeostasis and task perseverance in stressful environments (Peterson et al., 2017; Polanco, 2016; Pomerantz, Paukner, & Terkel, 2012).

Behaviors that are not repetitive but are unique to animals kept in captive settings are called abnormal behaviors. These behaviors are difficult to study because they usually occur at low frequencies and show marked variation across time, among individuals, populations, and species (Birkett & McGrew, 2013; Birkett & Newton-Fisher, 2011; Cheyne, 2006; Lopresti-Goodman, Kameka, & Dube, 2012). A notable exception is the sequence of regurgitation and reingestion behavior that is commonly seen in captive apes (Baker & Easley, 1996; Birkett & Newton-Fisher, 2011). Even in this case, however, its relationship to stress and welfare remains unclear (Baker & Easley, 1996; Hopper, Freeman, & Ross, 2016). Although the interpretation of anomalous and abnormal behavior is a subject of open debate, common STBs are often used by animal welfare scientists as indicators of poor welfare in an animal's past or current setting (Cheyne, 2006; Latham & Mason, 2008; Mason & Latham, 2004; McCann et al., 2007; Pomerantz et al., 2013). When observed across changes in spatial density, rates of SDBs and STBs reflect the heightened aggression risk and seem to complement both conflict-avoidance and tension-reduction strategies (Baker & Aureli, 1997; Cordoni & Palagi, 2007; Duncan et al., 2013; Judge et al., 2006). As Duncan et al. (2013) note, a lack of aggression does not evidence a lack of stress. In addition to simply comparing aggression rates between conditions, non-social behavior may add to our understanding of how the environment affects captive primates.

## Spider Monkey Biology and Society

Spider monkeys (genus *Ateles*) are widely kept in zoos (Davis et al., 2009), sanctuaries (Trayford & Farmer, 2013), and even in laboratories (see Muñoz-Delgado, Sánchez-Ferrer, Pérez-Galicia, Canales-Espinosa, & Erkert, 2014; Rodas-Martínez, Canales, Brousset, Swanson, & Romano, 2013). Despite their abundance in captivity, research into their welfare is scarce and most understanding of spider monkeys comes from field research (Davis, 2009).

There may be as many as seven distinct species of spider monkey (Morales-Jimenez et al., 2015). Overall, long-term field studies of spider monkeys are few and represent only a few species (Shimooka et al., 2008). Nonetheless, some patterns of behavior appear to be consistent across sites and are considered to be characteristic of most, if not all, spider monkey populations. Spider monkeys spend most of their time in the upper canopies of tropical forests (van Roosmalen, 1985) and only rarely come to the ground (Campbell et al., 2005; Link & Di Fiore, 2013). These monkeys live in loose communities of 15-56 individuals in which adult females tend to outnumber adult males and territories are relatively consistent across years (Ramos-Fernandez, Smith-Aguilar, Schaffner, Vick, & Aureli, 2013). Unlike many species of primate, spider monkeys do not move collectively as a one- or multi-male unit. Instead, these communities are almost always split into parties called *subgroups* which vary in membership and cohesion throughout the day (Eisenberg & Kuehn, 1966; Symington, 1987a; van Roosmalen, 1985). These high rates of fission and fusion (Aureli et al., 2008) parallel those of chimpanzees and bonobos (Chapman, 1990; Chapman, Wrangham, & Chapman, 1995;



Symington, 1990) and differ from those of many similarly-sized arboreal primates (Robbins, Chapman, & Wrangham, 1991).

The most evident explanation for such fluid fission-fusion dynamics is the ephemeral and seasonal nature of resources in tropical forests. Spider monkeys are obligate frugivores and thus rely on ripe fruit, a resource that varies in abundance, distribution, and quality throughout the year (Di Fiore et al., 2008; González-Zamora et al., 2009). When the availability of food resources is variable, flexibly adjusting subgroup size effectively reduces both scramble and contest competition within spider monkey communities (Asensio, Korstjens, & Aureli, 2009; Asensio, Korstjens, Schaffner, & Aureli, 2008; Aureli, Schaffner, Asensio, & Lusseau, 2012; Smith-Aguilar et al., 2016) and may even enable them to temporarily persist in heavily disturbed habitats (Champion, 2013; Schaffner, Rebecchini, Ramos-Fernandez, Vick, & Aureli, 2012).

Because spider monkey society is fluid and flexible, the different reproductive strategies of males and females correspond with sexually-segregated patterns of association (Chapman, 1990; Fedigan & Baxter, 1984; Hartwell et al., 2014; Ramos-Fernández, Boyer, Aureli, & Vick, 2009) and interaction (Slater et al., 2009). Family units are composed of individual adult females and their immature offspring, and seek to maximize the acquisition of resources while ensuring the survival of their infants (Chapman, Walker, & Lefebvre, 1990; Chapman, 1990). Females almost always disperse from their natal community upon reaching sexual maturity (Symington, 1987b, 1990). Aggression between females is generally limited to the collective exclusion of recent immigrants and rarely leads to physical injury (Asensio et al., 2008). Females emit more

individually-recognizable contact calls, called *whinnies*, than males do (Dubreuil, Notman, & Pavelka, 2015); these calls are used to maintain appropriate spacing during foraging and movement (Ramos-Fernández, 2005, 2008; Teixidor & Byrne, 1999)

Conversely, males are philopatric (remain in the same community for life) and a community's males are usually closely related to one another (Shimooka et al., 2008; Spehar, Di Fiore, Schmitt, & Link, 2009). Immature males gradually spend less time with their mothers as they age and develop close, equitable relationships with the other males in the group as they reach sexual maturity (Rodrigues, 2007; Schaffner, Slater, & Aureli, 2012). These bonds are reinforced through frequent affiliative interactions, which include embracing, allogrooming, facial greetings, and socio-sexual behaviors (Ahumada, 1992; Aureli & Schaffner, 2007; Busia, Denice, Schaffner, & Aureli, 2016; Eisenberg, 1976; Schaffner, Slater, et al., 2012; Slater et al., 2009).

Such strong and equitable bonds allow male spider monkeys to defend their territories from neighboring groups (Aureli, Di Fiore, Murillo-Chacon, Kawamura, & Schaffner, 2013; Aureli, Schaffner, Verpooten, Slater, & Ramos-Fernández, 2006; Wallace, 2008b) and exert social control over females despite being sexually monomorphic (Campbell, 2003; Slater, Schaffner, & Aureli, 2008). While observations of direct sexual coercion and infanticide are rare (Gibson et al., 2008), scramble competition among adult males (Gibson, 2010) can lead to infanticide and lethal violence against younger males (Alvarez et al., 2015; Campbell, 2006; Rebecchini, Schaffner, & Aureli, 2011; Valero, Schaffner, Vick, Aureli, & Ramos-Fernández, 2006; Vick, 2008). Older males appear to be dominant over younger ones (Schaffner, Slater, et al., 2012),

but wild spider monkeys do not appear to have linear dominance hierarchies (Aureli & Schaffner, 2008). Many of the aforementioned aspects of spider monkey society are comparable to those of chimpanzee societies, including reciprocated bonds between males (Mitani, 2009), competition for food among females (Miller et al., 2014; Murray, Mane, & Pusey, 2007), coalitionary patrols and raids by males (Mitani & Watts, 2005), and social mechanisms for alleviating tension when subgroups meet (Okamoto, Agetsuma, & Kojima, 2001).

In captivity, the social behavior of spider monkeys has only rarely been studied (Davis, 2009). The degree to which spider monkeys utilize different coping strategies has not been thoroughly examined in a manner that excludes confounding factors (e.g., indoor-outdoor housing and seasonal weather, Cox, 1998). In large captive groups, male and females usually assume the sexually-segregated association patterns of their wild counterparts (Anaya-Huertas & Mondragon-Ceballos, 1998; Klein & Klein, 1971; Rondinelli & Klein, 1976) and exhibit similar communication mechanisms and social behaviors (Eisenberg, 1976; Eisenberg & Kuehn, 1966; McDaniel, Janzow, Porton, & Asa, 1993). Although Pastor-Nieto (2001) and Ahumada (1992) found that grooming may allow spider monkeys to create long-term bonds, research at the United Kingdom's Chester Zoo revealed that spider monkeys employed embraces, not grooming, to reduce tension in risky situations (Schaffner & Aureli, 2005). The authors suggested that the partitioning and size of the expansive exhibit ensured that inhabitants could choose their associates, thus decreasing stress and optimizing welfare (Schaffner & Aureli, 2005).

In terms of coping with stressors, Davis et al. (2005) showed that the presence of unfamiliar humans increased the stress response of the Chester Zoo's spider monkeys and Davis (2009) demonstrated that social dynamics within the group have implications for individual welfare. A survey of zoos housing spider monkeys revealed intense patterns of male-male aggression that may be the result of inappropriate social groupings and management strategies (Davis et al., 2009). Davis (2009) also suggested that scratching, an example of SDB, may be an indicator of how spider monkeys experience changes in the captive environment. Given the chimpanzee-like ability of spider monkeys to cope with stressors through social mechanisms, captive spider monkeys should use comparable strategies to moderate aggression across changes in spatial density.

### Spider Monkey Conservation and Reintroduction

A better understanding of spider monkey social behavior could also contribute to the success of conservation efforts. Like the majority of specialized and large-bodied primates (Estrada et al., 2017), spider monkey populations are in decline across their entire range (Ramos-Fernandez & Wallace, 2008). Two species of spider monkeys, *A. hybridus* and *A. g. fusciceps*, are two of the most endangered primate species in the world (Schwitzer et al., 2015). Habitat loss due to deforestation and habitat degradation due to anthropogenic disturbance are pervasive threats to all spider monkey populations (Estrada & Coates-Estrada, 1988; Estrada et al., 2017; Felton, Felton, Foley, & Lindenmayer, 2010; Mittermeier, Kinzey, & Mast, 1989; Ramos-Fernandez & Wallace, 2008; Rimbach et al., 2013; Velazquez-Vazquez et al., 2015).

