Spatial Cohesion of Blond Capuchins (*Sapajus flavius*) in an Atlantic Forest Fragment

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Abstract

Spatial Cohesion of Blond Capuchins (*Sapajus flavius*) in a Forest Fragment

Jack Creeggan

The blond capuchin (*Sapajus flavius*) is an Endangered species of capuchin monkey largely confined to Atlantic Forest fragments in northeastern Brazil, where dispersal is restricted, and resources are limited. In this thesis, I investigated how the spatial cohesion and group movements of blond capuchins were affected by the conditions of the forest fragment they inhabited. My first manuscript (Chapter 2) focused on forest strata use (for age/sex classes), and group cohesion according to the strata used. My second manuscript (Chapter 3) looked at group movement and leadership in age/sex classes. My study site was a 90 hectare forest fragment located on the border of the states of Paraíba and Pernambuco in Brazil (7°52'85,2"S; 34°96'29,4"O), with a group of ~120 blond capuchins. My collaborators and I collected 633 group scans samples, with 15119 individual observations (October 2021 to July 2022), recording age, sex, location and behaviour of each individual. I found that capuchin use of forest strata varied among age/sex classes, a finding that suggests behavioural adjustments to avoid direct competition in this small fragment. I found that capuchin group movement could be characterized as two waves, with adults in the front wave and juveniles in the back wave, a finding that suggests adults reach preferred foods before juveniles. My work contributes to our understanding of how capuchins use forest fragments and underscores the need for further research in forest fragments to better inform conservation practices for this and other threatened primate species, and the biodiversity of the Atlantic Forests.

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Contribution of Authors

Chapter 2:
Creeggan, Jack, Miller, Kyle, Peruzzo, Simone, Pereira, Italo, Ferreira, Renata G. and Turner, Sarah E., Behavioural plasticity through differential strata use by blond capuchins (*Sapajus flavius*) in a forest fragment (in preparation for the International Journal of Primatology)

Jack Creeggan contributed to conceptualization of the project, funding acquisition, methods, data collection, data analysis and interpretation, and visualization of results; he wrote the original draft and participated in review & editing. Kyle Miller, Simone Peruzzo, and Italo Pereira contributed to methods development and data collection. Kyle Miller also contributed to data processing and wrote the program used to parse GIS data. Sarah E. Turner and Renata G. Ferreira contributed to conceptualization of the project, supervision, funding acquisition and resources, methods development, data analysis and interpretation, and manuscript review and editing.

Chapter 3:
Creeggan, Jack, Miller, Kyle, Peruzzo, Simone, Pereira, Italo, Turner, Sarah E., and Ferreira, Renata G. Adult leadership among blond capuchin monkeys during periods of higher food availability in an Atlantic Forest fragment (in preparation for Animal Behaviour)

Jack Creeggan contributed to conceptualization of the project, funding acquisition, methods, data collection, data analysis and interpretation, and visualization of results; he wrote the original draft and participated in review & editing. Kyle Miller, Simone Peruzzo, and Italo Pereira contributed to methods development and data collection. Kyle Miller also contributed to data processing and wrote the program used to parse GIS data. Sarah E. Turner and Renata G. Ferreira contributed to conceptualization of the project, supervision, funding acquisition and resources, methods development, data analysis and interpretation, and manuscript review and editing.

All authors reviewed the final manuscript and approved of the contents.

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List of Acronyms and Abbreviations

Emmeans: Estimated Marginal Means

GIS: Geographic Information System

GPS: Global Positioning System

Inf: Infinite

IUCN: International Union for Conservation of Nature

J1: Juvenile Class 1

J2: Juvenile Class 2

J2-3: Juvenile Class 2 & 3

J3: Juvenile Class 3

S1: Stratum 1

S2: Stratum 2

S3: Stratum 3

S4: Stratum 4

Chapter 1: Introduction

1.1 General Introduction: Blond capuchins in forest fragments

According to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, there are only ~1000 blond capuchins (*Sapajus flavius*) left in the wild (A. B. Martins et al., 2020). Classified as Endangered, their numbers are decreasing, leaving blond capuchins vulnerable to human-caused threats such as deforestation and hunting (A. B. Martins et al., 2020). This decrease in population is especially troubling since capuchin monkeys provide important ecosystem services, such as seed dispersal and pollination, insect control, and in tree regeneration by breaking rotten branches and bark (Sales et al., 2020). It is likely that if there is no longer sufficient habitat to support capuchin populations, many plants and animals that depend on capuchins will be threatened with extinction as well (Sales et al., 2020). With this in mind, it is increasingly important that the areas blond capuchins inhabit are protected from development and negative human impacts. Much of the Atlantic Forest that blond capuchins have historically inhabited has been replaced by agriculture, and although some populations have learned to supplement their diet by foraging on crops on these agricultural lands, many crops lack nutrients found in the blond capuchin's natural diet (Dantas et al., 2022; Lins & Ferreira, 2019). To manage and create protected areas for blond capuchins, it is important to first determine how these protected areas should be designed so that their value to the conservation of blond capuchins can be maximised. To do this, we must gain an understanding of how blond capuchins use resources in their habitat, how they choose where they place themselves in their habitats, and how they move as groups and as individuals in fragmented habitats. This knowledge can then be used to develop conservation plans and define new areas where capuchins could be reintroduced. The blond capuchins living in the fragment I studied make up around 10% of the total remaining population of this species. Therefore, information on the spatial cohesion and movement of this group that could inform the expansion of the fragment or efforts to link the fragment to other fragments would be valuable to the conservation of the species.

In this thesis, I investigated the broad question of how small habitat area and restricted resources interact with the group spatial cohesion and movements of blond capuchins in a forest fragment in Paraíba, Brazil. Spatial cohesion refers to the distance between individuals and the number of individuals within a certain radius of another individual. I have examined this question in two manuscripts. The first manuscript, Chapter 2: Behavioural plasticity through differential strata use by blond capuchins (*Sapajus flavius*) in a forest fragment, looks at the relationship between age/sex class and use of forest strata, as well as individual distance to the centroid (median point position) of the group and strata level, and posits that blond capuchins may be exhibiting behavioural plasticity by foraging in different strata depending on age/sex class in order to avoid direct competition. The second manuscript, Chapter 3: Adult leadership among blond capuchin monkeys during periods of higher food availability in an Atlantic Forest fragment, looks at the relationship between movement leadership and age/sex class, as well as individual distance to the centroid and age/sex class, and posits that females may be leading group movements more than other age/sex classes due to the increased resource restrictions of the forest fragment.

1.2 Literature Review

1.2.1 Natural history of *Sapajus flavius*

Sapajus flavius, the blond capuchin (also spelled as “blonde capuchin”), is believed to have been first described in western science in 1648 by the German naturalist George Marcgrave. However, blond capuchins may have appeared earlier in a fresco commissioned by Pope Leo X in the 16th century, suggesting that they may have been encountered by early European colonisers and brought back to Europe (Masseti & Veracini, 2010; Oliveira & Langguth, 2006). Marcgrave gave these monkeys the name “caitaia” and described them as a monkey with long yellow hair, a rounded head, and an arched tail. A collection of paintings brought back to Holland by the Dutch governor of Brazil at the time contained what is likely an early drawing of a blond capuchin monkey (**Figure 1.1**), possibly painted by Marcgrave, although there is no recorded artist (Oliveira & Langguth, 2006).

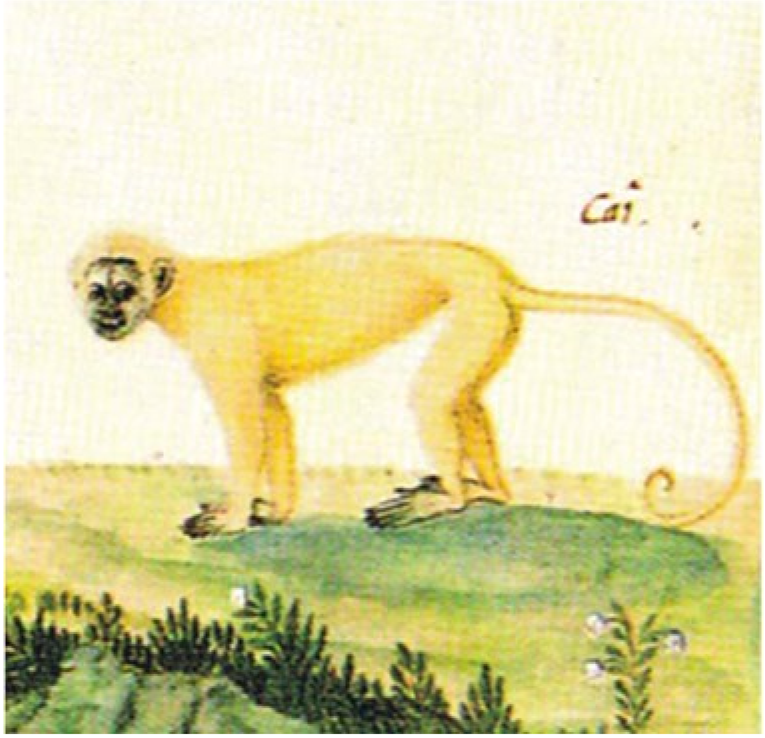

Figure 1.1 A drawing from the “Libri Principis,” likely drawn sometime between 1637 and 1644 by an unknown artist. The drawing matches many of the descriptions written by Marcgrave, notably the complete yellow coat and the arched tail from (Oliveira & Langguth, 2006).

Despite this early description, blond capuchins were not officially recognized as a distinct species until 2006. Prior to this, they had been described by naturalists as other species of capuchins, such as the black-striped capuchin (*Cebus libidinosus*) and the white-fronted capuchin (formerly *Cebus albifrons*), or had been considered taxonomically unidentifiable, mostly due to a lack of specimens. Upon its official designation, blond capuchins were given the name *Cebus flavius* by Oliveira & Langguth*,* taken from *Simia flavia*, a name given to the blond capuchin by another German naturalist named Johann Christian Daniel von Schreber in 1774 (Oliveira & Langguth, 2006). In the same year Pontes et al., (2006) also discovered a small population of blond capuchins, and thinking they had found a new species, proposed the name *Cebus queirozi, (Cebus flavius* remained the official name, however, having been proposed first). Blond capuchins at this time were well known to the people living in northeastern Brazil where the blond capuchin was somewhat notorious for raiding the crops that surrounded the Atlantic Forest fragments they inhabited (**Figure 1.2a)**. Oliveira and Langguth (2006) had thought that the blond capuchin was restricted to this area~~.~~ However, soon after blond capuchins were sighted by Ferreira et al. (2009) in the Caatinga biome, a relatively dry and rocky area with a much shorter canopy height than the Atlantic Forest (**Figure 1.2b)**. There were no official records of the release of any capuchin monkeys in this area, and elderly locals reported the presence of capuchins for at least 40 years prior, which led Ferreira et al. (2009) to propose that this population may represent a larger distribution of the species that was present prior to the drying of the Caatinga two million years ago and again 200 years ago following colonization of the area (Ferreira et al., 2009).

a)

b)

Figure 1.2 a) The edge of an Atlantic Forest fragment. The majority of blond capuchins inhabit fragments like this (A. B. Martins et al., 2020). **b)** A group of blond capuchins amongst the rocks in the Caatinga Biome. Notably, the Caatinga is much closer to a savannah-like biome than the Atlantic forests that blond capuchins were originally believed to exclusively inhabit, with rocky, hilly terrain and little to no presence of an arboreal canopy (photo by A. Roque, taken from Ferreira et al. 2009).

The capuchin monkey genus *Cebus* was split into two genera in 2014, after Lynch Alfaro et al. (2014) cited distinct morphological and behavioural differences between untufted, or "gracile," capuchins, and tufted, or "robust," capuchins. Gracile capuchins retained the name *Cebus* and robust capuchins were given a new genus name *Sapajus* (Lynch Alfaro et al., 2012, 2014). As a member of the robust capuchin genus, the blond capuchin was given the scientific name *Sapajus flavius*.

1.2.2 Study Species and Habitat

Blond capuchins (*Sapajus flavius)* are characterised by a yellow-gold coat and have black hands and feet **(Figure 1.3)**. They also sometimes have a rectangular white "cap" on top of the head that stretches down to the top of the ears. Blond capuchins are smaller than most other capuchin monkeys with an average weight of 2 to 3 kg and an average body length of 40 cm (Oliveira & Langguth, 2006; Pontes et al., 2006). Males are typically larger than females, possessing larger canine teeth as well (A. Martins et al., 2015). Males also possess a sagittal crest, a dorsal-ventral ridge on the top of the skull, that females do not possess, and older males will sometimes have a small throat pouch that grows with age (Lynch Alfaro et al., 2012; Pontes et al., 2006).

Figure 1.3 An adult female blond capuchin with an infant riding on her back. Both individuals have a near-uniformly yellow-gold coat, with the adult female having a visible white cap on the top of her head (Photo by Ítalo Ferreira Pereira).

