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Ranging Behavior, Group Cohesiveness, and Patch Use in Northern Bearded Sakis (Chiropotes sagulatus) in Guyana

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Ranging Behavior, Group Cohesiveness, and Patch Use in Northern Bearded Sakis (*Chiropotes sagulatus*) in Guyana.

By

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Graduate School of Arts and Sciences of

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of Doctor of Philosophy

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Abstract

I conducted a 15 month study of the activity patterns, diet, ranging behavior, and group cohesiveness of northern bearded sakis (*Chiropotes sagulatus*) in a continuous lowland rainforest in southern Guyana. My study combined observational data with a novel GIS-based method for assessing food patch quality to assess how bearded sakis adjusted their ranging and grouping patterns in response to changes in resource quality.

My study group consisted of at least 65 animals, making it the largest group of *Chiropotes* yet reported. Bearded sakis were highly active, spending most of their time traveling (40% of activity) and feeding (35% of activity). Compared to other platyrrhines, they spent relatively little time resting. Sakis changed their activity patterns monthly, increasing foraging effort when fruit was most abundant, and increasing resting when fruit was most scarce.

Consistent with their dental adaptations for seed predation, seeds made up 75% of feeding time. Sakis consumed over 215 plant species during the study period, including many types of dry and fleshy fruits. Due to their ability to exploit food items of varies states of maturity, sakis often used the same tree species for three months or more. Monthly seed consumption was correlated with fruit availability. When seeds became scarce seasonally, they incorporated a high percentage of insects, flowers, and mature fruit in their diet.

The study group had home and day ranges that were larger than previously reported for *Chiropotes* anywhere in its geographic range. Sakis exhibited a highly fluid social structure that likely mitigates the effects of intragroup feeding competition despite their large group size. Throughout much of the year, the group moved like an amoeba through their home range, with expansions and contractions dictated by intragroup social dynamics and not changes in food patch quality. When resources became scarcer, and food patch quality was lower, the group divided into smaller, independently functioning foraging parties.

The results of this study suggest that their unique sclerocarpic seed predator niche may necessitate bearded sakis range over large areas to balance the effects of seed secondary compounds. High predation pressure may explain the large group sizes of the genus.

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CHAPTER 1: INTRODUCTION

Theoretical Framework

The relationship between feeding competition, primate group size, and ecological conditions has been the subject of intensive study for the past three decades. Specifically, researchers have focused on the effect of the distribution and availability of food resources on grouping patterns and ranging behavior (Leighton and Leighton 1982, Terborgh 1983, Symington 1988, White and Wrangham 1988, Chapman 1988, 1990, Strier 1989, van Schaik 1989, Janson 1992, Pinto et al. 1993, Phillips 1995, Sterk et al. 1997, Kirkpatrick et al. 1998, Koenig et al. 1998, Stevenson et al. 1998, Pruetz 1999, Chapman and Chapman 2000, Dias and Strier 2003). In many of these studies, an underlying assumption is that food patch size in some way constrains the size of primate groups. This assumption is based on ecological models derived from the predictions of optimal foraging theory (Schoener 1971, Krebs et al. 1974, Charnov 1976). According to these models, selection for efficient foraging results in forager group sizes that allow feeding rates within a patch to be maximized. As a group of foragers begins to deplete a patch, its mean rate of nutrient intake begins to decline due to reduced densities of food items (scramble competition) or contests with other animals (contest competition). Larger patches can accommodate larger foraging groups because of a greater abundance/density of food items. For any patch size, however, a point is reached at which the costs of feeding competition (i.e., reduced rate of nutrient intake) become high enough that it is more efficient to leave a patch and travel to another. The length of time until this point is reached is determined by the quality of and distance to the other patches available to the forager.

The effect of patch size (and feeding competition) on forager group size depends on both the abundance and quality of food items a patch contains, and the density and spatial distribution of all available patches (Chapman 1990, Chapman and Chapman 2000). The density of patches affects foraging efficiency due to the travel costs involved in traveling from one patch to another. Similarly, the distribution of patches determines the distances animals must travel after leaving a depleted patch.