The widespread fragmentation of suitable habitat makes forest-dwelling species susceptible to hunting pressure; this synergistic interaction of deforestation and exploitation causes local extinctions of spider monkeys and other atelid primates across the Neotropics (Michalski & Peres, 2005; Ohl-Schacherer et al., 2007; Peres & Palacios, 2007; Peres, 2000, 2001; Ravetta & Ferrari, 2009; Urquiza-Haas, Peres, & Dolman, 2009). Atelids are vital dispersers of large seeds and contribute to the heterogeneity of tropical forests (Link & Di Fiore, 2006; Russo, Campbell, Dew, Stevenson, & Suarez, 2005). Functional extinction of these seed dispersers leads to biodiversity loss and ecosystem collapse (Estrada et al., 2017; Levi & Peres, 2013; Peres, Thaise, Schietti, Desmoulières, & Levi, 2015) and may even exacerbate the effects of human-induced climate change (Poorter et al., 2015).

Ethnographies point out that subsistence hunters of neotropical primates often take infant monkeys as pets after pulling them from their killed mothers (Cormier & Urbani, 2008; Mittermeier et al., 1989). These infants may be kept in local communities or sold as exotic pets in the illegal wildlife trade (Duarte-Quiroga & Estrada, 2003; Fialho, Ludwig, & Valença-Montenegro, 2016; Shanee, 2012; Shanee, Mendoza, & Shanee, 2015). Confiscated, abandoned and surrendered spider monkeys may end up in rescue centers, zoos, or sanctuaries (IUCN, 2002), some of which may attempt to rehabilitate them to improve welfare (e.g., Anaya-Huertas & Mondragon-Ceballos, 1998) or to prepare them for release (Bello Santa Cruz et al., 2014; McKinney & Schutt, 2005; Trayford & Farmer, 2013).

Despite being a complex and difficult process (Campbell, Cheyne, & Rawson, 2015; Feliu & Seres, 2013; Ongman, Colin, Raball, & Humle, 2013), welfare-based rehabilitation and release of displaced primates may serve to relieve pressure from crowded sanctuaries and raise awareness for conservation efforts (Baker, 2002; Beck et al., 2007; Feliu & Seres, 2013; Guy, Curnoe, & Banks, 2014). Attempts to reintroduce displaced spider monkeys into areas where they have been extirpated have yielded promising results, but successes have been modest and the long-term ecological effects of such reintroductions remain uncertain (Bello Santa Cruz et al., 2014; McKinney & Schutt, 2005; Milton & Hopkins, 2006). As with all primate reintroductions, confirming that individuals exhibit appropriate social behaviors is a vital step to ensure individual survival and overall success (Dellatore, 2007; Goossens et al., 2005; Le Hellaye, Goossens, Jamart, & Curtis, 2010)

Wildtracks, a Belizean non-profit that has been entrusted with the rehabilitation of all displaced nonhuman primates since 2010 (Wildtracks, 2015), aims to reintroduce black-handed spider monkeys (*Ateles geoffroyi*) into protected areas of Belize from which they disappeared decades ago (Meerman & Boomsma, 1993). Wildtracks maintains rehabilitated spider monkeys in four social groups at the Primate Rehabilitation Centre and is actively trying to prepare them for release. Because Wildtracks regularly provides three of these groups access to an additional enclosure on a rotating basis, the regimented management routine allowed me to examine how changes in the amount of available space affected the social behaviors of the captive spider monkeys.

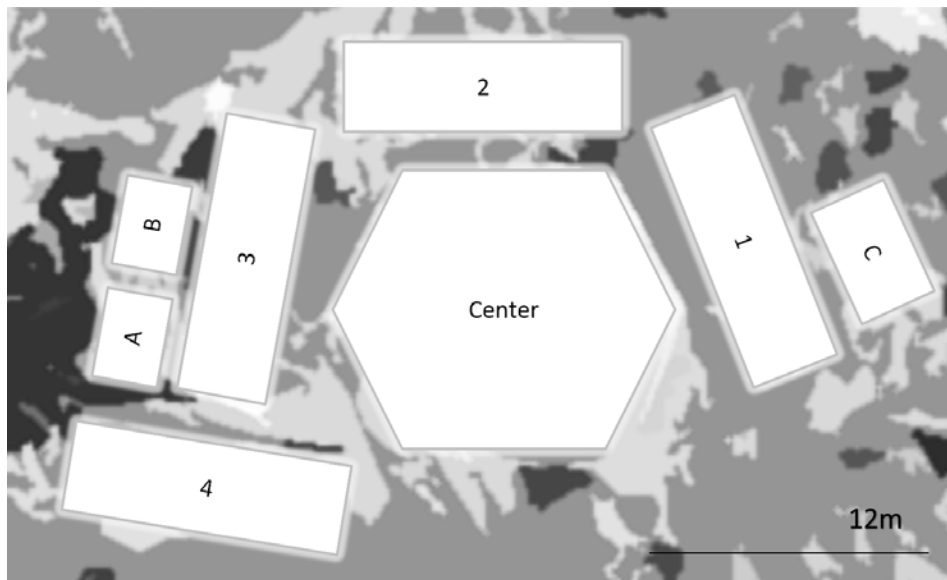
I hypothesized that patterns of behavior would follow both the coping model (de Waal, 1989) and the coping hypothesis (Rushen, 1993). I also hypothesized that the anticipation of meals would lead to increased stress-related behavior in the time intervals preceding expected meals (Bassett & Buchanan-Smith, 2007; Bloomsmith & Lambeth, 1995). The undertaking of a social integration during the study also provided me with an opportunity to determine whether a being housed with a social partner and increased space would have a similar effect on the behavior of two solitary-housed individuals. The study is a crucial piece of a comprehensive investigation to assess the reintroduction potential of these individuals by observing how they interact with their social and ecological surroundings.

## CHAPTER III

### METHODS

#### Study Site and Subjects

I conducted this study at the Wildtracks Primate Rehabilitation Centre (often referred to inclusively as just “Wildtracks”) near the coastal community of Sarteneja ( $18^{\circ} 21' 12''\text{N}$ ,  $88^{\circ} 8' 46'' \text{W}$ ) in the Corozal District of northeastern Belize. Wildtracks houses spider monkeys who are candidates for future release ( $N = 17$ ) in a complex of eight chain-link enclosures (all outlined and labeled in Figure 1). Rectangular enclosures 1-4 are called *satellite enclosures* and measure 12.2 meters long, 3.7 meters wide and 5.5



*Figure 1.* Spider monkey enclosures at Wildtracks. This diagram shows the spatial arrangement of the spider monkey enclosures at the study site. Satellite enclosures are labeled from 1-4 and single enclosures are labeled as A, B, and C.



Table 1

*Group Demographics of the Spider Monkeys in This Study*

<u>Group</u>	<u>Enclosure</u>	<u>ID</u>	<u>Age</u>	<u>Sex</u>	<u>Background</u>
1	Satellite (1)*	FG	Infant	M	Captive-born***
	Satellite (1)*	FY	Adult	F	Pet trade
	Satellite (1)*	PA	Adult	F	Pet trade
	Single (C)	FR	Adult	M	Pet trade
2	Satellite (2)*	CL	Subadult	M	Private menagerie
	Satellite (2)*	DU	Subadult	F	Pet trade
	Satellite (2)*	MA	Adult	F	Closed Zoo
	Satellite (2)*	ME	Subadult	F	Unknown
	Satellite (2)*	PE	Subadult	F	Pet trade
3	Satellite (3)*	PO	Adult	M	Pet trade
	Satellite (3)*	PP	Adult	F	Pet trade
	Satellite (3)*	RK	Adult	F	Pet trade
	Satellite (3)*	TR	Adult	F	Pet trade
4	Satellite (4)	CP	Juvenile	F	Unknown
	Satellite (4)	IZ	Juvenile	F	Pet trade
	Single (A)	MI**	Adult	F	Pet trade
	Single (B)	SV**	Adult	F	Pet trade

\* With variable access to the Center Enclosure on a rotating basis

\*\* MI and SV were integrated during the study

\*\*\* Offspring of FR and FY, born after FR's relocation

meters high (see Appendix A, Table A1 for dimensions and comparisons to other sites).

These enclosures house well-integrated social groups of 2-5 spider monkeys (group compositions are summarized in Table 1). For husbandry and enrichment purposes, caregivers manually operate sets of doors to give three of these groups access to an octahedral “Center” enclosure (see Appendix A for dimensions) on a rotating basis.

Through this routine, individuals in these three groups were interchangeably housed in two different housing conditions with different amounts of available space and

Table 2

Definitions of Housing and Feeding Conditions

<u>Condition</u>	<u>Definition</u>
<u>Housing Conditions</u>	
Normal Space	Only one enclosure, a satellite enclosure (1-4), is accessible
Increased Space*	Two enclosures, a satellite enclosure (1-3) and the Center enclosure, are accessible; the individual may be located in either enclosure
Choice*	Two enclosures, a satellite enclosure (1-3) and the Center enclosure, are accessible; the individual is located within the satellite enclosure
Solitary	The individual is enclosed in a single enclosure (A-C) with no access to another enclosure
Integrated	The individual is located in a single enclosure (A-B) with access to another adjacent single (A-B)
<u>Feeding Conditions</u>	
No meal	The individual is not scheduled to receive a meal within the next 60 minutes and has not received a meal within the last 60 minutes
Before Meal (0-15, 15-30, or 30-60)	The individual is scheduled to receive a meal within the next 0-15, 15-30, or 30-60 minutes
After Meal (0-15, 15-30, or 30-60)	The individual was scheduled to receive a meal within the last 0-15, 15-30, or 30-60 (irrespective of whether the meal was served or not)

*\* Note: these two conditions are not mutually exclusive*

numbers of available spaces (Table 2). Giving monkeys access to the Center enclosure in addition to their satellite enclosure resulted in a nine-fold increase in the amount of available space. Caregivers only restricted monkeys to the Center enclosure for brief periods of time. Three additional individuals were housed in smaller, separate enclosures (Figure 1, Table 1). One will be reintegrated upon release due to safety concerns; the

other two were integrated with each other during this study. None of these individuals or the residents of the fourth satellite enclosure were given access to the Center enclosure during the study.