Sapajus flavius is listed as Endangered on the IUCN Red List of Threatened Species (A. B. Martins et al., 2020). Endemic to northeastern Brazil, blond capuchins primarily inhabit Atlantic

Forest fragments. Blond capuchins living in forest fragments have reduced access to resources because their home range is restricted by forest fragment size, and some groups therefore have begun relying on foraging on the sugarcane crops that often surround their fragments (Bezerra et al., 2014; Lins & Ferreira, 2019; Medeiros et al., 2019). In one particular case, a group of blond capuchins was found to be supplementing half their yearly diet with just sugarcane, reaching up to 70% of their diet in the dryer months (Lins & Ferreira, 2019). While access to sugarcane and other crops has likely been a key factor allowing blond capuchins to survive in small and crowded habitats, it also creates problems. Compared to the blond capuchin's natural diet, sugarcane is much less nutritious, and while it does allow them to meet caloric requirements, nutrient requirements are likely not being met in times when the rate of sugarcane consumption is high (Dantas et al., 2022; Lins & Ferreira, 2019).

During months with higher precipitation, when wild fruit abundance is higher, fruit is the preferred food of the blond capuchin, with arthropods and other food sources constituting a higher percent of their diet during months when fruit is less available (Lins & Ferreira, 2019). Blond capuchins have been known to feed on the fruits from *Chrysobalanus icaco* (cocoplum), *Inga tripa*, *Montrichardia linifera*, *Annona glabra* (pond apple), *Symphonia globulifera* (boarwood), and *Calophyllum brasiliense*, among others (Medeiros et al., 2019).

1.2.3 Socio-Ecology and Habitat Use

Living in groups can provide many potential fitness benefits for primates, such as greater safety from predators, and benefiting from the knowledge of other group members for finding and defending food, but group living also comes with costs that animals have to trade-off against the benefits (Hill & Dunbar, 1998; Van Schaik, 1983). One trade-off is increased intra-group competition over food (Van Schaik, 1983; Wrangham, 1980). Competition over food can vary depending on the availability and dispersion of food sources. A group feeding on a concentrated clump of food will lead to direct, or contest competition, between individuals. Contest competition can involve aggressive or physical altercations with other individuals in order to maintain access to food, with more dominant individuals tending to have greater access to food (Sterck et al., 1997). In response to contest competition, individuals will sometimes form coalitions with one another to assist in the control of concentrated food patches (Ferreira et al., 2006; Vogel et al., 2007). Conversely, in situations where food is less clumped and more scattered, individuals in groups will spread apart and end up engaging in indirect, or scramble competition. Individuals engaging in scramble competition will spend more time foraging the lower the quality of their habitat, and therefore devote less time to social activities. Coalitions can still be formed in scramble competition, but usually for purposes other than feeding (Ferreira et al., 2006; Young et al., 2014).

As a way of avoiding intragroup competition over food, primate groups will often split into subgroups or spread out during feeding and reform into a larger group when finished. This social organization is known as *fission-fusion* (Kappeler & van Schaik, 2002; Sueur et al., 2011). Chimpanzees, for example, were able to increase their maximum ecologically-tolerable group size by exhibiting fission-fusion behaviour, which was proposed by (Lehmann et al., 2007) to allow chimpanzee groups to inhabit areas they might otherwise not have been able to inhabit.

Janson, (1988) found that the group size of tufted capuchins (*Sapajus apella*) did not affect feeding rate, suggesting that fission-fusion behaviour offers capuchins a way to minimise the negative effects of group living while maintaining many of the positive effects. In response to high food abundance, groups will fission and spread out, but when predation risk is higher, groups will become larger and denser (Di Bitetti & Janson, 2001; Ferreira et al., 2008; Heesen et al., 2015; Luccas & Izar, 2021; Stanford, 1995). A similar behavior can be found on the individual level as well. Less dominant adult male tufted capuchins will position themselves on the periphery of the group, where predation risk is higher, to avoid aggression from the dominant male who typically occupies the centre of the group (Janson, 1990a). Juveniles, on the other hand, will position themselves in the centre of the group where predation risk is the lowest, even at the expense of optimal food availability, and will gradually move to the periphery as they age and begin to receive growing aggression from the dominant male (Janson, 1990b, 1990a).

Another way capuchins have been observed to minimize the negative effects of group living is through niche differentiation. Niche differentiation refers to different age/sex classes of individuals within a group feeding on different food resources. A study of white-faced capuchins (*Cebus imitator)* by Williamson et al., (2021) found that juveniles and females foraged on smaller branches than males, and that they foraged less often on the ground than males. Such niche differentiation is likely to be especially important for individuals living in large groups within small and dense habitats like forest fragments. Primates living in forest fragments are known to have much smaller home ranges and day range lengths than primates living in continuous habitats; as primates in forest fragments can have reduced access to resources (Teichroeb et al., 2022).

Nonhuman primates exhibit a wide range of social structures and dynamics, especially when it comes to movement leadership (Fichtel et al., 2011). For example, dominant male mountain gorillas (*Gorilla gorilla*), will often lead group movements (Fichtel et al., 2011), but many other primate species, including some capuchins, have instead been found to exhibit distributed leadership models (Anand & Radhakrishna, 2022; Boinski & Campbell, 1995; Ceccarelli et al., 2020; Fernández et al., 2013; Leca et al., 2003; Lee & Teichroeb, 2016; Sueur, 2011; Van Belle et al., 2013; C. Wang et al., 2020). Despite any individual being capable of leading group movements, leadership in primate groups with distributed leadership can still sometimes trend towards certain age/sex classes. Females have been found to be the predominant leaders in many primate species (Ceccarelli et al., 2020; Leca et al., 2003; Lee & Teichroeb, 2016; Van Belle et al., 2013). White-faced capuchins (*Cebus capucinus*) in particular were found to have no sex-based difference in the number of leadership attempts, but did find a female-bias in the number of *successful* leadership attempts (Leca et al., 2003). Socio-ecological models of female-bonded species (species where males migrate between groups and females generally stay within their natal group, as occurs in blond capuchins) suggest that females have a greater incentive to gather food than males because their fitness depends primarily on maintaining nutritional requirements for themselves and their offspring, whereas males' fitness depends primarily on having access to fertile females (Sterck et al., 1997; Trivers, 1972; Wrangham, 1980). Thus, female primates in groups with distributed leadership may be leading their groups due to their greater foraging incentive. I investigated this question for my thesis and hypothesised that female blond capuchins living forest fragments have a greater imperative to find food, and thus would be at the front of group movements more than other age/sex classes.

Blond capuchins live in large, multi-male, multi-female social groups, with up to 150 individuals or more. Males are generally individually dominant over females, and females do the majority of direct infant care (Bezerra et al., 2014; A. Martins et al., 2015). Blond capuchins do not have a mating season, and infants are born throughout the year. While males do not often directly care for infants, they have been observed in a protective position around mothers who are lagging behind the group, a behaviour interpreted as indirect paternal investment (Andrade et al., 2020; Bezerra et al., 2014; Medeiros et al., 2019), and males are sometimes observed carrying infants (Hamada-Fearnside, *in preparation*). Like many primates, blond capuchins have a large variety of vocalisations that are unique to the species. One study found a group of blond capuchins to have 29 unique call types corresponding with 10 behavioural categories (Bastos et al., 2015). Some of these calls were specific to particular age groups. For example, certain calls would only be used by juveniles, suggesting the presence of vocal learning. Some calls were also location specific, only used when the observed group was in the mangrove forest (Bastos et al., 2015).

Current understanding of capuchin group movement, inter-individual positioning within groups, and the relationships among these variable and habitat characteristics is still emerging, and understanding of movement ecology for groups inhabiting forest fragments is even more limited. Capuchins are an interesting taxon for study. Despite sharing a last common ancestor with primates in Asia and Africa over 30 million years ago, capuchins seemingly operate with a high level of intelligence more similar to our great ape cousins than other neotropical primates (Schrago & Russo, 2003), an intelligence illustrated by their problem-solving abilities and tool use (Bowler et al., 2015; Falótico, 2022; Medeiros et al., 2020; Souto et al., 2011). By researching the movement and spatial choice of blond capuchins, I seek not only to provide vital information on an Endangered species, but also provide context to the effects of fragmented habitats on primates in general.

Chapter 2: Behavioural plasticity through differential strata use by blond capuchins (*Sapajus flavius*) in a forest fragment.

2.1 Abstract

Habitat loss is one of the biggest threats facing primates, and the fragmentation that often results can lead to limited dispersal and crowding for forest-specialist primates. Primates with higher capacity for behavioural plasticity may therefore have an advantage in adjusting to disturbed environments. Here we investigated behavioural plasticity in Endangered blond capuchins (*Sapajus flavius*) through differential use of forest strata among age/sex classes. Our study site was a 90ha section of a 270ha Atlantic Forest fragment with a group of ~120 individuals in northeastern Brazil. We used scan sampling at 20-minute intervals to record individuals' location, age/sex class, and forest strata, and then used a Chi-Square analysis to evaluate the use of strata among age/sex classes, and a linear mixed effects model to test the interaction between strata and distance to the centroid of the group. Contrary to our predictions and findings of similar studies, we did not find that adult males were using the ground significantly more often than other age/sex classes. Instead, we found that males occupied the highest stratum significantly more than expected by chance, and juveniles occupied the highest stratum significantly less than expected by chance. We also found that group spread increased as strata level increased. Our results suggest that juveniles may be accepting sub-optimal foraging space as a trade-off for increased safety from avian predators and reduced risk of direct competition with adult males. Juveniles are important for the continued persistence of the group; if juveniles are potentially not meeting nutritional requirements as a way to accommodate risk and reduce competition, this may pose a problem for the continued survival of the local population. Further research into the behavior and cohesion of capuchin groups in fragments is needed to determine the full effects of low habitat area and fragmentation on blond capuchin populations.

2.2 Introduction

Habitat loss is one of the biggest threats to biodiversity and is the leading cause of population loss for most primate species, and the majority of primate species are now facing the threat of extinction (Estrada et al., 2017, 2022). Removal of primate habitat, particularly for conversion to agricultural land and roads, often results in habitat fragmentation (Bloomfield et al., 2020). While habitat loss and fragmentation is often cited as causing population changes and disturbances to space use patterns of primates, it can also alter their social interactions and group dynamics, making it difficult to model population growth and maintenance (Banks et al., 2007; Bloomfield et al., 2020; Bolt et al., 2022; Schwitzer et al., 2011; Stevenson et al., 2015). Because suitable primate habitat is declining rapidly and the fragmentation that results can limit dispersal potential and promote crowding for forest-specialist species, primates with higher capacity for behavioural plasticity may have advantages over other species in adjusting to disturbed habitats (Dunham, 2011; Gestich et al., 2022; Kalbitzer & Chapman, 2018; Nowak & Lee, 2013; Stewart et al., 2023; Swart & Lawes, 1996).

Behavioural plasticity is defined here as “the ability to adjust behaviour according to circumstance and need” (Stewart et al., 2023, p. 2). Behavioural Plasticity is often used synonymously with behavioural flexibility (Strier, 2022), and though there is some discussion on the distinction between these two terms (Audet & Lefebvre, 2017), here we use behavioural plasticity and flexibility interchangeably. Behavioural plasticity can be broadly divided into endogenous plasticity, where plasticity arises in response to internal changes, such as circadian rhythms or menopause, and exogenous plasticity, where plasticity arises in response to external changes (Stamps, 2016). Exogenous plasticity can arise in individuals in response to changes in climate, food availability, and habitat, but can also act as a response to changes in the dynamics of local conspecifics (Nowak & Lee, 2013; Stewart et al., 2023; Turner et al., 2012). For example, a study that experimentally increased the ratio of male guppies (*Poecilia reticulata*) to female guppies found that a higher frequency of harassment of females by males led females to more frequently inhabit deeper waters with a higher risk of predation (Darden & Croft, 2008). In primates, fission-fusion dynamics in social groups can sometimes be considered a function of behavioural or social plasticity, and can arise from both environmental changes and changes to the social group (Aureli et al., 2008; Stead & Teichroeb, 2019; Strier & Mendes, 2012). Splitting into smaller subgroups or spreading out is advantageous for foraging as it allows individuals to avoid competition and conflict with fellow group members and provides potential first access to food sources for individuals on the periphery (Di Bitetti & Janson, 2001; Ferreira et al., 2008; Heesen et al., 2015; Luccas & Izar, 2021; Teichroeb et al., 2022). However, individuals will re-form into larger groups with smaller group spread when the threat of predation is high (Stanford, 1995).

Capuchin monkeys in particular have been found to show a high capacity for behavioral plasticity in a variety of contexts; this trait that has allowed them to inhabit several different biomes, including Atlantic forests, Caatinga, coastal and mangrove forests, mountain forests, and urban areas (Ceballos-Mago & Chivers, 2013; Ferreira et al., 2009; A. Martins et al., 2015; Medeiros et al., 2019; Suzin et al., 2017). Part of this plasticity comes from capuchins’ generalist diet, which allows them to survive on a variety of foods. Capuchins have a varied diet of fruits and other vegetable parts, invertebrates, and small vertebrates, but have been found to be able to supplement their diet with crop foraging and provisioned food from humans in areas with high human impact and lower wild food availability (Lins & Ferreira, 2019; Suzin et al., 2017). Variation in use of forest strata is another form of behavioural plasticity that capuchins have been shown to exhibit; for example, male white faced capuchins (*Cebus imitator*) were found to forage for invertebrates on the ground significantly more than females and juveniles, which preferred to forage in higher strata (Williamson et al., 2021).