Meals consisted of ripe fruit and freshly-cut browse and were served to the spider monkeys four times a day on a consistent schedule. Caregivers did not serve meals to monkeys in the Center enclosure. On most days, caregivers began preparing fruit and browse at 6:30, 10:00, 14:00 and 16:00. Although it was blocked from view and quite far away, noise from the area where meals are prepared can sometimes reach the spider monkey complex. Fresh water was available *ad libitum* and enrichment was provided regularly in the form of novel climbing structures, swinging toys, scented items, and plant materials. All spider monkeys had some artificial and natural cover from the weather and for privacy. Except for the Center enclosure, which was constructed around a living zapote tree (*Manilkara zapota*: Sapotaceae) and was considerably taller than the rest, the interiors of all enclosures are essentially the same and were furnished with small trees, tree trunks, branches, ropes, hammocks and platforms. Only a small team of caregivers, workers, researchers, and managers had access to the complex and visitors were not usually brought to within view.

#### Sampling Schedule and Timeline

Between June 10 and September 7, 2017, a volunteer field assistant and I collected 337 hours of observational data using a focal-animal sampling method (Altmann, 1974). While one of us collected focal data, the other collected data for a

related study of the same individuals. We assigned numbers to the four groups, including the three solitary-housed individuals, then employed a fixed sampling rotation so that we would never be sampling the same individuals at the same time and our observations of each individual were spread evenly throughout the day. Each day was thus divided into four observational turns (roughly 6:00-9:00, 9:00-12:00, 12:00-15:00, and 15:00-18:00).

### Focal-Animal Sampling

During each observational turn, one observer conducted focal-animal samples (Altmann, 1974) on all the individuals in one of the four groups, thus sampling each individual once per day. For each of these samples, we continuously recorded the behavioral state of the focal individual (hereafter referred to as just “the focal”) according to an exhaustive ethogram (see Appendix B, Table B1). To record data, we used the Animal Behavior Pro application for iOS, which records the absolute start and end times of all behaviors and automatically calculates the durations of each (Newton-Fisher, 2015). We recorded the occurrence of any relevant events (such as vocalizations by the focal, arrival of caregivers with meals, changes in the focal’s location, changes in the focal’s enclosure access) so that contextual variables could be continuously recorded as well.

I assessed inter-observer reliability for focal-animal sampling at the beginning of this study. To assess reliability, both observers simultaneously conducted 10 focal-animal samples (totaling 200 min) on the same individuals. During this period, each observer recorded over 1,500 behaviors. I compared the frequencies at which each

observer recorded each behavior in the ethogram, then compared the two sets of observed frequencies using a Pearson's product-moment correlation. I found a highly significant positive correlation between the two sets ( $r(25) = .995, p < 0.001$ ), indicating that inter-observer reliability was near perfect. All discrepancies between observers appeared to result from differences in visibility, not disagreements on how to classify observed behaviors.

### Aggression

Because comparing aggression rates was a key objective of this study and focal-sampling was not guaranteed to yield a sufficient sample size (see Cox, 1998; Kurtycz, Wagner, & Ross, 2014), we also systematically recorded all occurrences (Altmann, 1974) of aggression regardless of actor. The good visibility across enclosures, combined with the conspicuous manner in which spider monkeys perform and react to aggressive behaviors (Ordóñez-Gómez et al., 2015), ensured that any bouts of aggression would be noticed by one or both observers and recorded appropriately. We always recorded the behavioral components and contextual variables of each aggression using the same definitions shown in Appendix B and Table 2. *Post hoc*, I isolated aggressions that occurred between group members and categorized each instance of intragroup aggression as “high-severity” or “low-severity” based on its behavioral components. High-severity aggressions contained at least one component of physical contact (e.g., a bite, slap or grab) whereas low-severity aggressions did not.

Because we recorded aggressive behaviors by any individual, regardless of whether they were the current focal or not, I estimated individual rates of aggression in each housing and feeding condition using the equation:

$$A_{xc} = \frac{N}{\frac{F}{M} \times D}$$

where  $A_{xc}$  equals the aggression rate (aggressive behaviors per minute) of individual  $X$  in condition  $C$ ,  $N$  equals the number of aggressive behaviors by  $X$  in  $C$ ,  $F$  equals the amount of focal minutes  $X$  spent in  $C$ ,  $M$  equals the total amount of focal minutes in which  $X$  was the focal, and  $D$  is the total duration of all focal samples for all individuals. Thus, I could estimate the aggression rate of each individual in each housing condition using data obtained *ad libitum* while sampling other individuals. Although these results must be interpreted conservatively, this method provided a richer dataset and allowed for a more thorough comparison of aggression rates across conditions.

## Statistical Analysis

The Animal Behaviour Pro application saved focal samples as independent, comma-delimited spreadsheet (CSV) files, which I aggregated at the end of the study. Because we only recorded the times at which meals were served but did not continuously record feeding condition, I added these values *post hoc* according to the definitions of each condition (which are explained in Table 2). I performed all statistical analyses using R (R Core Team, 2013).

Parametric statistics were inappropriate and data transformations were difficult due to the limitations of my data set (multiple outliers and zero-values led to highly-

skewed distributions). Therefore, I limited my analysis to nonparametric tests. I tested for significant differences between “Normal” and “Increased Space” housing conditions using asymptotic, two-tailed Wilcoxon signed-rank tests, which use Pratt’s (1959) method for handling zeros and ties. In addition to comparing behavior between those conditions, I followed the lead of Kurtycz, Wagner, and Ross (2014) and isolated the potential effect of enclosure choice on rates and relative durations of each behavior (“Normal” vs. “Choice”) using similar signed-rank tests.

To test for differences in relation to expected meal times, I defined expected meal times as the average times at which meals were provisioned by caregivers. Following Bloomsmith and Lambeth (1995), I then binned behavioral data according to the time interval (in minutes) until the next expected meal or time since the last meal was served. I aggregated the data into bins representing the time intervals outlined in Table 2. I used Kruskal-Wallis tests for multiple comparisons to determine which behaviors varied across time intervals, then tested for pairwise differences using paired Wilcoxon signed-rank tests. I adjusted the resulting  $p$ -values to control for false discovery rates (Benjamini & Hochberg, 1995)

I constructed plots using the ggplot2 package (Wickham, 2009) in RStudio (RStudio Team, 2015). Because of the small sample size and striking individual variation, I could not reliably test for any effects of sex, age, or rearing history. I also chose to omit the infant FG from most analyses, as his behavior was radically different from that of older individuals (Vick, 2008). For all tests, the sample size was the number of individuals who were housed in the conditions tested. I set all  $\alpha$ -values at 0.05.

## Ethical Statement

All protocols were approved by Central Washington University's Institutional Animal Care and Use Committee (Protocol #A111501) and followed the Code of Best Practices for Field Primatology as published by the International Primatological Society (Riley, Mackinnon, Fernandez-Duque, Setchell, & Garber, 2014).



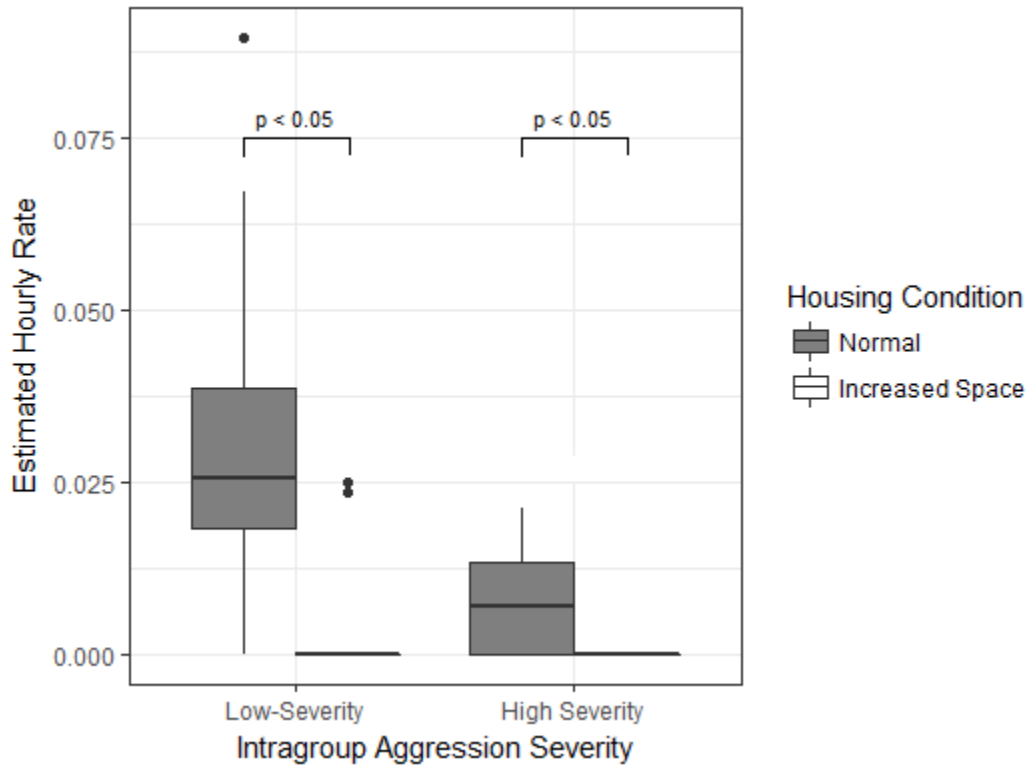
## CHAPTER IV

### RESULTS

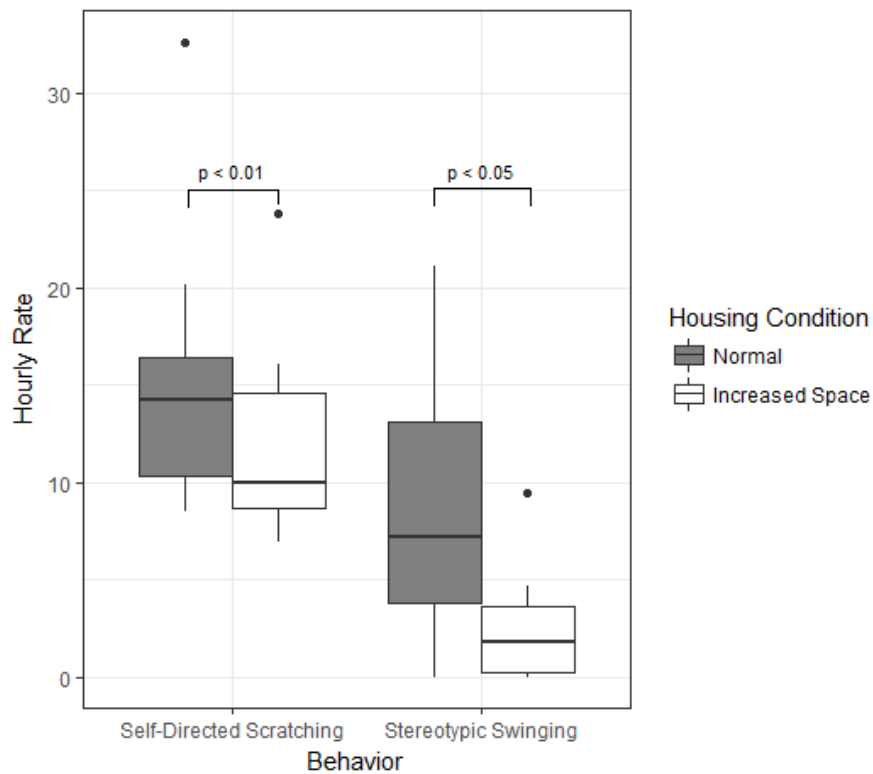
#### Increased Space

Between the “Normal” and “Increased Space” conditions, there were no significant differences in median rates of all aggressions, self-grooming, yawning, allogrooming, sitting in proximity, or social play (see Appendix C, Table C1 for the corresponding  $Z$  and  $p$ -values). Whinny vocalizations tended to be more frequent in the “Increased Space” condition, although this trend was marginally insignificant (Wilcoxon  $Z = -1.89$ ,  $p = .06$ ). Despite the consistency of overall aggression rates, rates of intragroup aggression ( $Z = 2.55$ ,  $p < .05$ ), high-severity intragroup aggression ( $Z = 2.39$ ,  $p < .05$ ), and low-severity intragroup aggression ( $Z = 2.55$ ,  $p < .05$ ) were all lower in the “Increased Space” condition (Figure 2). We did not observe any instance of high-severity aggression between individuals housed in the “Increased Space” condition. Rates of stereotypic behaviors ( $Z = 2.55$ ,  $p < .05$ , including stereotypic swinging,  $Z = 2.55$ ,  $p < .05$ ) and self-directed behaviors ( $Z = 2.60$ ,  $p < .01$ , including scratching,  $Z = 2.70$ ,  $p < .01$ ) were lower in the “Increased Space” condition (Figure 3). There was no significant difference in the proportions of time spent moving ( $p = .58$ ) or inactive, although the latter was only marginally insignificant (45.3% of non-feeding time in the “Normal” condition, 58.4% in the “Increased Space” condition,  $p = .06$ ). I did not analyze for differences in feeding and co-feeding behavior, as caregivers occasionally withheld the third meal from the monkeys to encourage them to move into the satellite enclosures. Appendix C (Table C1) shows the median hourly rates of each behavior in each space

condition, as well as the sample sizes, degrees of freedom, and results of the signed-rank tests.



*Figure 2.* The effect of housing with increased space on intragroup aggression. This box plot compares median individual rates of intragroup aggression between “Normal” and “Increased Space” housing conditions. Outliers are represented as black dots. Intragroup aggression is categorized by severity and *p*-values denote differences that were statistically significant between conditions.

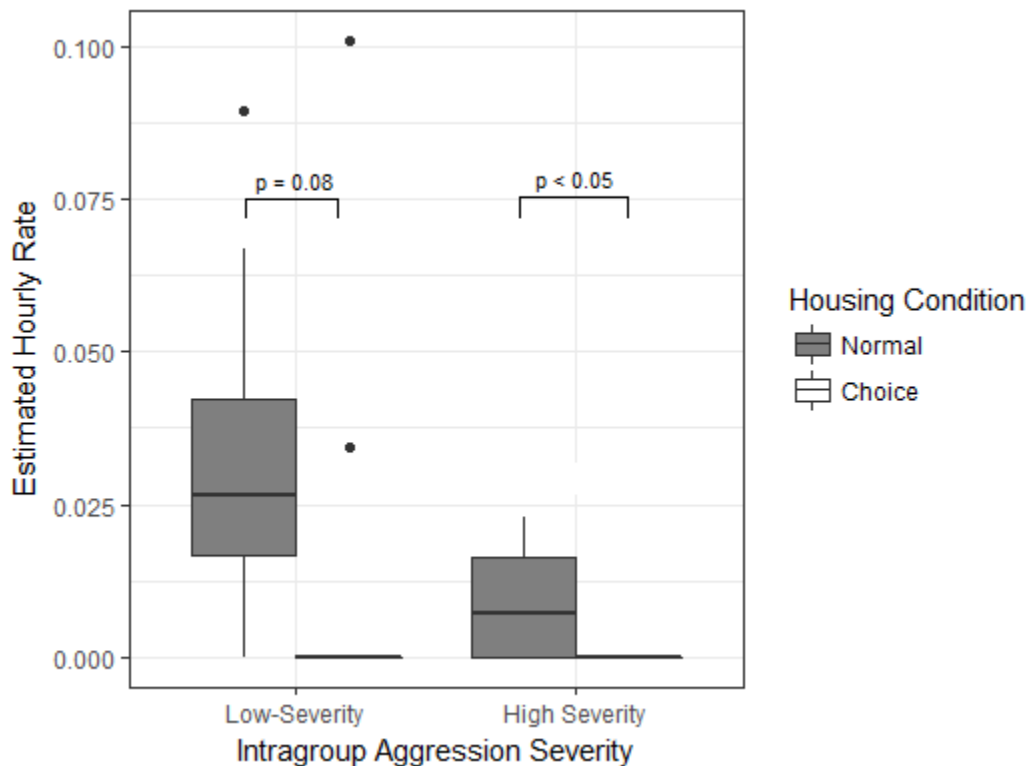


*Figure 3.* The effect of housing with increased space on non-social behaviors. This box plot compares median individual rates of two non-social behaviors (scratching, the most frequent SDB, and swinging, the most prevalent STB) between “Normal” and “Increased Space” housing conditions. Outliers are represented as black dots. *P*-values denote differences that were statistically significant between conditions.

#### Enclosure Choice

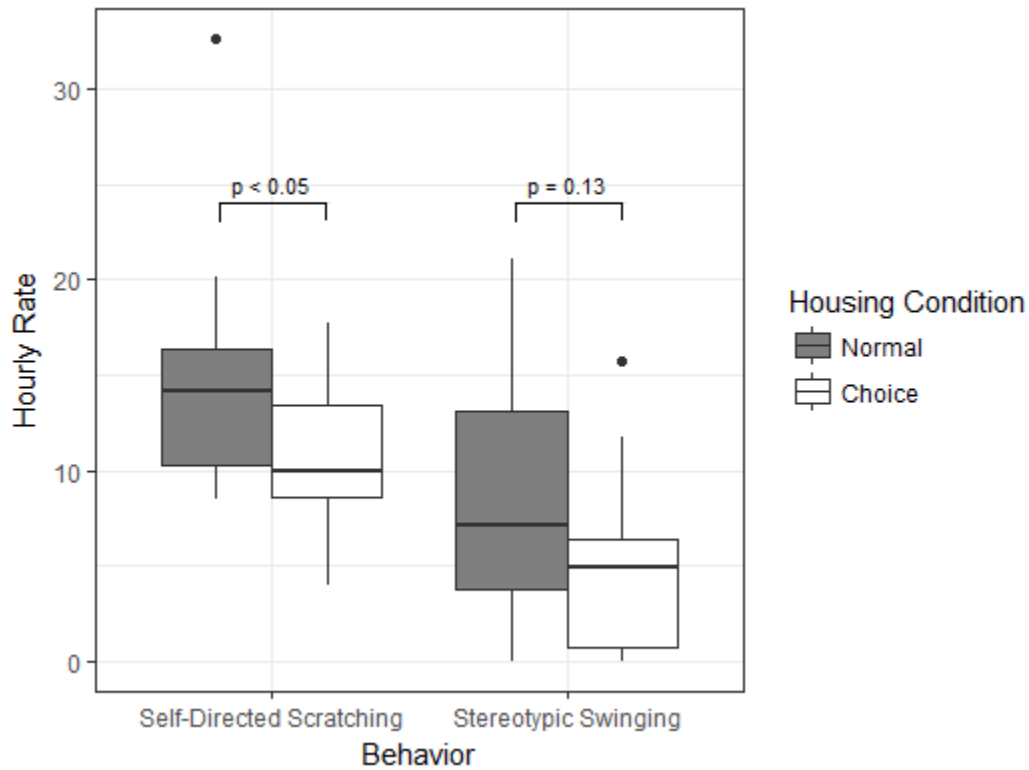
Between the “Normal” and “Choice” conditions, there were no significant differences in median rates of all aggressions, stereotypic behavior, stereotypic swinging, self-grooming, yawning, allogrooming, social play, whinny vocalizations, feeding alone, or co-feeding (see Appendix C, Table C2 for the corresponding *Z* and *p*-values).