Blond capuchins (*Sapajus flavius*) are a species of tufted capuchin endemic to the Atlantic Forest of northeastern Brazil and are an Endangered species, largely due to habitat loss and human encroachment (Martins et al., 2020). Many groups are confined to forest fragments, that is small areas of forest, surrounded by other landscape and land use types. Living in forest fragments can restrict dispersal and food availability, and thus typically capuchins in forest fragments have to supplement their diet with crop foraging. Many of the agricultural crops grown near blond capuchin populations are monocultures of crops like sugarcane grown at an industrial scale and for non-food uses, so crop foraging provides few nutrients compared to caloric intake (Lins & Ferreira, 2019). Intragroup conflict among capuchin groups often arises during foraging, and while significant injury resulting from aggression in capuchins is rare, females and juveniles are at a higher risk of injury when in conflict with the typically larger and stronger males (Lins & Ferreira, 2019; A. Martins et al., 2015). As dispersal between fragments is often restricted, males cannot emigrate to different groups or form new groups like they would normally, and thus in order to persist, all age/sex classes are forced to exhibit behavioural and social plasticity to deal with the challenges that arise from this (Sterck et al., 1997; Wrangham, 1980).

We therefore hypothesized that blond capuchins living in forest fragments would show differences in each age/sex class’s use of forest strata, a kind of micro niche differentiation, as a function of behavioural plasticity to reduce conflict and competition between individuals and allow for larger groups to persist in the fragment. From this hypothesis, we predicted that males would be observed more often on the ground and females and juveniles less often on the ground when foraging for insects and non-patched fruit. Additionally, we hypothesized that blond capuchins behaved as though the forest floor in fragments was more dangerous than the canopy and understory, as we expected that contact and risk from humans is higher in fragments than in continuous habitats. We therefore predicted that group spread would be smaller in lower strata and larger in higher strata.

2.3 Methods

2.3.1 Study Group and Site

Our study site was a 90-hectare section of a 270ha forest fragment located near the cities of Caaporã, Paraíba and Goiana, Pernambuco State in Brazil (7°52'85,2"S; 34°96'29,4"O) **(Figure 2.1)**. The group has been studied since 2005, and the highest number of individuals that we observed in the group was 127 (Lins & Ferreira, 2019). There is another group of blond capuchins on the opposite side of the fragment, although they are not habituated, and population numbers are unclear. The northwestern part of the fragment is flooded and capuchins from each group rarely venture outside of their respective southeast and southwest sides of the fragment, so between group encounters are relatively rare.

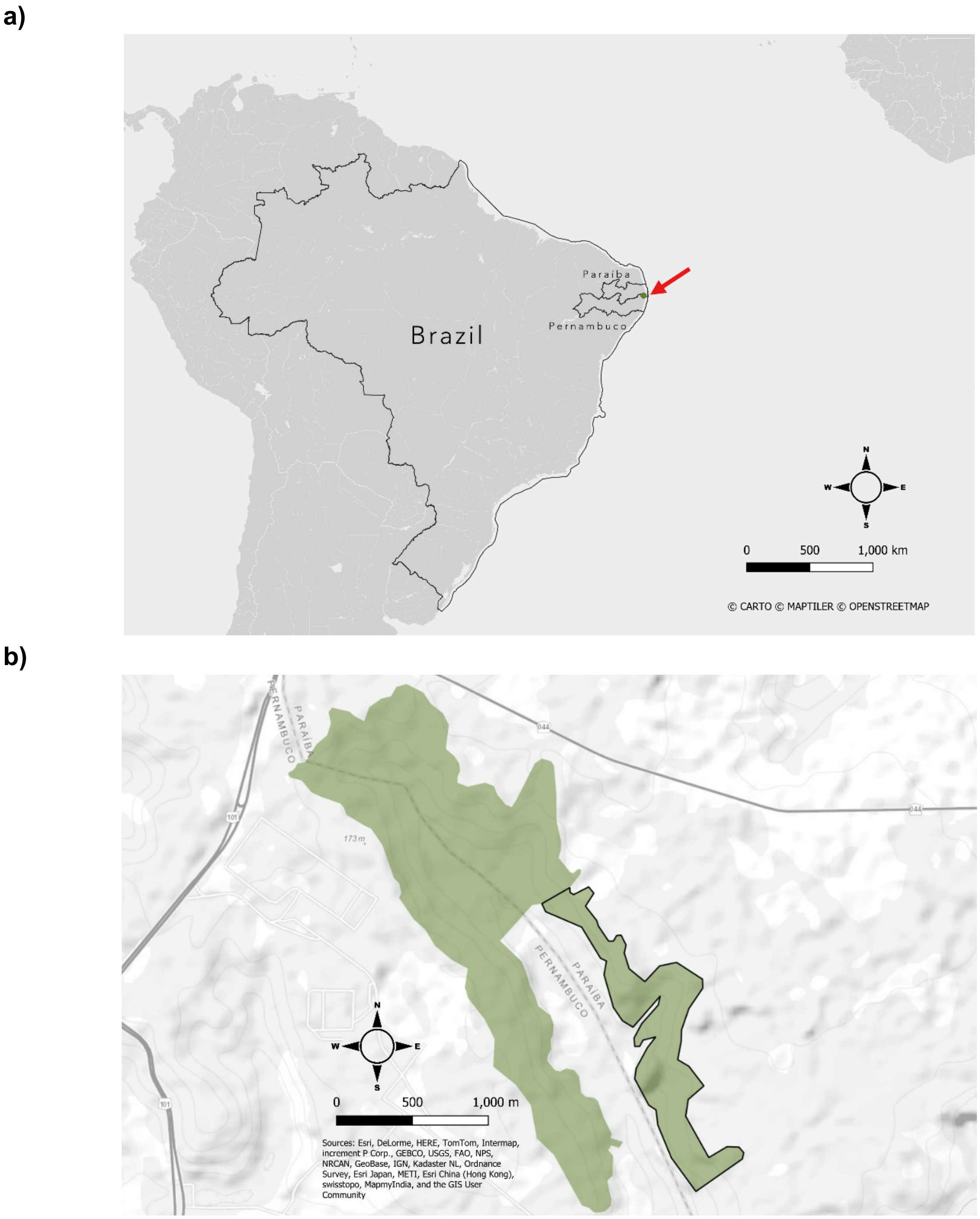

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Figure 2.1 a) The location of the study site (green dot with red arrow pointing to it) relative to Brazil. The borders of the states of Paraíba and Pernambuco are also visible. **b)** The study site, located on the border of the states of Paraíba and Pernambuco, Brazil, with the forest fragment coloured in green and the specific area of outlined in black.

The fragment was surrounded by industrial sugarcane farming; however, sugarcane has since been replaced with other crops in much of the surrounding area. During the study period, the capuchins fed frequently (almost daily) on sugarcane (Lins & Ferreira, 2019). However, unlike some occurrences of primate crop foraging, human-animal conflict did not arise from the capuchins foraging on sugarcane, likely because the crops were owned by large-scale industry, and so individual livelihoods were not impacted by capuchin crop foraging behaviours the way they would be for small-scale local or subsistence farmers. The landscape surrounding the forest fragment is relatively impermeable for capuchin monkeys. While monkeys have been observed foraging on crops near the forest edge, large monoculture plantations and roads do not provide suitable habitat for capuchins, and there is no evidence to suggest that capuchins leave this forest fragment or move to others in the surrounding area (Hamada-Fearnside, 2023).

2.3.2 Data collection

We used a scan sampling method to collect data on behaviour, individual and group locations (Altmann, 1974). Samples were conducted at 20-minute intervals, about four to five times a day, over 131 days, with a total of 633 scans with 15119 individual observations collected from October 2021 to July 2022. We alternated with data collection in the morning (~06:30 - ~11:30) or afternoon (~11:30 - ~17:30). Upon arriving at the field site, we would search for the study group for 10 to 120 minutes, and once we found the group, we would follow it, positioning ourselves in the centre of the group during scan sampling. We used an application called Locus Map (*Locus Map 4 Outdoor Navigation*, 2024), to enter data, scanning each visible individual and recording the time, their GPS location based on their proximity to the observer, their age/sex class, the forest strata in which they were located, and their behavior at the time of the scan.

Age/sex classes were divided into adult males, adult females, adult males with infants, adult females with infants, sub-adults, and juveniles (categorized as Juvenile class 1 (J1, 6mo - 1yr), class 2 (J2, 1yr - 2yrs) or class 3 (J3, 2yrs - 4yrs) following Izawa (1980) and Hamada-Fearnside (2023). We divided the forest floor-to-canopy crown into four Strata: Stratum 1 (S1) referring to capuchins on the ground to 0.3 metres above the ground, Stratum 2 (S2) for 0.3 to 5m above the ground, Stratum 3 (S3) for 5 to 15m above the ground, and Stratum 4 (S4) for 15m and higher in the canopy. Behavior for each individual was recorded and later grouped into 7 broad activity budget categories: Locomotion and Foraging (“lof”), Foraging on sugarcane (“for cane”), Foraging on African Oil Palm or Jackfruit (“for de.ja”), Affiliative social interactions (“affiliative” e.g., grooming, copulation, playing), Agonistic interactions (“agonistic”), Inactive/ Rest (“resting”), Non-locomotion vigilance or individual stationary behaviour (“alert”), and Other (“others”).

Observations were later separated by month, and then further separated into two seasons based on the level of fruit production by trees: the non-productive season (April - January), and the productive season (February - March) (Pereira, *in preparation*).

2.3.3 Statistical Analysis

We processed our data using a program written for Python (by KM) that organized the raw data, extracted metadata from each of our scans, and calculated the distance to the centroid (center location calculated from median distances to the central point) of the group for each individual scanned capuchin monkey. Males with infants and subadults were removed from the analysis due to small sample size, with the number of observations in these classes too low compared to other age/sex classes for our statistical analyses. We combined juveniles classed as 2 and 3 together (Juvenile class 2-3) out of concern that we could not distinguish between the two classes reliably.

We used Chi-square tests to test the relationship between age/sex class and strata. We ran one test for the observations in the non-productive season and one for the observations in the productive season to account for differences in fruit availability.

For this analysis, we only included observations where the associated behaviour was “locomotion and foraging.” We excluded non-foraging observations since we were interested in examining behavioural plasticity with strata use during foraging. We excluded observations of foraging on clumped foods (e.g., foraging on African oil palm (*Elaeis guineensis*), foraging on jackfruit (*Artocarpus heterophyllus*), and foraging on sugarcane (*Saccharum*), as these resources typically required foraging in a particular strata level. For example, African oil palm fruit only grows at the top of its main trunk body, and as such the strata level of capuchins foraging for African oil palm fruit is dependent on how tall the tree is, rather than where the capuchins have chosen to be. Sugarcane grows relatively low to the ground, so foraging on sugar cane can only occur on the ground stratum.

To test the relationship between strata and distance to centroid, we first transformed distance to centroid to a logarithmic distribution based on the results of a descriptive test of the distribution, and then ran the following linear mixed effects model in R (Bates et al., 2003; Delignette-Muller & Dutang, 2015; R Core Team, 2023):

Distance to Centroid ~ age/sex * strata * season + 1/scan.total

We used scan.total, the sequential number of a particular scan, as a random factor to reduce auto-correlation and control for the differential number of individuals in each scan. We then ran a pairwise estimated marginal means (Emmeans) test (*as used in* Borgeaud et al., 2021) with a Tukey adjustment (Lenth, 2017; R Core Team, 2023), which allowed us to adjust for the other variables in the model when comparing the estimated means (based on the model) of different groups within variables, with strata and season as interactions to determine the relationship between distance to centroid and each level of strata, as well as account for seasonal differences.

This research complied with all field study guidelines recommended by the International Primatological Society (*Code of Best Practices for Field Primatology*, 2014), and with the policies of Concordia University's Animal Research Ethics Committee (*Procedures for the Ethical Use of Animals in Research and Teaching*, 2022). This study obtained certification of Ethical Acceptability for Research or Teaching Involving the Use of Animals (STurner, protocol number 30016343). All procedures were approved by the University of Rio Grande do Norte's bioethics committee (RFerreira, SISBIO 76835-3).

2.4 Results

2.4.1 Age/Sex Class Differences in Strata Use

After removing observations of foraging on sugarcane and clumped foods, our sample included 3098 observations of females, 613 of females with infants, 597 of Juveniles (class 1), 4324 of Juveniles (class 2-3), and 5116 of males. The mean number of individuals in each scan was 30.9, 30.1 in the productive season and 31.2 in the non-productive season. 10930 observations were taken in the non-productive season, and 2818 were taken in the productive season. Altogether, 1553 of these observations were in S1, 3814 were in S2, 5209 were in S3, and 3172 were in S4.