Although there was no significant difference in between rates of all aggressions, rates of intragroup aggression were lower when individuals had choice of enclosure ( $Z = 2.04, p < .05$ ). Within the intragroup aggression category, rates of high-severity intragroup aggression were lower in the “Choice” condition ( $Z = 2.388, p < .05$ ) and there was a similar trend in rates of low-severity intragroup aggression between conditions that approached significance ( $p = .08$ , Figure 4). There were no occurrences of high-severity



*Figure 4.* The effect of housing with enclosure choice on intragroup aggression. This box plot compares median individual rates of intragroup aggression between “Normal” and “Choice” housing conditions. Outliers are represented as black dots. Intragroup aggression is categorized by severity and  $p$ -values denote differences that were statistically significant across conditions.

aggression between individuals housed in the “Choice” condition. Rates of self-directed behaviors ( $Z = 1.99, p < .05$ , including scratching,  $Z = 1.99, p < .05$ ) were also lower in the “Choice” condition (Figure 5). The rates at which individuals sat in proximity (within



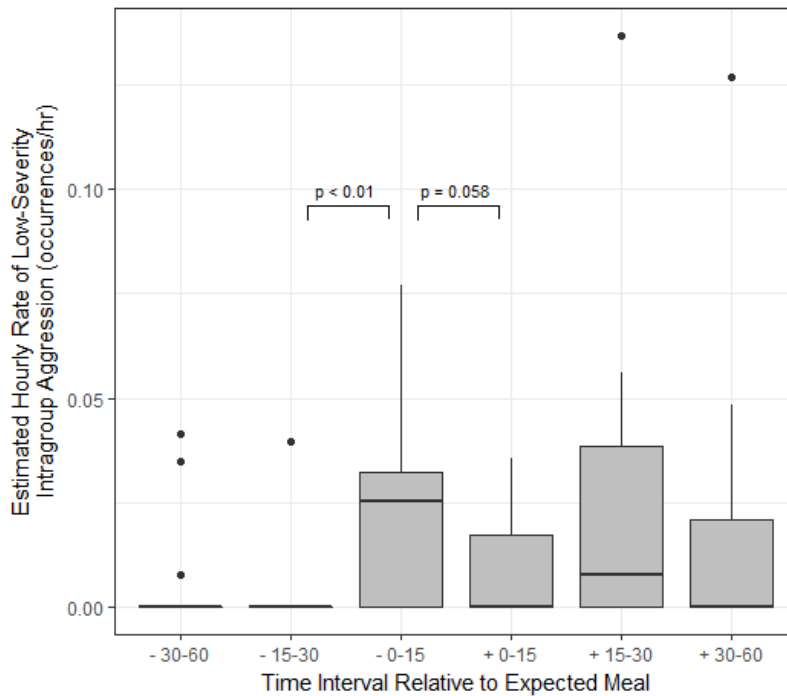
*Figure 5.* The effect of housing with enclosure choice on non-social behavior. This box plot compares median individual rates of two non-social behaviors (scratching, the most frequent self-directed behavior, and swinging, the most frequent and prevalent stereotypic behavior) between “Normal” and “Choice” housing conditions. Outliers are represented as black dots. *P*-values denote differences that were statistically significant across conditions or showed a trend towards significance.

one meter) with others were lower when they had a choice in enclosure ( $Z = 1.99, p < .05$ ). There were no significant differences in movement ( $p = .39$ ) or inactivity ( $p = .80$ ) between conditions. Appendix C (Table C2) shows the median hourly rates of each behavior in each condition, as well as the sample sizes, degrees of freedom, and results of the signed-rank tests.

### Expected Meals

The mean times at which caregivers served the first, second, third, and fourth meals were 7:12 ( $n = 124, SD = 12$  min), 10:37 ( $n = 74, SD = 11$  min), 14:41 ( $n = 124, SD = 11$  min), and 16:38 ( $n = 122, SD = 14$  min), respectively. Because the meals were distributed throughout the day, I omitted the few data that were more than 60 min before or after the closest expected meal time from these analyses. Appendix C (Table C3) shows median hourly rates of each behavior across feeding conditions, as well as the sample sizes and degrees of freedom. Across time intervals, there were no significant differences among median hourly rates of all aggressions, all stereotypic behaviors, stereotypic swinging, all self-directed behaviors (excluding yawning), self-directed scratching, self-grooming, allogrooming, sitting in proximity, social play, or whinny vocalizations (see Appendix C, Tables C4 for corresponding Kruskal-Wallis  $X^2$  and  $p$ -values).

Although there was no difference in rates of all aggressions, rates of intragroup aggression varied across time intervals (Kruskal-Wallis  $X^2(16, 5) = 11.4, p < .05$ ). Rates of high-severity intragroup aggression did not vary relative to expected meals



*Figure 6.* The effect of expected meals on low-severity intragroup aggression. This box plot compares median individual rates of low-severity intragroup aggression across time intervals relative to the closest expected meal time. Outliers are represented as black dots. Adjusted *P*-values denote differences that were statistically significant between successive intervals.

( $X^2(16, 5) = 2.71, p = .75$ ) but rates of low-severity intragroup aggression did ( $X^2(16, 5) = 13.16, p < .05$ , Figure 6). Pairwise comparisons between these rates showed that low-severity intragroup aggression increased significantly between the 15-30 min and 0-15 min intervals before expected meals ( $Z = -2.93, p < .01$ , Figure 6). There was also a decrease in low-severity aggression rates between the 15 min before and 15 min following expected meals; this trend approached significance ( $Z = -1.47, p = .06$ , Figure

6). Differences in rates of yawning were highly significant across time intervals ( $X^2(16, 5) = 26.46, p < .001$ ) although this was skewed by a consistent decrease in yawning as the day progressed; this consistent decrease was evidenced by differences in yawning across successive observational turns ( $X^2(16, 3) = 20.682, p < .001$ ). There were no significant differences in movement ( $X^2(16, 5) = 8.99, p = .11$ ) or inactivity ( $X^2(16, 5) = 9.14, p = .10$ ) across intervals. Appendix C shows the results of the Kruskal-Wallis tests for all behaviors across the same time intervals (Table C4) and the results of pairwise comparisons between successive intervals with adjusted  $p$ -values (Table C5).

### Social Integration

During this study, caregivers opened the door separating two adult females, MI and SV, which gave each individual continuous access to the two spaces and an opportunity to socialize with the other. Both before and after this social integration, both females exhibited very low hourly rates of aggression, allogrooming, sitting in proximity, social play, and whinnies (see Table C6 in Appendix C). MI's hourly rates of stereotypic behavior (always a form of stereotypic swinging) and overall self-directed behavior (especially scratching and self-grooming) were lower after the integration (STB: 21.54 before/14.55 after; SDB: 25.54 before/18.12 after). MI also spent considerably more of her time inactive (43.4% before/53.5% after), an effect that was not as pronounced for SV (49.8% before/52.4% after). SV showed a slight increase in stereotypic behavior after the integration, but hourly rates of self-directed behaviors decreased (STB: 12.98



before/15.58 after; SDB: 11.65 before/8.28 after). Table C6 (Appendix C) shows rates of all behaviors for each female in the “Solitary” and “Integrated” conditions.

## CHAPTER V

### DISCUSSION

#### Space and Aggression

There was limited evidence that these individuals utilized social behavior to cope with space restrictions or variable amounts of available space. The patterns we observed contradicted the widely-supported coping model (de Waal, 1989) and were suggestive of a more direct relationship between space and aggression that followed the density-aggression model (Calhoun, 1962). Other authors have noted the potential confounding factors of studies that support the coping model; these factors include access to the outdoors and the presence of different features (Kurtycz et al., 2014). The Wildtracks complex provided a near-ideal setting for testing the coping model, as all enclosures are outdoors, contain similar features, and have the same infrequent exposure to humans. Furthermore, the Wildtracks monkeys had been familiar with the Center enclosure for almost two years before the start of my study, thus minimizing the potential effects of novelty and uncertainty.

For the 11 individuals who had rotating access to the Center enclosure, the nine-fold increase in the amount of available space every third day resulted in decreased rates of intragroup aggression and a complete absence of high-severity aggression. The remarkable rarity of intragroup aggression (only three occurrences in the “Increased Space” condition across the entire study) indicates that having access to the Center enclosure momentarily reduces the risk of conflict and injury within groups. Therefore, it

appears that having such a dramatic increase in the amount of available space on a regular basis could improve welfare by reducing stressful conflicts and minimizing injury risk.

Intensified aggression between captive spider monkeys has been attributed to space restrictions and inappropriate management practices (Davis et al., 2009; Klein & Klein, 1971). Some researchers have suggested that these stressful and risky conflicts can be alleviated by giving spider monkeys the opportunity to fission and fusion at will, thereby spending more time with preferred associates and less time with potential agonists (Davis et al., 2009; Schaffner & Aureli, 2005). While the satellite enclosures housed monkeys in social densities that were similar to those at other captive sites, the Center enclosure alone provided individuals with as much space as some large, outdoor zoo exhibits (Appendix A, Table A1) and seemed to allow individuals to effectively avoid conflicts.

Interestingly, there was a complete absence of embraces during this study. The exchange of embraces (and simultaneous pectoral sniffs) has been widely reported as the key tension-reducing behavior in wild, captive, and rehabilitated spider monkey groups (Aureli & Schaffner, 2007; Eisenberg, 1976; Klein & Klein, 1971; Pastor-Nieto, 2001; Schaffner & Aureli, 2005). The reason why we did not observe any embraces is unclear. We did note that many individuals appeared to solicit pectoral sniffs by presenting their chests to caregivers and researchers; two females, FY and PE, regularly attempted to embrace and sniff caregivers through the caging. The Wildtracks directors reported that FY and another female, PA, embraced shortly after FY gave birth to her first infant. This

event occurred approximately 15 months before I began data collection for this study. Both field and captive studies have shown that embraces facilitate alloparental interactions in such contexts (Evans, Pavelka, Hartwell, & Notman, 2012; Schaffner & Aureli, 2005; Slater, Schaffner, & Aureli, 2007; Watt, 1994). Even orphaned infants in the nursery showed a fixation with their own sternal glands while affiliating with caregivers. In summary, there is some evidence that these spider monkeys are capable of embracing.

Alternatively, I propose that the lack of embraces lends partial support to the conflict avoidance strategy proposed by Judge and de Waal (1993). Unlike the tension-reducing strategy of primates following de Waal's coping model (1989), an expected rise in aggression may be countered by an inhibition of social behavior. The findings that embraces were nonexistent and allogrooming was uniformly infrequent both suggest that these spider monkeys may be inhibiting social behavior in all contexts. This inhibitory strategy has been reported in chimpanzees (Aureli & de Waal, 1997) and seems to be the predominant strategy by which they cope with short-term crowding (Duncan et al., 2013; Videan & Fritz, 2007). Behavioral inhibition is a necessary cognitive ability of socially complex species with high fission-fusion dynamics (Amici, Aureli, & Call, 2008). The low rates of aggression and social behavior found in this study parallel those of captive chimpanzees housed in similar conditions (Aureli & de Waal, 1997; Duncan et al., 2013; Ross et al., 2010; Videan & Fritz, 2007) and suggest that these spider monkeys are capable of avoiding conflict to cope with temporary space restrictions. We also noted that the Wildtracks spider monkeys took turns rather than bypass each other in doorways;

even in the Center enclosure, individuals seemed to take longer travel routes if the shortest route brought them into close proximity with another individual. A related study of patterns of proximity between individuals may reveal patterns of avoidance in certain conditions. There is evidence from field studies that females actively avoid encounters with adult males (Chapman, 1990; Slater et al., 2008; Smith-Aguilar et al., 2016), and it will be useful to know whether captive females do the same.

Although this strategy may reduce conflict, the avoidance of group members and inhibition of social behavior may be detrimental to individual well-being. Previous studies by Baker and Aureli (1997) and Duncan et al. (2013) showed that self-directed behaviors, especially scratching, increased when individuals were housed in stressful conditions. I found a similar effect of space restrictions on self-directed and stereotypic behaviors; these behaviors are frequently used by primatologists as indicators of anxiety, uncertainty, or heightened arousal (Maestripieri et al., 1992; Mason, 2006). It appears that these individuals use non-social mechanisms of coping with stressors, especially stereotypic swinging and self-directed scratching, in accordance with the coping hypothesis (Rushen, 1993). These mechanisms also seem to facilitate the behavioral inhibition required for short-term conflict avoidance (Aureli et al., 1995). Therefore, notwithstanding the low rates of affiliation, the reduction in self-directed and stereotypic behaviors and absence of severe aggression suggest that having access to an additional enclosure dramatically improves the welfare of these spider monkeys.

## Enclosure Choice

Using the method described by Kurtycz et al. (2014), I attempted to distinguish the effects of enclosure choice from those of increased space. Therefore, this analysis tested for how the perception of additional space affected individual behavior while accounting for the possibility that individuals might have used the two enclosures for different behaviors. Even when they were located in the satellite enclosure, focals who had access to the Center enclosure (i.e., housed in the “Choice” condition) showed lower rates of intragroup aggression and self-directed behaviors. There are two explanations for this difference that are not mutually exclusive: increased escape opportunities and increased spacing between individuals. The perception of available space has been cited as a key determinant of stress and agonism in captive chimpanzees, with increased complexity leading to greater capacity to escape aggressors (Caws & Aureli, 2003; Herrelko et al., 2015). Therefore, it is possible that access to a second enclosure prevented conflicts from escalating in severity. In fact, not a single instance of high-severity aggression occurred between individuals housed in the “Choice” condition. The alleviatory effect of additional space may be amplified by the expansive height of the Center enclosure. Given that spider monkeys often avoid attackers by changing their height relative to their aggressor (Klein & Klein, 1971), the increased vertical space may serve to improve welfare as it does with captive chimpanzees and gibbons (Anderson, 2014; Caws, Wehnelt, & Aureli, 2008).

## Meal Predictability

The effect of choice was not limited to space use, however. In the wild, spider monkeys have opportunities to choose where, when, and what to eat based on predictable patterns of availability. In this free-ranging context, alterations in the predictability and availability of food resources may be stressful (e.g., Rimbach et al., 2014). How meal provisioning affects captive spider monkeys, however, remains uncertain.

In general, I found few significant differences across time intervals, but the increased rate of low-severity intragroup aggression right before expected meals may indicate anticipation of food provisioning. Wild spider monkeys, especially adult females, engage in frequent disputes during foraging that rarely result in severe aggression (Asensio et al., 2008). Therefore, an increase in minor conflicts around expected meal times may be normal. However, given that low-severity aggression was not injurious, whether increased competition before meals impacts welfare is unclear.

Our observations suggested that the monkeys could occasionally hear caregivers preparing fruit and browse even though all of the preparation was performed out of sight. On the rare days when meal preparation took longer than usual, the anticipation of meals may have resulted in increased stress responses and possibly even anxiety (Waitt & Buchanan-Smith, 2001). The finding that most behaviors did not vary across time intervals may reflect my decision to aggregate the data into shorter bins (15-30 minutes each). However, given that four meals were served each day, the effect of anticipation may be blunted by the high frequency of meals. Indeed, caregivers have noted that some individuals voluntarily forego the fourth meal to remain in the Center enclosure

overnight. In captive settings where only one or two meals are served, the impact of predictability may be much more pronounced. Since meals were evenly distributed in the morning and afternoon when spider monkeys are the most active (Symington, 1987a; van Roosmalen, 1985) and there seem to be no obvious effects on rates of stress-related behavior, it appears that these practices are conducive to good spider monkey welfare.

### Social Integration

The opportunity to observe MI and SV before and after their integration provided some insight into how the change impacted their welfare. The few reports of social integration between captive spider monkeys highlight the unpredictability and variability of this process. For example, Klein and Klein (1971) reported that attempted integrations were rarely successful (although they also noted that their colony was abnormally crowded). By contrast, integration of an adult male into an established group at the Chester Zoo was relatively relaxed and successful (Davis, 2009). In general, integrations between males seem to be much more tense and risky than those between females (Davis, 2009; Davis et al., 2009), possibly because spider monkey males are generally philopatric and fiercely territorial (Aureli & Schaffner, 2008; Schaffner, Slater, et al., 2012).

Following the observed integration, the two adult females rarely interacted and were almost never in proximity to one another. This lack of affiliation does not necessarily constitute incompatibility; in the wild, female spider monkeys associate in patterns that are often indiscernible from random aggregations (Ramos-Fernández et al., 2009), and affiliative interactions between unrelated females are rare (Slater et al., 2009). Pastor-Nieto (2001) suggested that allogrooming facilitates long-term tolerance and



sharing of resources in captive spider monkeys, but these patterns develop over long periods of time. Since caregivers continued to provision individuals in separate enclosures, tolerance during feeding was not an immediate priority for MI and SV.

Although having a social partner did not seem to produce any instantaneous benefits for either individual, the continuous access to two enclosures that accompanied the integration may have caused the observed changes in non-social behavior. MI's behavior changed dramatically following the integration; she exhibited lower rates of stereotypies and self-directed behaviors but spent considerably more time inactive. SV showed less self-directed behaviors as well. These changes are indicative of decreased arousal and suggest that the associated spatial changes had a calming effect. Although they documented more frequent affiliation, similar calming effects were observed in laboratory-housed rhesus macaques following social integration (Baker et al., 2012, 2014). The mere presence of a conspecific, combined with access to more space, may help captive primates cope with the stressors of captivity by buffering the stress response (Gilbert & Baker, 2011). The integration of MI and SV, at least in the short-term, appeared to improve the welfare of both individuals in the weeks that followed.

#### Implications for Future Research and Management

Throughout this study, we documented various behaviors that did not fit the descriptions of any behaviors previously described for this genus. Stereotypic behavior in captive spider monkeys, for example, has only been reported sporadically (Márquez-Arias et al., 2014; Pomerantz et al., 2013); detailed descriptions are absent from the

literature. During this study, all individuals exhibited stereotypic swinging except for TR, an adult female, and FG, the male infant. In addition to widespread swinging, MA frequently engaged in stereotypic rocking, and two individuals, IZ and PO, exhibited a stereotypic head-rolling behavior. The “smush-face” behavior frequently exhibited by several individuals also appeared to be stereotyped. Although we recorded them as non-stereotypic SDBs, compulsive masturbation and certain forms of self-touching (e.g., MI’s eye-poking) may actually be stereotypic in origin. Although it was apparently exhibited by some individuals, I chose not to regard stereotypic pacing as a discrete behavior, as it was often difficult to discern from regular, non-stereotypic locomotion. Therefore, our interpretations of stereotypic behavior may be too conservative.

It is important to note that stereotypies are prevalent in orphaned and confiscated nonhuman primates (Botero, MacDonald, & Miller, 2013; Lopresti-Goodman et al., 2012; Moore, Cabana, & Nekaris, 2015; Wobber & Hare, 2011). Thus, there is no evidence that these behaviors result from the Wildtracks setting. Studies of how rates of stereotypies change over long time spans may provide more insight into how the rehabilitation process benefits individual welfare. However, these results indicate that immediate changes in the captive environment may influence the rates at which these stereotypic behaviors are expressed and possibly demonstrate how captive spider monkeys subjectively experience these changes.