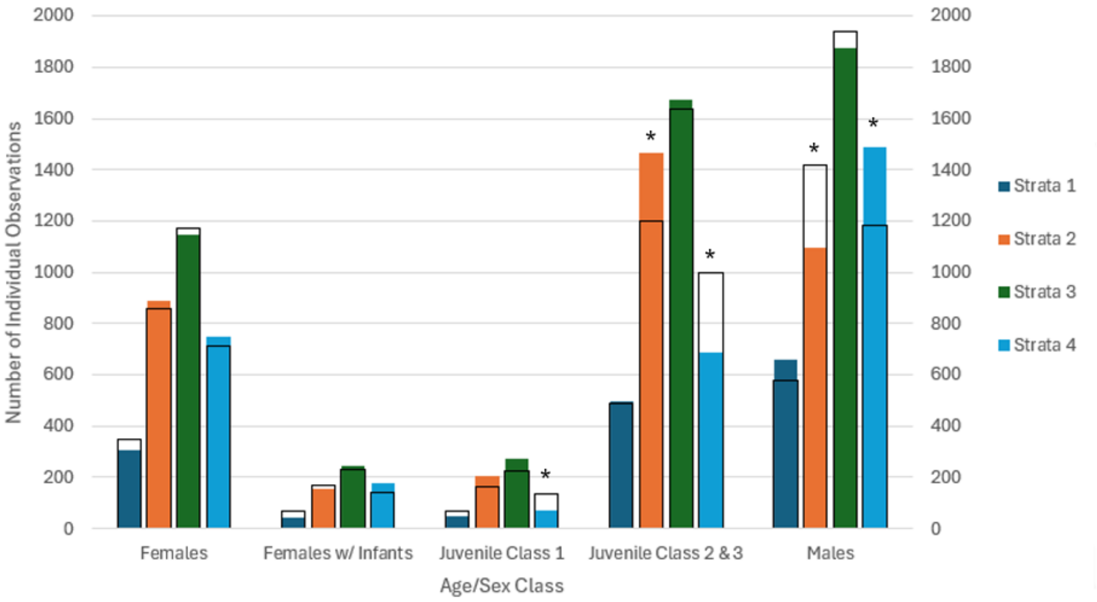


Figure 2.2 The observed (coloured bars) and expected (black outline) observations of each age/sex class in each stratum across both seasons. Significant results are notated with "*", for p-values of <0.05.

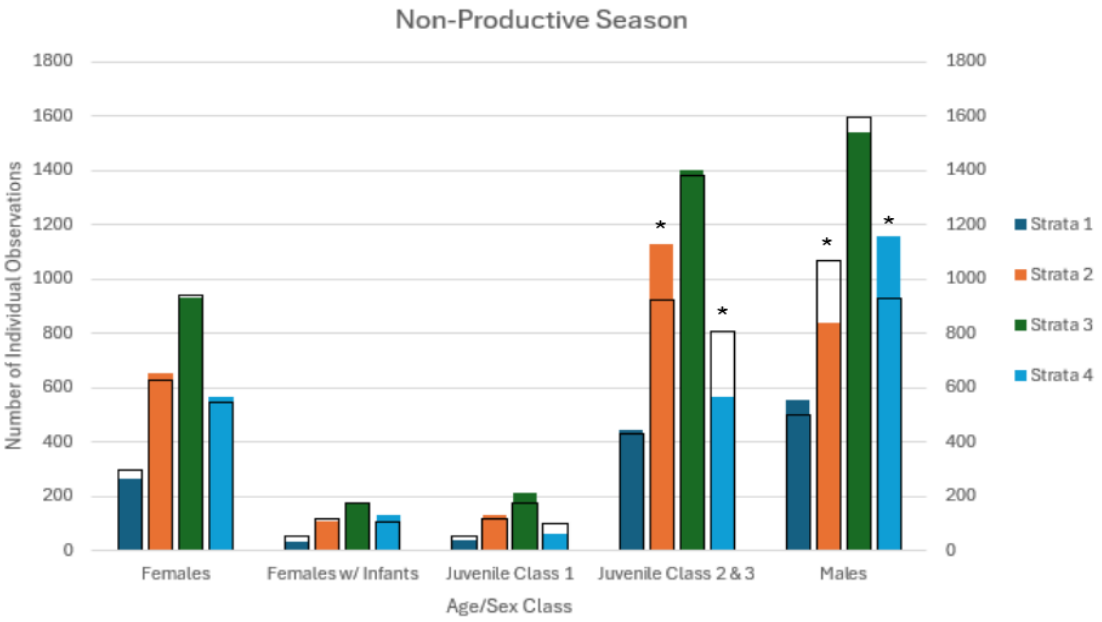


Figure 2.3 The observed (coloured bars) and expected (black outline) observations of each age/sex class in each stratum for the non-productive season. Significant results are notated with "*", for p-values of <0.05.

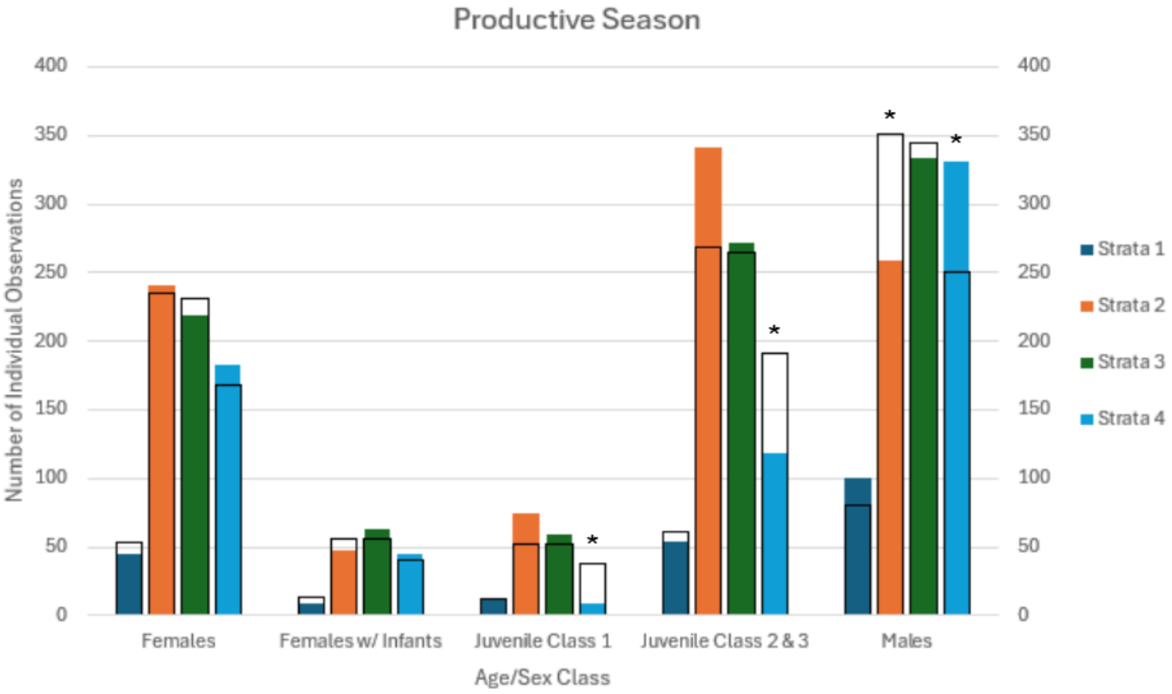


Figure 2.4 The observed (coloured bars) and expected (black outline) of each age/sex class in each stratum in the productive season. Significant results are notated with "*", for p-values of <0.05.

Across both seasons, males used S2 significantly less than expected and S4 significantly more than expected by chance ($\chi^2(12, n = 13748) = 406.64, p < 0.001$) **(Figure 2.2**). Juveniles class 2-3 used S2 significantly more than expected in the non-productive season, and used S4 significantly less than expected in both seasons (*non-productive* ~ $\chi^2(12, n = 10930) = 279.31, p < 0.001$ | *both seasons* ~ $\chi^2(12, n = 13748) = 406.64, p < 0.001$) **(Figure 2.2 & 2.3)**. Juveniles in Class 1 used S4 significantly less than expected, but only in the productive season when results were separated by season (*both seasons* ~ $\chi^2(12, n = 13748) = 406.64, p < 0.001$ | productive ~ $\chi^2(12, n = 2818) = 143.95, p < 0.001$) **(Figure 2.2 & 2.4)**.

2.4.2 Strata Use and Distance to Centroid

For distance to current centroid, the total mean for our study was 30.1m, with a median of 24.1m, a range of 0.1 to 260.7m, standard deviation of 24.4m, and a standard error of 0.2. In the non-productive season, the mean distance to current centroid was 29.7m, with a median of 23.9m, a range of 0.1 to 260.7m, standard deviation of 23.9m, and a standard error of 0.22. In the productive season, the mean distance to current centroid was 31.3m, with a median of 24.9, range of 0.2 to 235.2m, standard deviation of 25.9m, and standard error of 0.43. The mean distance to centroid of the whole group increased during the productive season by 1.61 metres, and the median by 1.08 metres, but this difference was not statistically significant (Emmeans, $z(\text{inf}) = -0.374$, $p > 0.05$).

Strata	**Non-Productive Season**		**Productive Season**		**Both Seasons**	
	Mean	Median	Mean	Median	Mean	Median
1	24.9	20.1	27.0	23.8	25.4	20.5
2	27.0	22.3	31.0	24.6	28.2	23.0
3	31.0	24.8	31.5	25.5	31.1	24.9
4	33.5	27.4	33.6	25.5	33.6	27.1

Table 2.1 The mean and median distance (m) to centroid for each stratum in the non-productive and productive season, as well as both seasons together.

Across both seasons, mean distance to centroid was highest in S4, and decreased with strata level **(Table 2.1)**. Both S3 and S4 showed significant differences in individual distances to centroid from all other strata, and only the relationship between S1 and S2 was not statistically significant (**Table 2.2)**. When accounting for season, these relationships remained significant in each season, although they were not as strong in the productive season **(Table 2.2)**. Mean distance to centroid tended to increase for each stratum from the non-productive season to the productive season, although none of these differences were found to be statistically significant. These increases were larger in S1 and S2 (2.1 and 4m respectively), than in S3 and S4, where the mean distance to centroid only increased in the productive season by 0.5 and 0.1 metres respectively **(Figure 2.5)**.

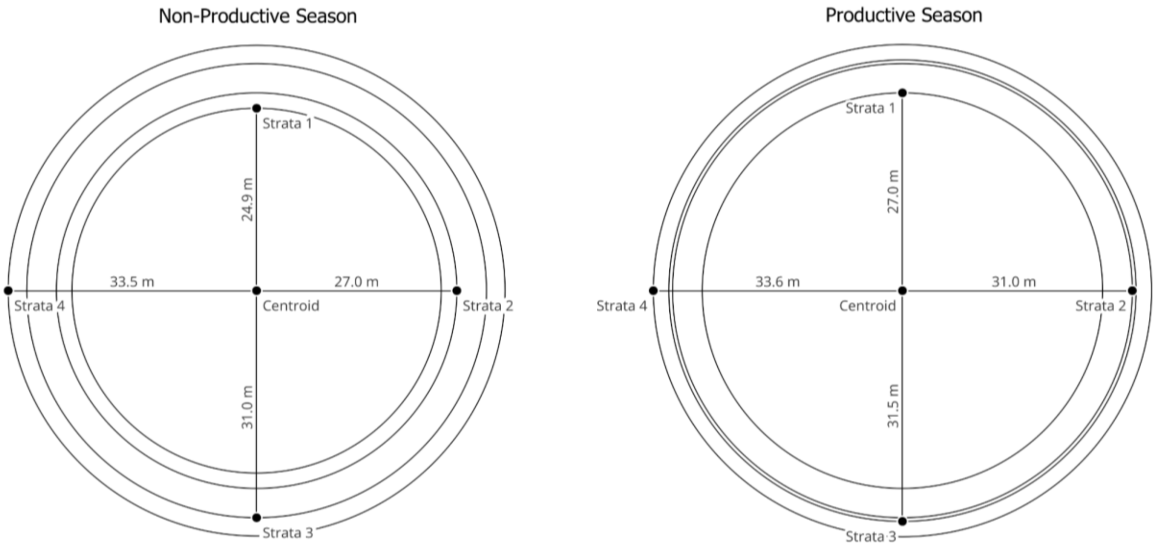


Figure 2.5 Mean distance to centroid of each stratum for non-productive and productive seasons. Across both seasons, individual distances to centroid were significantly higher in S4 than in other strata, and in S3 than in the strata below it **(Table 2.2)**.

Season	**Interaction**	**Estimate**	**Standard Error**	**Degrees of Freedom**	**Z Ratio**	**P Value**
Non-Productive	S1 - S2	-0.05104	0.035182	Inf	-1.45082	1
Non-Productive	S1 - S3*	-0.19507	0.034049	Inf	-5.72906	1.62E-07
Non-Productive	S1 - S4*	-0.27075	0.038641	Inf	-7.0068	3.90E-11
Non-Productive	S2 - S3*	-0.14403	0.022455	Inf	-6.41403	2.27E-09
Non-Productive	S2 - S4*	-0.21971	0.028974	Inf	-7.58284	5.41E-13
Non-Productive	S3 - S4*	-0.07568	0.026376	Inf	-2.86931	0.065818
Productive	S1 - S2	-0.08926	0.055692	Inf	-1.60269	1
Productive	S1 - S3*	-0.17207	0.057055	Inf	-3.01582	0.041006
Productive	S1 - S4*	-0.29785	0.069849	Inf	-4.26423	0.000321
Productive	S2 - S3*	-0.08281	0.035011	Inf	-2.36528	0.28826
Productive	S2 - S4*	-0.20859	0.05331	Inf	-3.91287	0.001459
Productive	S3 - S4*	-0.12578	0.052648	Inf	-2.38915	0.270202

Table 2.2 Results of the Emmeans post-hoc test of strata and distance to next centroid in both seasons. Significant interactions are notated with “*”, where twice the standard error does not cross zero when added to the estimate. Infinite of “Inf” degrees of freedom indicates that estimates are tested against a standard normal distribution rather than a *t* distribution (Lenth, 2017).

2.5 Discussion

Our initial prediction, based on the findings of Williamson et al., (2021), that males would be observed more than expected on the ground and females and juveniles would be observed less than expected on the ground, was not supported by our findings. We found no differences in ground use according to age/sex class in our study **(Figure 2.2)**. Females did not forage significantly less on the ground, despite previous studies of female strata use showing that females tend to use higher strata (De Petrillo & Rosati, 2021; Williamson et al., 2021). Our results suggest that females in this group may have been engaging in unusual risky behavior for increased food access. We found that in both the productive and non-productive seasons males used S4 significantly more than expected, and juveniles in class 2-3 used S4, the top of the canopy, significantly less than expected **(Figure 2.2)**. These findings may indicate that males were monopolizing S4 for premier access to fruit from tall trees, as suggested by Janson (1990b, 1990a). This suggestion is also supported by the finding that juveniles class 1 used S4 significantly less than expected in the productive season, when fruit on tall trees is most plentiful **(Figure 2.4)**. A previous study of this group found that occurrences of direct competition were highest when individuals were consuming sugarcane, what was, at the time of our study, a staple fallback food for this group (Lins & Ferreira, 2019). As the group supplemented much of their diet with sugarcane, juveniles may have been more cautious of direct competition with males in general due to conflicts that may have occurred during sugarcane foraging (Lins & Ferreira, 2019). Notably, females and females with infants did not show a significant greater or lesser use of S4 in either season. This result is consistent with group dynamics reported for other capuchin species, in that more dominant males have been found to monopolize food patches and desirable group positions, while still tolerating females in their vicinity (Di Bitetti & Janson, 2001; Howard et al., 2018; Janson, 1990b, 1990a). Our result that juveniles class 1 used S4 significantly less than expected in the productive season is unusual however, as dominant males have been observed to tolerate young juveniles as well as females near their feeding positions (Janson, 1990b). Our result may be explained by males becoming more aggressive in S4 in the productive season in order to monopolize food patches that are not present in the non-productive season.

That S4 was used significantly less frequently than expected by chance by juveniles could also be due to predator avoidance and/or conflict avoidance with adult males. Capuchins, especially juveniles, are vulnerable to predation by birds of prey (Suscke et al., 2017), and juveniles may be avoiding areas with increased predation risk at the cost of foraging success, a tradeoff that has been observed in juvenile brown capuchins (*Cebus apella*) (Janson, 1990a). Males may also be occupying S4 more than expected for this reason. Male blond capuchins are larger than other age/sex classes and therefore face a lower risk of predation from birds (birds of prey big enough to hunt adults, such as harpy eagles (*Harpia harpyja*), have not been cited near the forest fragment). Adult males may therefore be willing to tolerate riskier locations for foraging than smaller individuals (Martins et al., 2015). However, in this case we would also expect to see a significantly less than expected use of S4 by females and females with infants, yet we found no significant relationship. It should be noted though that the only avian predators spotted near our study site are crested caracara (*Caracara plancus*), which are only capable of capturing infants or juveniles (Travaini et al., 2001), and thus it is possible that females and females with infants were choosing to avoid the researchers and other human contact on the ground by occupying high strata.

Group spread was larger in higher strata **(Figure 2.5)**, a result that supports our hypothesis, suggesting that blond capuchins as a group perceive the ground as riskier and the higher strata as less risky and therefore are willing to spread out further in higher strata. Primate groups have been found to reduce group spread when predation risk is higher, and increase group spread when foraging to avoid direct competition (Di Bitetti & Janson, 2001; Ferreira et al., 2008; Heesen et al., 2015; Luccas & Izar, 2021; Stanford, 1995). However, group spread may also be larger in higher strata because invertebrate availability may be lower (Elton, 1973), thus forcing the group to spread out more in higher strata to achieve the same invertebrate foraging returns that they otherwise would on the ground. Our findings on individual distance to centroid align with previous work on interindividual distance in our own study population as well as other capuchin populations. Lins and Ferreira (2019) found blond capuchins in our study group to have a mean interindividual distance of 25 ± 27 m^2, Luccas & Izar, (2021) found the mean interindividual distance in a group of black capuchins (*Sapajus nigritus*) to be 36m, and (Janson, 1990a) found that individual adult tufted capuchins (*Sapajus apella*) tended to stay 50m from the group at most.

Blond capuchins are primarily an arboreal species, and thus were often several meters high in the trees and sometimes a large distance away. Although we would only record age/sex class if we were confident in our identification, it is possible that the accuracy of age/sex identifications decreased as distance to the researcher and strata increased. Even though this is a well habituated group, it is also possible that the presence of researchers may have led to the capuchins using the canopy more often than they otherwise would have. This could also partially explain the disproportionate number of observations of males and older juveniles compared to other age/sex classes. During our study, males would sometimes perform threatening displays at researchers, and seemed much more willing to be within closer proximity (i.e., within 10m) to researchers than females. Older juveniles similarly were more willing to be within closer proximity to researchers than females, however we suspect this was due to curiosity towards researchers or a lack of life experience rather than aggression, as threatening displays were not seen in this age/sex class.

In this study, we tested the strata use of different age/sex classes of Endangered blond capuchins living in a forest fragment, and though we did not find sufficient evidence to show that male blond capuchins were using the ground more than other age/sex classes, we did find significant differences in how males and other age/sex classes used the higher strata. On top of relying on fission-fusion strategies and sugarcane as a fallback food, the varying use of strata levels by different age/sex classes during foraging provides an additional example of behavioural plasticity that likely contributes to the capuchins ability to survive in the restricted environment of a forest fragment (Lins & Ferreira, 2019). However, juveniles accepting sub-optimal foraging space in exchange for lower predation or conflict risk in a social group where direct competition peaks when the capuchins are foraging on their primary fallback food, and typical food resources are restricted due to a low habitat area, may be problematic for the continued development of juveniles in the group (Lins & Ferreira, 2019). Additionally, females engaging in risky behavior by foraging on the ground may also be problematic for the group, as females are a key age/sex class for ensuring the long-term persistence of the group. Future research should continue to examine the effects that low habitat area and the subsequent low resources have on capuchin behaviour and cohesion and should investigate the nutritional intake of individuals to determine if their adjustments through behavioural plasticity are allowing them to fulfill nutritional requirements. Many primates, including capuchins, are facing extinction, largely due to habitat loss (Estrada et al., 2017, 2022). Further understanding of how primates use their space and habitat will help to inform the habitat conservation and restoration projects that will be vital in preventing further biodiversity loss (Chapman & Peres, 2021).

Chapter 3: Adult leadership among blond capuchin monkeys during periods of higher food availability in an Atlantic Forest fragment

3.1 Abstract

Maintaining group cohesion while accounting for the needs of each individual is one of the main challenges that group-living animals face. In many group-living mammal species, older adult females will lead group movements, in part because they often have the highest nutritional needs of the group. Group-living animals can also dynamically adjust group size and spread to satisfy individual needs. Here we hypothesized that female blond capuchins (*Sapajus flavius*) living in a forest fragment would lead group movements in response to higher energy requirements compared with other age/sex classes. We also expected that overall group spread would be smaller when fruit was less abundant, and the group had to rely on crop foraging for more of their diet. We used scan-sampling at 20-minute intervals to record individuals' location, age/sex class, and strata in a 90ha section of an Atlantic Forest fragment in northeastern Brazil. Contrary to our predictions, we did not find that females led group movements significantly more than other age/sex classes, or that group spread was significantly smaller when fruit was less abundant. Instead, we found that all adult age/sex classes were significantly closer to the front of group movements compared to juveniles, when fruit was abundant, but were no longer significantly closer when fruit was less abundant. Our results suggest that individual needs contribute to group spread and group movement, that adults lead group movement, and that resource and dispersal limitations in forest fragments affect adult females, adult males and juveniles differently.

3.2 Introduction

All animals that live in groups face the challenge of making collective movements while maintaining group cohesion (Morales et al., 2010; Stutz et al., 2018). This can be especially difficult when individuals in groups have different nutritional requirements, predation risks, or habitat preferences (Van Schaik, 1983). Group-living animals have developed a variety of strategies to address this challenge. Ants use a combination of pheromones, touch, and sound to communicate foraging site locations, with each individual working for the benefit of the colony with no apparent overall patterns of foraging movement leadership (Jackson & Ratnieks, 2006). Schooling fish will observe each other for potential movements, with certain individuals, sometimes those with higher nutritional requirements, becoming temporary leaders and causing an "avalanche" of group movement that follows their initial movement (Múgica et al., 2022; Nakayama et al., 2016; Reebs, 2000). Pigeons (*Columba livia*) similarly make collective movements, although bolder individuals in groups tend to lead collective movements more often (Sasaki et al., 2018). In ungulates, an individual's age, sex, metabolic requirements, stress levels, and dominance rank can all influence whether they lead group movements. As a result, older females, who typically have the highest nutritional needs of the group, and typically hold higher dominance ranks than younger individuals, often lead group movements. Older female ungulates will also usually have more extensive social networks and social ties relative to individuals of other age/sex classes in their group, and consequently are often more successful at attracting followers when initiating movements (Ramos et al., 2021).

A female bias towards leading collective movements has been found to occur broadly in most mammal groups, including primates, although less so for primates compared to other mammalian taxa (Smith et al., 2022). Non-human primates exhibit more variation in social structure and dynamics than most other vertebrate taxa, largely due to their wide range of habitats and larger brain to body size ratio (Fichtel et al., 2011). In some species, such as chacma baboons (*Papio ursinus*) and black-handed spider monkeys (*Ateles geoffroyi*), males predominantly lead group movements (Chapman, 1990; Sueur, 2011). In other species, leadership is distributed among adult individuals, and is not significantly associated with dominance rank or age/sex class (Fernández et al., 2013; X. Wang et al., 2016). Many species exhibit distributed leadership, but show a sex-based bias towards where movements are headed or how successful movement attempts are (Ceccarelli et al., 2020; Leca et al., 2003; Lee & Teichroeb, 2016; Van Belle et al., 2013). Leca et al. (2003) found no sex-based difference in the number of movement start attempts among a semi-free-ranging group of white-faced capuchins (*Cebus capucinus*) but did find that females were significantly more often the leaders of successful movement attempts.

Many researchers have suggested that group leadership is dependent on energy requirements for reproductive success. Female primates, particularly those with infants, often have the highest energy requirements of their groups (Key & Ross, 1999), and in female-bonded species, fitness of female primates is primarily dependent on maintaining nutritional requirements for themselves and their offspring (Sterck et al., 1997; Trivers, 1972; Wrangham, 1980). The fitness of males in these species is conversely primarily dependent on maintaining access to females, and therefore they would be expected to have less interest in the direction of movement of the group, and more interest in staying in close proximity to females. Of the aforementioned species that did have males leading group movements, male chacma baboons have the highest nutritional requirements of the group, and male black-handed spider monkeys often move to the edge of their territory, possibly to have access to females from other groups, thus males in both of these species experience fitness benefits from leading group movements (Chapman, 1990; Sueur, 2011).