We also observed several non-stereotypic behaviors that seem highly unusual for spider monkeys but may not be associated with welfare. These included coprophilous behavior like that reported by Márquez-Arias et al. (2014), excavation and attempted

consumption of lizard eggs, masturbation using a water bottle fixed to the caging, partial burying of the tail by piling sand around it, the catching and subsequent carrying of live frogs and toads, and resting with the ventral surface flat on the ground with limbs splayed (a potential thermoregulatory behavior). Curiously, we observed DU draping provisioned browse over her neck and waist before swinging or leaping across the enclosure on numerous occasions. I speculate that this behavior may be a parallel to the “draping” behavior occasionally reported in wild hominoids (McGrew & Marchant, 1997; Nishida, Matsusaka, & McGrew, 2009) and commonly seen in enculturated apes (Carrasco, Posada, & Colell, 2009; Subiaul, 2016).

The degree to which these unusual behaviors are socially-transmitted remains unclear. There is evidence that spider monkeys, like large-bodied apes (Whiten, 2000; Whiten & van Schaik, 2007), have traditions that vary among wild populations and demonstrate a behavioral capacity for culture (Santorelli et al., 2011). In chimpanzees, even rehabilitated individuals housed in a rescue center have spontaneously innovated new traditions and transmitted them to group members (van Leeuwen, Cronin, & Haun, 2014). The tail-wrapping behavior described by Klein and Klein (1971) and coprophilia mentioned by Márquez-Arias et al. (2014) may also be socially-transmitted behaviors among captive spider monkeys. If there is indeed cultural variation among captive spider monkeys, especially in rehabilitation centers, a thorough assessment of how this variation affects management, welfare, and conservation would be appropriate (Whitehead, 2010).

It is also unclear whether having access to increased space on every third day affected the behavior of the monkeys on the other days. Because our study groups had

been habituated to this pattern of management for some time, I was unable to examine this possibility. Whereas three of the groups housed in satellite enclosures had intermittent access to the Center enclosure at the time of this study, the two juveniles housed in a fourth satellite enclosure did not. The ongoing plan to integrate them with other individuals, possibly nursery-reared orphans or MI and SV, will likely be followed by introduction to the Center enclosure on an intermittent basis. Close monitoring and systematic observation of their behavior may provide insight into how temporary access to a second enclosure impacts welfare on a broader scale.

Perhaps the most interesting implication of these results is that the relationship between available space and social behavior may translate to the reintroduction process. If allowing intermittent access to the Center enclosure dramatically changes the behavior of these individuals, these findings may help Wildtracks managers to predict how the spider monkeys will transition from a pre-release enclosure to the wild. Reintroduction has been lauded as a potential welfare tool (Guy et al., 2014) provided that released individuals interact in a species-specific manner (Le Hellaye et al., 2010) and appropriately cope with the stressors of their new environments (Dellatore, 2007). Thorough post-release monitoring (Beck et al., 2007) will likely allow a more conclusive examination of how the processes of rehabilitation and reintroduction impact the welfare of captive spider monkeys.

## CHAPTER VI

### CONCLUSION

This study shows that spider monkeys have diverse coping mechanisms, and that these mechanisms become less necessary as individuals are allowed a greater degree of available space and choice. Rates of conspecific aggression and self-directed behaviors seemed to be the most affected by changes in available space and enclosure choice. However, I found no evidence of social behavior being used to regulate tension; thus, these findings do not support de Waal's coping model (1989). Instead, the observed behavioral changes suggest the existence of an alternative, imperfect strategy based on conflict avoidance (Aureli & de Waal, 1997; Aureli et al., 1995) and self-directed displacement (Rushen, 1993). The absence of high-severity aggression when individuals were allowed to choose their enclosure suggests that increased space and choice reduce the risk of stressful conflict and injury. Thus, having access to the Center enclosure seems to dramatically improve the welfare of these spider monkeys. I also noted similar behavioral changes in two solitary-housed females who were socially integrated during this study.

Across groups and enclosures, I found few significant behavioral differences in relation to expected meals, suggesting that food was provisioned in a manner accordant with spider monkey welfare. Further analysis of data collected at this site can determine whether the presumed effects of space and choice influence the patterns in which individuals associate with one another. Subsequent studies of these spider monkeys

during later stages in the rehabilitation and reintroduction process may also reveal how a complete removal of artificial space restrictions affects their behavior. Comparing these patterns to those of wild individuals will be a key component in assessing reintroduction success. Additionally, this study provides further evidence that spider monkey behavior is flexible, variable, and influenced by environmental conditions. Thorough examinations of captive spider monkey behavior may reveal new patterns of sociality and thereby aid various management and conservation efforts.

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## APPENDIX A

Table A1

### *Housing of Spider Monkeys in Captivity*

<u>Source(s)</u>	<u>Housing Type</u>	<u><i>n</i>*</u>	<u><i>A</i> (m<sup>2</sup>)</u>	<u><i>V</i> (m<sup>3</sup>)</u>	<u><i>D</i> (<i>n/V</i>)</u>
Pomerantz et al. (2013)	NA	8	43.0	NA	NA
Watt (1994)	Wire-mesh exhibit with small holding area	17	140.0	420.0	0.040
Rodrigues et al. (2015)	Mixed-species indoor exhibit	8	929.0	863,097	0.000
Rodrigues et al. (2015)	Off-exhibit night housing	~2	15.6	38.1	0.052
Pastor-Nieto (2000, 2001)	Temporary outdoor enclosures plus feeding area	9	39.8	NA	NA
Davis et al. (2005); Schaffner & Aureli (2005)	Outdoor/indoor exhibit with off-exhibit areas	7.5	963.0	NA	NA
Ordóñez-Gómez et al. (2015)	Outdoor cage	7	17.4	55.6	0.126
Anaya-Huertas & Mondragon-Ceballos (1998); Ordóñez-Gómez et al. (2015)	Outdoor cage (urban surroundings)	10	37.2	223.2	0.045
Scheel & Edwards (2012)	Indoor exhibit/off-display rooms	2.33	145.0	580.0	0.004
Eisenberg (1976)	Outdoor enclosure (summer months only)	4.5	15.0	45.0	0.100
Márquez-Arias et al. (2014); Rodas-Martínez et al. (2013)	Covered outdoor exhibit	14.5	105.0	315.0	0.046
Campbell, Shideler, Todd, & Lasley (2001)	Outdoor exhibit	3.5	NA	440.0	0.008
Cruz-Aguilar et al. (2015)	Covered, outdoor solitary enclosure	1	4.9	9.8	0.102
This study	Outdoor "satellite" enclosure	3.25	44.8	244.2	0.013
This study	Outdoor "single" enclosure	1	22.2	66.6	0.015
This study	Outdoor "Center" enclosure	3.66	166.3	2012.0	0.002

\* Average number of individuals in each enclosure, excluding infants

## APPENDIX B

Table B1

### *Ethogram for Focal-Animal Sampling*

<u>Behavior</u>	<u>Definition</u>
<u>Affiliative Social Behaviors (ASB)</u>	
Allogrooming*	Gently manipulating another individual's fur or skin using the mouth or digits
Embracing*	Sniffing the neck or pectoral region of another individual, often with one or both arms wrapped around them, sometimes accompanied by an <i>ook-ook</i> or <i>whinny</i> vocalization
Greeting*	Extending the lips and chin outward towards another individual, often accompanied by a low <i>ook-ook</i> or <i>whinny</i> vocalization
Sexual*	Copulating with, presenting genitalia to, or grappling with another individual
Sitting in Proximity*	Being inactive with another individual in close proximity
Socially playing*	Wrestling, chasing, or exchanging approaches and retreats with another individual in a non-aggressive manner
Supporting*	Wrapping an arm around, joining, or protectively standing behind another participant in an aggressive interaction
Grabbing*	Restraining another individual with a closed hand
Biting*	Using teeth to wound another individual
<u>Environmental Behaviors</u>	
Feeding Alone	Extracting, processing, or consuming food with no other individuals in close proximity (within one meter)
Co-Feed*	Feeding with another individual in close proximity
Drink	Consume water
Human interaction	Interacting with one or more humans in a non-aggressive manner
Inactive	Sitting, laying, hanging, or standing without performing any other behavior or having any other individual in close proximity
Moving	Changing spatial position by locomoting (brachiating, jumping, climbing, clambering, bounding, walking or running)
Non-socially playing	Interacting with or manipulating an object or manipulating one's own body in a playful, inquisitive manner
Not visible	Out of the observer's sight (activity unknown)
Other	Performing a behavior not described in the ethogram



Table B1 (continued)

<u>Behavior</u>	<u>Definition</u>
Rubbing	Brushing of the anal or genital region, chest, or face along a surface, or using one or both hands to brush an item or substance against their own fur or skin
Sniffing/Licking	Examining a surface or object by smelling or tasting it
<u>Parental Behaviors</u>	
Carrying*	Moving with an infant holding on
Nursing*	Sitting as an infant suckles milk ( <i>vice versa</i> for infant)
Presenting*	Showing the chest, abdomen or lower back to an infant
Riding*	Clasping onto another individual as they move (infants only)
<u>Self-Directed Behaviors (SDB)</u>	
Masturbating	Stimulating one's own genitalia using the mouth, digits, or tail
Self-other	Performing any SDB not described in the ethogram
Scratching	Raking of the digits across one's own fur or skin
Self-grooming	Gently manipulating one's own fur or skin using the mouth or digits
Self-touching	Placing one's hand, foot or tail on their own body and keeping it in that location without moving it
<u>Stereotypic Behaviors (STB)</u>	
Head-rolling	Rapidly rotating the head in a clockwise or counter-clockwise motion
Rocking	Moving the torso backwards and forwards repetitively while in a sitting position; head is usually angled downward and the hands usually clutch onto the tail or hind limbs
Smush-facing	Pressing one's face into the caging so that the nose appears flattened or the mouth is pushed open
Swinging	Repetitively moving one's body back and forth while hanging by the arms and/or tail and remaining in the same general location
<u>Vocalizations</u>	
Bark	Emitting alarm calls (repetitive sequences of sharp vocalizations) while displaying heightened vigilance
Chirp**	A sharp, high-frequency vocalization in an alert or frightened context
Long call**	An extremely loud, harsh call used to advertise location to distant individuals
Squeak**	A sharp, high-frequency vocalization in an affiliative or playful context