Another way that group-living animals cope with the challenges of living in groups and satisfy individual needs is by dynamically adjusting group size and spread (Sueur et al., 2011). Many primates modify group size and spread in response to predation risk and food availability, forming large, dense groups when predation risk is high, and splitting into subgroups or spreading out when predation risk is low and food availability is high (Di Bitetti & Janson, 2001; Ferreira et al., 2008; Heesen et al., 2015; Luccas & Izar, 2021; Stanford, 1995). The likelihood of group fissioning is higher in species where individuals have higher variation in their energy needs (Sueur et al., 2011). Within groups of capuchin monkeys (*Sapajus* and *Cebus spp.*), smaller and more vulnerable individuals, such as juveniles, have been found to occupy the centre of the group where predation risk is lowest. However, in the centre of the group, food availability is also lowest as alpha males often monopolize central food patches (Janson, 1990a, 1990b). Less dominant adult males will conversely occupy the periphery of the group where predation risk is higher, but risk of competition with the more dominant alpha male is lower and the potential to have first access to food patches is higher (Bezerra et al., 2014; Di Bitetti & Janson, 2001; Janson, 1990b). Group dynamics and space use are also dependent on the variability of a group's environment (Sueur et al., 2011). A study of yellow-breasted capuchins (*Sapajus xanthosternos*) in an environment with the presence of human hunters as well as a variety of non-human predators found that space use was highly correlated with predator avoidance rather than food availability (Suscke et al., 2021). A similar study of tufted capuchins (*Sapajus apella*), in an environment with very little or no human presence, found instead that the group's space use was positively correlated to food availability (Gómez-Posada et al., 2019).

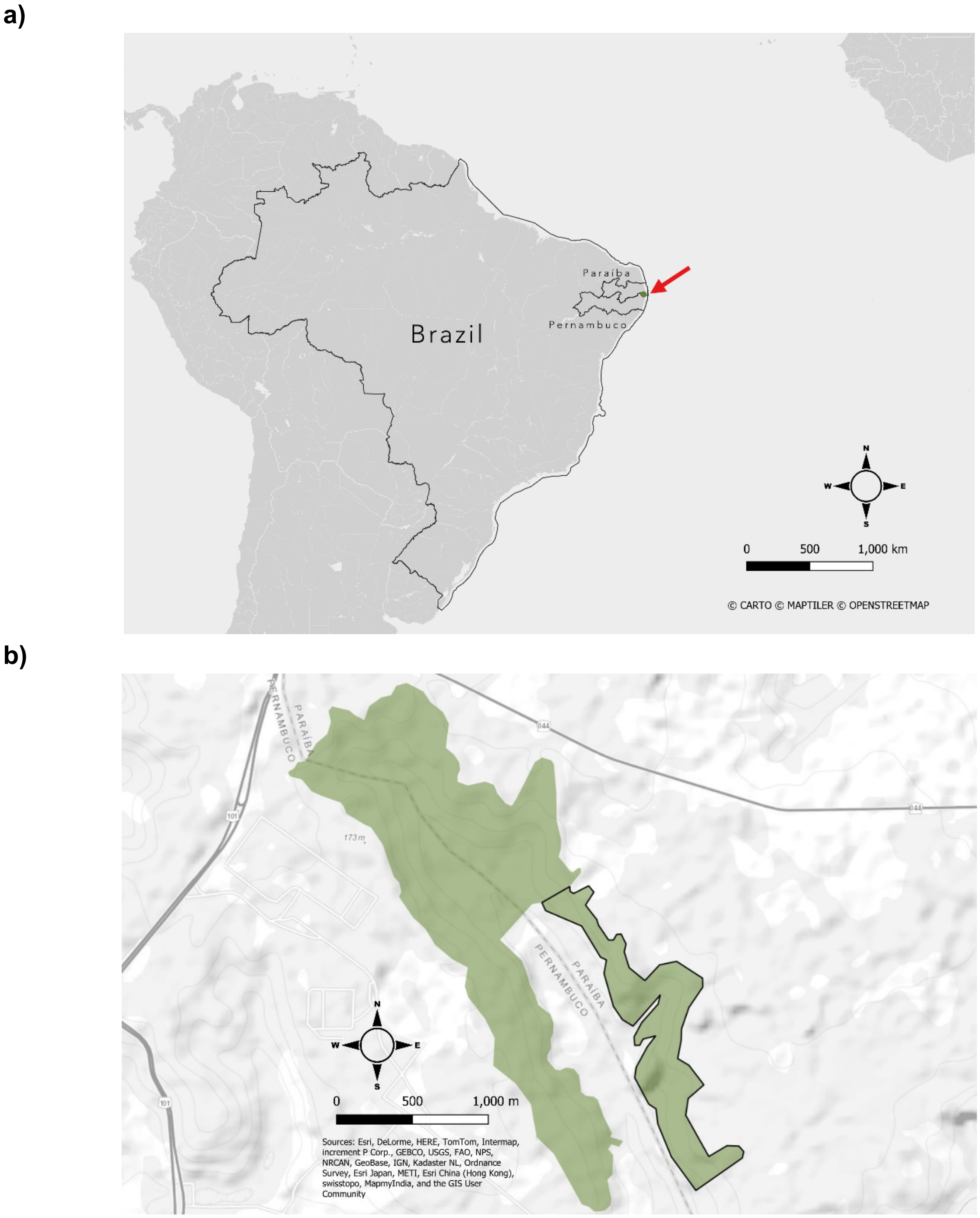
Blond capuchins (*Sapajus flavius*), are an Endangered species, and like many primates, are at high risk of extinction due largely to habitat loss, with only an estimated 1000 individuals remaining (Da Silva et al., 2019; A. B. Martins et al., 2020). Much of their former habitat in the Atlantic Forests of northeastern Brazil has been replaced by agricultural and residential development, leaving only a few relatively small isolated forest fragments (Filho et al., 2021; Lynch Alfaro et al., 2014). These isolated forest fragments are often degraded habitat and provide fewer natural resources for blond capuchins, forcing them to achieve substantial parts of their caloric requirements through crop foraging (Freitas et al., 2008; Lins & Ferreira, 2019; Mota et al., 2018). However, crop foraging, especially of sugarcane, often only fulfills caloric requirements, while not necessarily meeting other nutritional needs, and capuchins have been shown to prefer fruit when it is available (Lins & Ferreira, 2019).

We therefore hypothesized that female blond capuchins in forest fragments have a greater imperative to find food than other age/sex classes and predicted that female blond capuchins and females with infants would be at the front of group movements significantly more than other age/sex classes. We also expected group spread would be smaller when fruit was less available, and capuchins were forced to forage at the edge of the fragment where crops are available, but risk of human interaction is higher. We predicted from this that group spread would be significantly smaller in the season where fruit was less plentiful, and significantly larger in the season where fruit was more plentiful.

3.3 Methods

3.3.1 Field Methods

We conducted our study in a U-shaped 270ha forest fragment on the border of the states of Paraíba and Pernambuco in Brazil, near the cities of Caaporã and Goiana respectively (7°52'85,2"S; 34°96'29,4"O) **(Figure 3.1)**. Our study focused on the eastern side of the fragment, a 90ha segment on the Paraíba side, which is inhabited by a group of around 120 individuals, habituated to the presence of researchers and studied since 2009. There is another group of unknown size on the western side of the fragment, although interactions between the two groups are infrequent. Meetings between the groups have been observed in the northern part of the fragment connecting the two sides, but this area is mostly swamp and tends to be avoided by the capuchins.



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Sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community

Figure 3.1 a) The location of the study site (green dot with red arrow pointing to it) relative to Brazil. The borders of the states of Paraíba and Pernambuco are also visible. **b)** Map of the study site. The study site is located on the border of the states of Paraíba and Pernambuco, Brazil. The forest fragment is coloured in green, and the specific area of our study is outlined in black.

We used scan sampling to gather data on the capuchin monkeys (Altmann, 1974), recording the age/sex class, behaviour, and Global Positioning System (GPS) location of each individual monkey. Observations were recorded in Locus Map, an application for android phones (*Locus Map 4 Outdoor Navigation*, 2024), in 20 minute intervals, with a 20 minute break between each observation period. We categorized individuals according to 8 age/sex classes: adult male, adult male carrying an infant, adult female, adult female carrying an infant, juvenile class 1 (J1, 6mo - 1yr) juvenile class 2 (J2, 1yr - 2yrs), juvenile class 3 (J3, 2yrs - 4yrs), and sub-adult (Hamada-Fearnside, 2023; Izawa, 1980). Individuals whose age/sex class could not be determined were recorded as “not identifiable.”

For each day of data collection, we arrived at the field site and began searching for the group for 10 to 120 minutes, after which we positioned ourselves in the centre of the group and began scan sampling. We alternated between morning visits (~06:30 - ~11:30) and afternoon visits (~11:30 - ~17:30). Season was designated following data collection as either productive (February - March) or non-productive (April - January), based on the presence of fruit in fruit bearing trees and fruit traps (Pereira, *in preparation*).

3.3.2 Statistical Analysis

Distance to next centroid (center location calculated from median distances to the central point) and distance to current centroid were calculated using a program written for this data collection by Kyle Miller. We defined distance to next centroid as the distance of each individual in a scan to the centroid of the following scan, and distance to current centroid as the distance of each individual in a scan to the centroid of the current scan. In all analyses, we removed sub-adults and males with infants due to a low number of observations compared to other age/sex classes, and combined class 2 and 3 juveniles (J2-3) due to a lack of significant differences and relative difficulty of visual distinction between the classes compared to other age/sex classes. We removed scans that occurred more than 25 minutes after a previous scan so that the results of the analysis would not be skewed by movement intervals of longer than 25 mins (20 mins plus a 5 min buffer because field conditions did not always allow perfect precision in scanning intervals). We used 535 scans in total, 128 in the productive season and 407 in the non-productive season. For the purposes of the distance to next centroid analysis, the final scan of each day was removed. This resulted in a remaining 406 scans for this analysis, 101 in the productive season, and 305 in the non-productive season. We used the following generalized linear mixed effects model to test the relationship between distance to next centroid and age/sex class (Knudson, 2015; R Core Team, 2023):

Distance to Next Centroid ~ age/sex * season + 1/scan.total

Distance to next centroid data were transformed into a beta distribution after running a descriptive test of the distribution (Delignette-Muller & Dutang, 2015), and the sequential number of a particular scan was used as a random factor to control for autocorrelation and the number of individuals in each scan (“1/scan.total” in the model above).

To analyze the relationship between distance to current centroid and age/sex class, we used the following linear mixed effects regression model after log-transforming distance to current centroid data based on the results of a descriptive test of the distribution (Bates et al., 2003; Delignette-Muller & Dutang, 2015; R Core Team, 2023):

Distance to Current Centroid ~ age/sex * season + 1/scan.total

For both analyses, we ran a pairwise estimated marginal means (Emmeans) test (Lenth, 2017; R Core Team, 2023), which allows for the comparison of estimated means (based on the model) of different groups while adjusting for the other variables in the model, with a Tukey adjustment that included age/sex class and season as interactions to test the relationships between individual age/sex classes and distance to next/current centroid (*as used in* Borgeaud et al., 2021).

This research complied with all field study guidelines recommended by the International Primatological Society (*Code of Best Practices for Field Primatology*, 2014), and with the policies of Concordia University's Animal Research Ethics Committee (*Procedures for the Ethical Use of Animals in Research and Teaching*, 2022). This study obtained certification of Ethical Acceptability for Research or Teaching Involving the Use of Animals (STurner, protocol number 30016343). All procedures were approved by the University of Rio Grande do Norte’s bioethics committee (RFerreira, SISBIO 76835-3).

3.4 Results

3.4.1 Distance to Next Centroid and Age/Sex Class

The total mean distance to next centroid for our study was 123.4 metres, with a median of 107.8m, range of 1 to 606.5m, standard deviation of 84.6m, and a standard error of 0.76. The mean number of individuals per scan was 30.9 in total, 30.1 in the productive season and 31.2 in the non-productive season. In the productive season, the mean distance to next centroid was 118.9m, with a median of 101.5m, range of 1.3 to 506.7m, standard deviation of 85.5m, and a standard error of 1.55. In the non-productive season, the mean distance to next centroid was 124.8m, with a median of 109.2m, range of 1 to 606.5m, standard deviation of 84.6m, and a standard error of 0.87.

Age/Sex Class	**Non-Productive Season**		**Productive Season**	
	Mean	Median	Mean	Median
Males	122.7	107.9	115.1	98.0
Females	124.6	105.2	113.3	97.1
Females with Infants	139.7	123.8	120.7	99.2
Class 1 Juveniles	119.5	106.4	128.1	111.1
Class 2 and 3 Juveniles	126.2	111.4	125.8	109.6

Table 3.1 Distance to next centroid (mean and median distances) (m) for each age/sex class, in each season, and for both seasons combined.

In the productive season, males, females, and females with infants were at the front of group movements, with median distances to next centroid for the productive season within 2 metres of each other for these age/sex classes **(Table 3.1)**. All juveniles (J1 and J2-3) were significantly farther back from the adult age/sex classes, with median distances to centroid at least 11 metres back from the closest adult class **(Table 3.2)**.

Interaction	Estimate	Standard Error	Degrees of Freedom	Z Ratio	P Value
Females - Females with Infants	0.040467	0.034484	Inf	1.173495	1
Females - Class 1 Juveniles*	-0.07389	0.033613	Inf	-2.19836	0.698081
Females - Class 2 & 3 Juveniles*	-0.04957	0.01898	Inf	-2.61192	0.225088
Females - Males	-0.00109	0.018765	Inf	-0.05802	1
Females with Infants - Class 2 Juveniles*	-0.11436	0.043715	Inf	-2.61609	0.222355
Females with Infants - Class 2 & 3 Juveniles*	-0.09004	0.03383	Inf	-2.6616	0.194423
Females with Infants - Males	-0.04156	0.033705	Inf	-1.23294	1
Class 1 Juveniles - Class 2 & 3 Juveniles	0.02432	0.03278	Inf	0.741914	1
Class 1 Juveniles – Males*	0.072806	0.032737	Inf	2.22396	0.653778
Class 2 & 3 Juveniles – Males*	0.048486	0.017446	Inf	2.779224	0.136222

Table 3.2 Results of the Emmeans post-hoc test of age/sex class and distance to next centroid in the productive season. Significant interactions are notated with "*", where twice the standard error does not cross zero when added to the estimate. Infinite of "Inf" degrees of freedom indicates that estimates are tested against a standard normal distribution rather than a *t* distribution (Lenth, 2017).

In the non-productive season, qualitatively, we continued to see females at the front of group movements based on median distance to next centroid, along with class 1 juveniles. Males and juveniles (J2-3) made up the middle of the group, and females with infants often were far behind the rest of the group, although none of the relationships in this season were found to be statistically significant, aside from the difference between males and juveniles (J2-3) **(Table 3.3)**.

Interaction	Estimate	Standard Error	Degrees of Freedom	Z Ratio	P Value
Females - Females with Infants	0.013914	0.020889	Inf	0.666126	1
Females - Class 1 Juveniles	0.005309	0.020928	Inf	0.25366	1
Females - Class 2 & 3 Juveniles	-0.01664	0.01075	Inf	-1.54835	1
Females - Males	0.007564	0.010625	Inf	0.711856	1
Females with Infants - Class 2 Juveniles	-0.00861	0.026998	Inf	-0.31876	1
Females with Infants - Class 2 & 3 Juveniles	-0.03056	0.020236	Inf	-1.51012	1
Females with Infants - Males	-0.00635	0.020184	Inf	-0.31465	1
Class 1 Juveniles - Class 2 & 3 Juveniles	-0.02195	0.020289	Inf	-1.08204	1
Class 1 Juveniles - Males	0.002255	0.02027	Inf	0.111253	1
Class 2 & 3 Juveniles - Males*	0.024209	0.009315	Inf	2.598862	0.233833

Table 3.3 Results of the Emmeans post-hoc test of age/sex class and distance to next centroid in the non-productive season. Significant interactions are notated with “*”, where twice the standard error does not cross zero when added to the estimate. Infinite of “Inf” degrees of freedom indicates that estimates are tested against a standard normal distribution rather than a *t* distribution (Lenth, 2017).

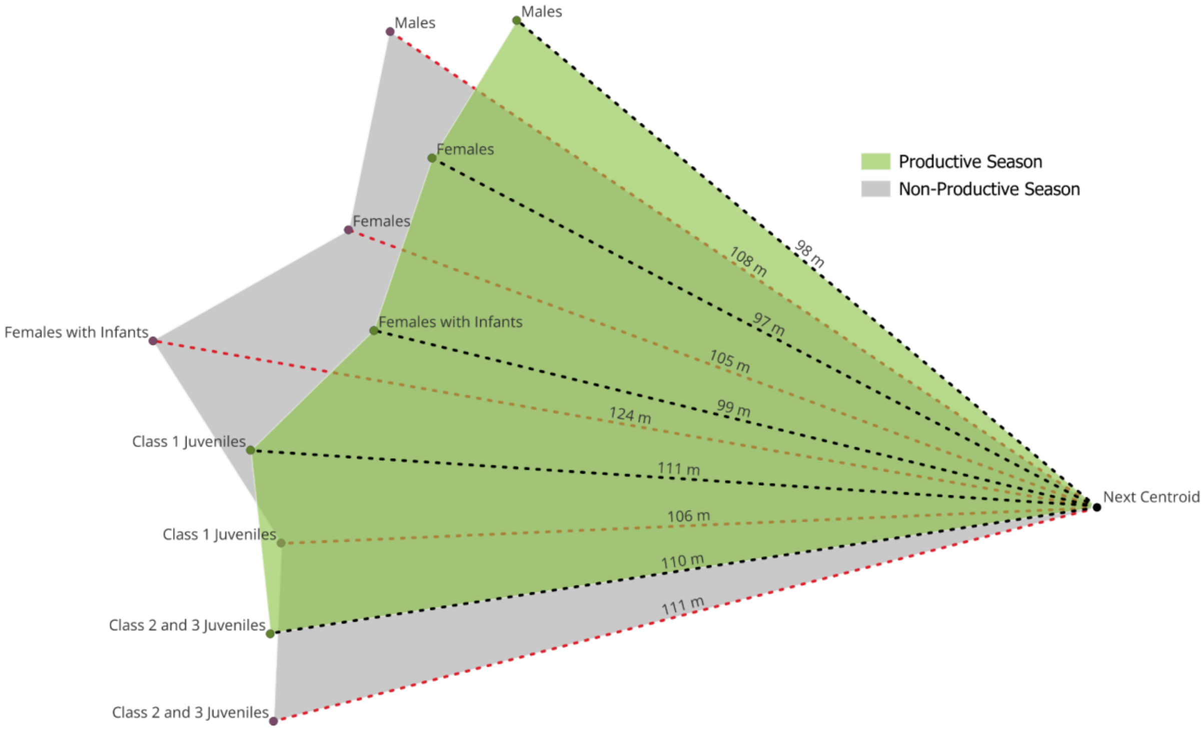

Figure 3.2 Median distance to next centroid for each age/sex class by season. In the productive season, juveniles are significantly further away from the next centroid than adult age/sex classes, but no significance is found in the non-productive season.

3.4.2 Distance to Current Centroid and Age/Sex Class

For distance to current centroid, the total mean for our study was 30.1m, with a median of 24.1m, range of 0.1 m to 260.7m, standard deviation of 24.4m, and a standard error of 0.2. In the non-productive season, the mean distance to current centroid was 29.7m, with a median of 23.9m, range of 0.1 to 260.7m, standard deviation of 23.9m, and a standard error of 0.22. In the productive season, the mean distance to current centroid was 31.3m, with a median of 24.9, range of 0.2 to 235.2m, standard deviation of 25.9m, and standard error of 0.43. The mean distance to centroid of the whole group increased during the productive season by 1.61m, and the median by 1.08m, but this difference was not statistically significant (Emmeans, *z*(inf) = -0.374, *p* > 0.05).

Age/Sex Class	**Non-Productive Season**		**Productive Season**	
	Mean	Median	Mean	Median
Males	31.1	25.1	34.1	27.8
Females	29.8	23.3	31.3	24.3
Females with Infants	30.6	23.6	30.6	23.0
Class 1 Juveniles	26.1	20.4	27.1	22.7
Class 2 and 3 Juveniles	28.4	23.1	28.9	24.1

Table 3.4 Mean and median distance to current centroid (m) across both seasons and for each season separately, for each age/sex class.

Males were typically on the periphery of the group across both seasons, having a median distance to current centroid 1.5m higher than the next highest age/sex class in the nonproductive season, and 3.5m higher than the next highest in the productive season **(Table 4)**. Males showed a significantly higher distance to centroid over all other age/sex classes in both seasons **(Table 3.5 & 3.6)** and showed the largest increase in median distance to current centroid between seasons of all age/sex classes (from 25.1 to 27.8m). Females, females with infants, and juveniles were closer to the centre of the group and did not show any significant differences between each other, aside from class 1 juveniles and females and class 1 juveniles and class 2 and 3 juveniles in the productive season **(Table 3.5 & 3.6)**. Females with infants were the only age/sex class to have a smaller median distance to current centroid in the productive season than in the non-productive season (23.0 compared to 23.6m).

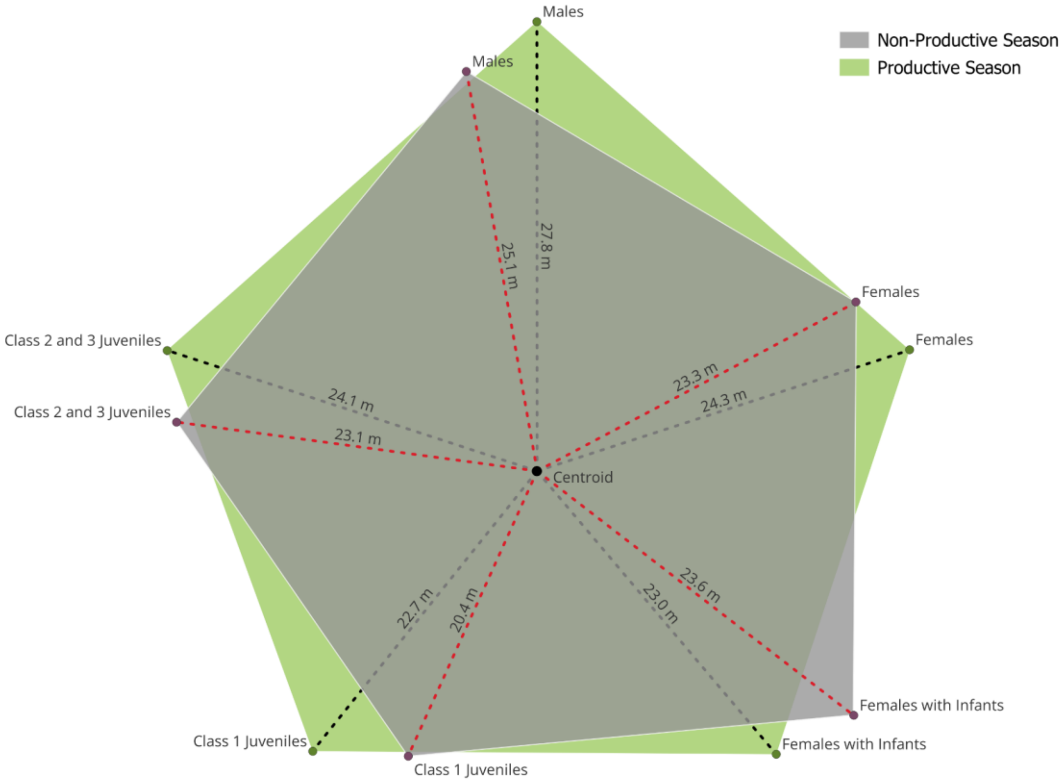

Figure 3.3 Median distance to current centroid for each age/sex class by season. Males were significantly further away from the centroid than other age/sex classes, and typically occupied the periphery.

Interaction	Estimate	Standard Error	Degrees of Freedom	Z Ratio	P Value
Females - Females with Infants	0.073004	0.049561	Inf	1.472993	1
Females - Class 1 Juveniles*	0.153722	0.051033	Inf	3.012199	0.064841
Females - Class 2 & 3 Juveniles	0.044134	0.027997	Inf	1.576416	1
Females - Males	-0.05594	0.0273	Inf	-2.0492	1
Females with Infants - Class 2 Juveniles	0.080718	0.064679	Inf	1.247982	1
Females with Infants - Class 2 & 3 Juveniles	-0.02887	0.04865	Inf	-0.59341	1
Females with Infants - Males*	-0.12895	0.048263	Inf	-2.67175	0.18864
Class 1 Juveniles - Class 2 & 3 Juveniles*	-0.10959	0.05002	Inf	-2.19088	0.71152
Class 1 Juveniles - Males*	-0.20966	0.049765	Inf	-4.21303	0.00063
Class 2 & 3 Juveniles - Males*	-0.10008	0.025629	Inf	-3.90487	0.002357

Table 3.5 Results of the Emmeans post-hoc test of age/sex class and distance to current centroid in the productive season. Significant interactions are notated with “*”, where twice the standard error does not cross zero when added to the estimate. Infinite of “Inf” degrees of freedom indicates that estimates are tested against a standard normal distribution rather than a *t* distribution (Lenth, 2017).

Interaction	Estimate	Standard Error	Degrees of Freedom	Z Ratio	P Value
Females - Females with Infants	0.022904	0.031327	Inf	0.731105	1
Females - Class 1 Juveniles	0.049108	0.031869	Inf	1.540926	1
Females - Class 2 & 3 Juveniles	0.019744	0.015965	Inf	1.236708	1
Females - Males*	-0.07291	0.015616	Inf	-4.6691	7.56E-05
Females with Infants - Class 2 Juveniles	0.026205	0.040966	Inf	0.639665	1
Females with Infants - Class 2 & 3 Juveniles	-0.00316	0.030397	Inf	-0.10395	1
Females with Infants - Males*	-0.09582	0.030259	Inf	-3.1666	0.038558
Class 1 Juveniles - Class 2 & 3 Juveniles	-0.02936	0.030958	Inf	-0.94851	1
Class 1 Juveniles - Males*	-0.12202	0.030886	Inf	-3.95074	0.001948
Class 2 & 3 Juveniles - Males*	-0.09266	0.013753	Inf	-6.73745	4.03E-10

Table 3.6 Results of the Emmeans post-hoc test of age/sex class and distance to current centroid in the non-productive season. Significant interactions are notated with "*", where twice the standard error does not cross zero when added to the estimate. Infinite of "Inf" degrees of freedom indicates that estimates are tested against a standard normal distribution rather than a *t* distribution (Lenth, 2017).