Table B1 (continued)

<u>Behavior</u>	<u>Definition</u>
Tschook**	A harsh, gurgling call used to restore contact with unseen or distant individuals
Vocal-other**	Any vocalization not described in the ethogram
Whinny**	A squeaky, two-toned contact call which is individually-recognizable and is mostly used in foraging and affiliative contexts

\* *Required the observer to record any partners/recipients*

\*\* *Recorded as events (without durations)*

# APPENDIX C

Table C1

## *The Effect of Increased Space on Individual Rates of Behaviors*

<u>Behavior</u>	<u>Individual Hourly Rate (occur./hr)</u>				<u>Wilcoxon signed-rank test</u>	
	<u>Normal</u>		<u>Increased Space</u>		<u>Z</u>	<u>p-value</u>
	<i>Mdn</i>	<i>SD</i>	<i>Mdn</i>	<i>SD</i>		
All Aggression	0.08	±0.13	0.01	±0.07	1.63	.103
Intragroup	0.04	±0.03	0.00	±0.01	2.55	.011
High-Severity	0.01	±0.01	0.00	±0	2.39	.017
Low-Severity	0.03	±0.03	0.00	±0.01	2.55	.011
All STB	12.46	±7.96	4.25	±3.35	2.55	.011
Swinging	7.17	±6.63	1.79	±2.97	2.55	.011
All SDB	19.88	±6.84	15.87	±6.34	2.60	.009
Scratching	14.20	±7.14	9.96	±5.13	2.70	.007
Self-Grooming	1.61	±1.54	1.10	±1.98	1.27	.203
Yawning	2.14	±0.98	1.68	±1.88	-0.56	.575
Allogrooming	0.22	±0.51	0.00	±0.40	0.88	.378
Sit in Proximity	1.66	±1.45	1.36	±1.20	0.76	.445
Social Play	0.37	±0.84	0.07	±0.92	0.48	.633
Whinny Vocal.	0.65	±2.55	1.11	±4.23	-1.89	.059
<u>Individual Proportion of Time (%)*</u>						
Moving	18.4	±13.2	15.3	±7.8	0.56	.575
Inactive	45.3	±19.6	58.4	±12.0	-1.89	.059

\* For non-feeding behaviors, percentages represent the percent of non-feeding time spent on that behavior

Note: for all behaviors,  $N = 11$ ; Reject  $H_0$  at  $p < .05$ ; signed-rank tests use Pratt's method for handling zeros and ties

Table C2

*The Effect of Enclosure Choice on Individual Rates of Behaviors*

<u>Behavior</u>	<u>Individual Hourly Rate (occur./hr)</u>				<u>Wilcoxon signed-rank test</u>	
	<u>Normal</u>		<u>Choice</u>		<u>Z</u>	<u>p-value</u>
	<i>Mdn</i>	<i>SD</i>	<i>Mdn</i>	<i>SD</i>		
All Aggression	0.08	±0.13	0.00	±0.21	0.51	.610
Intragroup	0.04	±0.03	0.00	±0.03	2.04	.041
High-Severity	0.01	±0.01	0.00	±0	2.39	.017
Low-Severity	0.03	±0.03	0.00	±0.03	1.74	.083
All STB	12.46	±7.96	6.82	±5.37	1.53	.126
Swinging	7.17	±6.63	4.92	±5.23	1.53	.126
All SDB	19.88	±6.84	15.87	±5.10	1.99	.047
Scratching	14.20	±7.14	9.99	±4.16	1.99	.047
Self-Grooming	1.61	±1.540	1.38	±2.66	0.76	.445
Yawning	2.14	±0.98	0.84	±1.78	1.17	.241
Allogrooming	0.22	±0.51	0.00	±0.49	1.09	.276
Sit in Proximity	1.66	±1.45	1.42	±1.15	1.99	.047
Social Play	0.37	±0.84	0.00	±3.61	-0.05	.958
Whinny Vocal.	0.65	±2.55	1.44	±4.40	-1.58	.114
<u>Individual Proportion of Time (%)*</u>						
Moving	18.4	±13.3	23.1	±13.2	-0.87	.386
Inactive	45.3	±19.6	45.6	±12.8	-0.26	.799
Feeding Alone	9.3	±2.9	6.4	±9.8	0.66	.508
Co-Feeding	0.3	±0.3	0.1	±0.5	0.76	.445

\* For non-feeding behaviors, percentages represent the percent of non-feeding time spent on that behavior

Note: for all behaviors,  $N = 11$ ; Note: Reject  $H_0$  at  $p < .05$ ; signed-rank tests use Pratt's method for handling zeros and ties

Table C3

*Median Rates of Behaviors Relative to Expected Meals*

<u>Behavior</u>	<u>Mean Individual Hourly Rate (occur./hr)</u>					
	<u>Minutes Before Expected Meal</u>			<u>Minutes After Expected Meal</u>		
	<u>30-60</u>	<u>15-30</u>	<u>0-15</u>	<u>0-15</u>	<u>15-30</u>	<u>30-60</u>
All Aggression	0.01	0	0.04	0.02	0.03	0.03
Intragroup	0	0	0.03	0	0.01	0
High-Severity	0	0	0	0	0	0
Low-Severity	0	0	0.03	0	0.01	0
All STB	7.52	10.47	14.00	6.36	6.28	5.06
Swinging	4.14	9.10	8.85	4.65	6.28	3.90
All SDB	20.82	20.33	18.40	14.75	12.31	17.39
Scratching	13.66	13.54	14.05	9.65	10.04	12.23
Self-Grooming	2.08	1.98	1.10	1.34	1.04	1.13
Yawning*	2.55	1.53	1.07	0.48	0	0
Allogrooming	0	0	0	0	0	0
Sit in Proximity	1.16	1.14	1.50	0.44	0.59	1.18
Social Play	0.07	0	0	0	0	0
Whinny Vocal.	0.61	0.36	1.39	0.88	1.01	0.57
<u>Individual Proportion of Time (%)**</u>						
Moving	15.8	26.7	33.2	23.5	21.5	16.9
Inactive	48.5	43.0	34.7	43.4	47.6	51.2

\* Yawning was excluded from SDB as rates of yawning showed a unique temporal distribution across the day

\*\* For non-feeding behaviors, percentages represent the percent of non-feeding time spent on that behavior

Note: for all behaviors,  $N = 16$ . Standard deviations of medians are not shown

Table C4

*Kruskal-Wallis Tests of Data From Table C3*

<u>Behavior</u>	$X^2$	$p$ -value
All Aggression	7.00	.221
Intragroup	11.40	.044
High-Severity	2.710	.745
Low-Severity	13.16	.022
All STB	7.66	.176
Swinging	6.27	.281
All SDB	8.04	.155
Scratching	8.93	.112
Self-Grooming	4.02	.547
Yawning*	26.46	.000
Allogrooming	10.29	.067
Sitting in Proximity	4.37	.498
Social Play	0.35	.996
Whinny Vocal.	3.50	.624
<u>Individual Proportion of Time**</u>		
Moving	8.99	.110
Inactive	9.14	.104

\* Yawning was excluded from SDB as rates of yawning showed a unique temporal distribution across the day

\*\* For non-feeding behaviors, percentages represent the percent of non-feeding time spent on that behavior

Note: For all tests,  $N = 16$  and  $df = 5$ ; Reject  $H_0$  at  $p < .05$

Table C5

*Wilcoxon Signed-Rank Tests of Select Data From Table C4*

<u>Times Relative to Expected Meal (min)</u>	<u>Intragroup Aggression</u>		<u>Low-Severity Aggression</u>		<u>Yawning*</u>	
	<i>Z</i>	<i>p</i> **	<i>Z</i>	<i>p</i> **	<i>Z</i>	<i>p</i> **
- 30-60 vs. - 15-30	1.21	.227	0.96	.336	1.76	.079
- 15-30 vs. - 0-15	-2.50	.012	-2.93	.003	0.80	.422
- 0-15 vs. + 0-15	1.84	.066	1.89	.058	1.79	.074
+ 0-15 vs. + 15-30	-1.36	.174	-1.47	.142	1.89	.058
+ 15-30 vs. + 30-60	0.49	.625	0.54	.587	-2.08	.037

\* Yawning was excluded from SDB as rates of yawning showed a unique temporal distribution across the day

\*\* Adjusted using Benjamini and Hochberg's method to control for false discovery rate (1995)

Note: For all tests,  $N = 16$  and  $df = 5$ ; Reject  $H_0$  at  $p < .05$ ; signed-rank tests use Pratt's method for handling zeros and ties

Table C6

*Individual Rates of Behavior Before and After Social Integration*

	<u>Individual Hourly Rate (occur./hr)</u>			
	<u>MI</u>		<u>SV</u>	
	<u>Solitary</u>	<u>Integrated</u>	<u>Solitary</u>	<u>Integrated</u>
All Aggression	0.01	0.00	0.00	0.00
STB (Swinging)	21.54	14.55	12.98	15.58
All SDB	25.54	18.12	11.65	8.28
Scratching	17.69	12.77	6.34	4.97
Self-Grooming	1.89	0.96	3.10	0.97
Yawning	0.91	1.10	0.89	0.69
Allogrooming	0.00	0.00	0.00	0.00
Sit in Proximity	0.00	0.14	0.00	0.00
Social Play	0.00	0.00	0.00	0.00
Whinny Vocal.	0.15	0.14	1.03	0.14
	<u>Individual Proportion of Time (%)*</u>			
Moving	12.0	13.7	1.9	4.2
Inactive	43.4	53.5	49.8	52.4
Feeding Alone	3.0	0.7	8.6	10.6
Co-Feeding	0.0	0.0	0.0	0.0

\* For non-feeding behaviors, percentages represent the percent of non-feeding time spent on that behavior