3.5 Discussion

We found that in this 90ha section of a forest fragment, a blond capuchin group with a mean of 30.9 observed individuals maintains a mean distance of 30.1m to the current centroid and moves a mean distance of 123.4m every 20 minutes (as measured by distances between centroids).

We tested the prediction that female blond capuchins and those with infants would be at the front of group movements significantly more than other age/sex classes, and while females had the lowest median distance to next centroid, we did not find that females or females with infants were significantly closer to the next centroid compared to all other age/sex classes; our data did not support our prediction. This may be because of the presence of sugarcane as a fallback food that may allow females and females with infants to satisfy their greater energy requirements without having to lead the group from fruit patch to fruit patch (Key & Ross, 1999; Lins & Ferreira, 2019). Another possibility is that males were following females and trying to maintain close proximity with females to maximize their reproductive success (Sterck et al., 1997; Trivers, 1972; Wrangham, 1980), but this interpretation requires further analysis to verify.

In the productive season, we found that group movement could be characterized as occurring in two waves of movement: Males, females, and females with infants were often in the first wave at the front of group movements, while juveniles often made up the second wave at the back of group movements **(Figure 3.2)**. This result is consistent with results from other studies in the literature that have found adults to be the primary leaders in primate group movements (Fernández et al., 2013; Janson & Di Bitetti, 1997; Lee & Teichroeb, 2016). The separation between adults and juveniles could be due to the adults having an increased familiarity with the area, thus allowing them to move with less hesitation than juveniles when deciding group movements (Janson & van Schaik, 1993). As the productive season is when the capuchins' preferred food (fruit) is more available, these results could also indicate a greater energetic and nutritional need from adults to reach these foods before other members of their group. Juveniles may lack this urgency, or may not be able to keep up with the adults due to their less developed movement abilities (Paukner & Suomi, 2008). This interpretation is further supported by our result that showed that the median distance to next centroid for juveniles remained relatively unchanged between seasons, while the median distance to next centroid of the adult age/sex classes was somewhat larger (although not statistically significantly so) in the non-productive season by 8.1m for females, 9.9m for males, and 24.6m for females with infants **(Figure 3.2)**.

In the non-productive season, there were no significant differences in distance to next centroid between adults and juveniles. We suggest that this likely reflects the capuchins' diet during these months, which consisted largely of arthropods and sugarcane taken from the agricultural fields that surround the forest fragment. Arthropods are a non-clumped food resource that can be found everywhere in the forest fragment, and such resources encourage scramble competition rather than direct competition (Ferreira et al., 2008; Lins & Ferreira, 2019). Conversely, direct competition is common during sugarcane consumption, although this is likely because sugarcane requires substantial processing time and individuals compete for already-processed pieces of sugarcane (Lins & Ferreira, 2019), and not because individuals are seeking to monopolize clumped foods as they would with fruit (Ferreira et al., 2008; Janson, 1988). Being on the periphery of the group or at the front of group movements can provide individuals with first access to clumped foods (Bezerra et al., 2014; Janson, 1990a), but as arthropods and sugarcane were widely available, there was likely little to no benefit for individuals to be at the front of the group when these foods are the majority of their diet.

Our data did not support our prediction that group spread would be significantly smaller in the non-productive season, although we did find a non-significant decrease in median group spread during the non-productive season. Males were significantly more often on the periphery of the group in both seasons and had the highest median distance to current centroid **(Figure 3.3)**. This result is consistent with existing literature on male spatial positioning in capuchin groups, where the alpha male has been found to monopolize the ideal location of the centre of the group, and thus forces less dominant males to the periphery of the group (Ferreira et al., 2006; Janson, 1990b; Robinson, 1981). As migration between groups is largely restricted to this forest fragment, males are less able to leave and join new groups or to form their own groups, than they otherwise would in continuous environments (Jack & Fedigan, 2004). Despite this, our findings on overall group spread are similar to those from other studies of group spread in capuchins (Janson, 1990a; Lins & Ferreira, 2019; Luccas & Izar, 2021). It is possible that less dominant males are tolerated in the group because by occupying the periphery, they provide protection and vigilance against predation for the rest of the group. This behaviour is consistent with the "hired-gun hypothesis," where males maintain their permanence by participating in intergroup conflicts and defending against predators (Bshary et al., 2022; Rubenstein, 1986; Scarry, 2017). Although intergroup conflicts were rare in our study group, as the only nearby group was separated by a large area of flooded forest and an open field, females may still allow males to occupy the periphery of the group, especially if individuals are more risk averse due to increased human disturbance (Suscke et al., 2021).

Since we attempted to position ourselves at the centre of the group when taking scan samples, we were not able to observe every individual in the group due to the large size of the group, vegetation density, and canopy cover in the forest. This meant that we could not always definitively identify the initiators of group movements, as had been done in several studies that have investigated group leadership in primates (Ceccarelli et al., 2020; Fernández et al., 2013; Leca et al., 2003; Lee & Teichroeb, 2016; Van Belle et al., 2013; X. Wang et al., 2016). Because of this, while our data did not support it, we cannot reject the hypothesis that females were leading group movements. Additionally, even though the group is habituated to researcher presence, it is possible that the capuchins may have altered their spatial positioning in response to our presence; during observation we noticed that males and juveniles often tolerated being within a few metres of us, but females tended to maintain a relatively further distance from us. Further research into movement leadership and group positioning of free ranging arboreal primates should seek to use methods that avoid these issues, (e.g., using GPS collars to track individuals).

Our study provides information on the group movement behaviors of capuchins living in heavily restricted forest fragments. This analysis helps us to understand how individuals in disturbed areas alter their behavior and provides insight into how these disturbed areas may be affecting different age/sex classes. Capuchins provide many ecosystem services (e.g. seed dispersal), so increasing knowledge on group movement and leadership dynamics in fragmented landscapes is vital for developing conservation management of Endangered species and ecosystems (Sales et al., 2020). As primate habitat continues to be lost to human development and encroachment, an increasing number of primate species will have to deal with the challenges of living in forest fragments (Chapman & Peres, 2021; Estrada et al., 2017; Taubert et al., 2018). Habitat conservation and restoration practices will continue to be increasingly valuable for creating and expanding protected areas (Chapman & Peres, 2021), and these practices will benefit from an understanding of how species at risk use and move within their habitats.

Chapter 4: Conclusion

I investigated how the spatial cohesion, group movements, and group behavior of blond capuchins are affected by the conditions of disturbed habitats. My initial prediction in my first manuscript, based on the findings of (Williamson et al., 2021), that males would spend more of their time on the ground compared to other age/sex classes, was not supported by the data. I found instead that in both seasons, males used stratum 4 significantly more than expected by chance, while juveniles in classes 2 and 3 used this stratum significantly less than expected. This difference in use of stratum 4 may be because more dominant males are monopolizing areas of the canopy where fruit grows the most, as has been observed in other capuchin species (Di Bitetti & Janson, 2001; Howard et al., 2018; Janson, 1990b, 1990a). However, dominant males in other capuchin species have been observed to tolerate young juveniles in their vicinity when monopolizing fruit patches (Janson, 1990b), so the additional finding that juveniles in class 1 used stratum 4 significantly less than expected in the productive season is unusual, although this may reflect a greater desire from males to monopolize fruit patches in months when fruit is most available. Predator avoidance could also be a contributing factor causing juveniles to avoid stratum 4, as they are at greater risk of predation from crested caracara (*Caracara plancus*) when in the highest parts of the canopy (Travaini et al., 2001).

However, our results show that juveniles are occupying sub-optimal foraging positions, which could be a problem for the long-term viability of the group, as juveniles are an important age/sex class for ensuring group persistence. Sugarcane acts as a fallback food for the capuchins, and may have been allowing juveniles to still reach caloric requirements despite their foraging positions, though because the capuchins do not eat the plant material itself, sugarcane does not fulfill the same nutritional requirements that their preferred diet of fruit normally would (Lins & Ferreira, 2019).

In my second manuscript, I predicted, based on the socio-ecological model of female-bonded primate groups (Sterck et al., 1997; Trivers, 1972; Wrangham, 1980), that females and females with infants would be at the front of group movements more than other age/sex classes. Although we did find that females had the lowest median distance to next centroid of all age/sex classes, we did not find significant results to support this prediction. This could be due again to the presence of sugarcane as a fallback food (Lins & Ferreira, 2019), allowing females to satisfy energy requirements, and therefore not have as great of an incentive to lead group movements towards feeding opportunities. However, like juveniles, females (and especially females with infants) are an important age/sex class for ensuring the long-term persistence of the group and may also not be fulfilling nutritional requirements using sugarcane as a fallback food. Further investigation into the nutritional intake of the group will be needed to determine if juveniles and females are experiencing a nutritional deficit as a consequence of their foraging habits in the fragment.

In the productive season, a two-wave movement pattern emerged, with adult classes at the front of movements, and juveniles trailing significantly behind. This pattern aligns with previous studies showing adult primates as leaders in group movements (Fernández et al., 2013; Janson & Di Bitetti, 1997; Lee & Teichroeb, 2016). In the non-productive season, this pattern was no longer present. This pattern only appearing in the productive season could be the result of the capuchins shifting more of their diet to sugarcane and arthropods when fruit is no longer available, as sugarcane and arthropods are widely distributed around and in the fragment and thus do not incentivise being at the front of group movements as strongly as fruit does (Ferreira et al., 2008; Lins & Ferreira, 2019).

In my first manuscript, I investigated the relationship between group spread, or distance to centroid, and strata. In my second manuscript, I investigated the relationship between distance to centroid and age/sex class. My prediction from my first manuscript, that group spread would be smaller in lower strata, was supported by my data, as I found that group spread increased as strata increased. This finding is consistent with literature that shows that primate groups dynamically adjust group size and spread according to risk (Di Bitetti & Janson, 2001; Ferreira et al., 2008; Heesen et al., 2015; Luccas & Izar, 2021; Stanford, 1995). Although juveniles may be occupying Stratum 4 less to avoid predation from crested caracara, adult males and females do not face this risk, and therefore may feel safest spreading out in Stratum 4 at the top of the canopy due to its distance from ground-based disturbances (i.e., researchers, local people, sugarcane harvesters, and other farmers and workers). However, the high group spread in Stratum 4 could also be due to a lower availability of invertebrates in this stratum, thus achieving the same foraging returns as lower strata may require larger group spread (Elton, 1973). It is possible that the high group spread in Stratum 4 could be male driven, as males were observed in Stratum 4 more than any other age/sex class and were found to have the highest median distance to centroid of all age/sex classes. Less-dominant males have been found to tend towards occupying the periphery of the group in other capuchin groups (Ferreira et al., 2006; Janson, 1990b; Robinson, 1981), and may be tolerated in the group because by occupying the periphery, they provide protection and vigilance for the rest of the group (Bshary et al., 2022; Rubenstein, 1986; Scarry, 2017). This periphery protection and vigilance service may also apply to the vertical axis as well for protection against avian predators, possibly explaining the relatively high number of males in Stratum 4 and the high group spread, though further research into the response of males to the presence of avian predators would be required to verify this claim.

Although I did not record observations of age/sex class without being quite certain that they were accurate, it is possible that the accuracy of my observations decreased as the capuchins' horizontal distance from me, as well as strata, increased. Furthermore, identifying the leaders of group movements was not possible in this study due to extensive tree cover and large group sizes that made it difficult to identify the exact borders of the group while in the field. Individual identification is also not possible in this group -- blond capuchins have a uniform coat and most lack distinct individual features that are observable from the ground. While a few have notable scars or other injuries, most were not individually identifiable in our study (Oliveira & Langguth, 2006). Despite the fact that this capuchin group has been habituated, it is possible that they may have altered their spatial positioning in response to the presence of researchers, an inference that is supported by my observation in the field that males would sometimes perform displays of aggression towards us and females tended to be further away from us than other age/sex classes.

My work shows how primates may be adjusting to living in disturbed environments and underscores the need for further research into the spatial behaviour and group dynamics of primates in fragmented habitats. Specifically, investigation into the nutritional intake of individuals in age/sex classes that are more vulnerable to predation (i.e., juveniles) and may have specific nutritional needs associated with growth (juveniles) or pregnancy and lactation (females), would bring further understanding of the effects that forest fragment conditions have on the primates that are confined to living within them. Furthermore, this type of research would also build knowledge on the trade-offs that different age/sex classes within primate groups make in order to survive. Additionally, investigation into the roles that subordinate males fulfill in groups when unable to disperse, such as predator vigilance, would provide further understanding as to how group-living individuals adjust their behaviour to live in forest fragment conditions. As habitat loss is currently the largest threat to primate biodiversity, the conservation and expansion of protected areas is vital for preventing the extinction of vulnerable primate species (Chapman & Peres, 2021; Estrada et al., 2017), and as human development continues to encroach on primate habitat, more and more primate species will be forced to deal with the challenges of living in forest fragments (Taubert et al., 2018). Thus, understanding how primates move and function as groups in forest fragments will help inform the conservation of vulnerable primates.

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