Chapman and Chapman (2000) combined these predictions with evidence from studies on feeding competition and group size in primates to formulate the "ecological constraints model (ECM)" of group size. According to Chapman and Chapman (2000: 567), the critical assumption of this model is "when resource availability is constant, the addition of new members leads to increased intragroup feeding competition, necessitating increased travel. The need for increased travel can result from larger groups depleting patches quickly, necessitating that the group visit many patches."

The ECM is widely accepted as one of the most robust explanations of primate group size. Yet most studies used to support the model focus on a subset of primates with similar ecological requirements and social organization (*Ateles*: Chapman 1988, 1990, Chapman et al. 1995, Symington 1987, 1988, 1990; *Brachyteles arachnoides*: Milton 1984, Strier 1989, Dias and Strier 2003; *Pan*: Chapman et al. 1994, 1995, White and Wrangham 1988, Wrangham 2000). Researchers have generally used either positive relationships between feeding party size and feeding patch size, or positive relationships between day range and group size as evidence to support the ecological constraints model (Klein and Klein 1977, Leighton and Leighton 1982, Symington 1988, White and Wrangham 1988, Wrangham et al. 1993, Wrangham 2000). Most of these researchers have studied primates living in fission-fusion social systems, in which primates from a single community forage in subgroups that change composition and size throughout the day. Thus, animals can respond to small scale temporal changes in food availability with flexible subgrouping.

However, the ECM predicts that the effects of ecological variables on group size should vary for primates with different ecological requirements. Specifically, the differential distribution of leaves vs. fruit should produce different effects on folivores vs. frugivores. According to Isbell (1991), the relationship between primate group size and home range size is primarily determined by food abundance while the relationship between group size and day range length is determined by food distribution. She concluded that frugivore day range length increases with increasing group size because frugivorous primates exploit highly clumped food patches. Because of the clumped distribution of these patches, frugivorous primates cannot increase group spread sufficiently to limit scramble competition. Thus, larger frugivore groups deplete such patches quicker than smaller groups and must travel to more patches to obtain the same amount of nutrients. In contrast, the scattered distribution of leaves allows folivorous primates to spread out during foraging, mitigating the costs of feeding competition. Therefore, day range length does not increase in folivores when group size increases.

Despite the prevalence of models based on feeding competition, few researchers have tried to quantitatively document scramble competition. Especially problematic in studies of scramble competition are the definition of a feeding patch and the assessment of food availability (Oates 1987, Chapman 1988, Isabirye-Basuta 1988, Isbell et al. 1988, Symington 1988, Byrne et al. 1990, Chapman et al. 1994, Pruetz 1999, Vogel and Janson

2007). Traditionally, researchers have defined "patch" as the individual feeding crown (measured as diameter-breast-height, or DBH) (Leighton and Leighton 1982, Nakagawa 1989, Strier 1989, Phillips 1995, Pruetz 1999, Vogel and Janson 2007, 2011). Others have defined a patch as the area in which an individual primate can continuously move and eat (Wrangham and White 1988, Chapman 1988, 1990) or a "localized aggregation of food items…separated from other such aggregations by regions of markedly lower food density" (Temerin and Cant 1983: 336). However, all of these definitions are difficult to use operationally and a patch must be defined according to the specific questions one wants to address (Preutz 1999). Patch size can be defined from the perspective of an individual within a social group or in relation to the entire social group. Defining a patch in relation to a specific individual does not allow for an assessment of how entire social groups perceive food resources. Yet the ability for a patch to accommodate all members of a primate group is critical for testing models of the effect of feeding competition on primate group size. In addition, it is difficult to quantify areas of lower food density in relation to areas of high food density (Nakagawa 1989, Pruetz 1999). According to Pruetz (1999: 10), "Greater standardization, comparability, and accuracy of measures of food abundance and distribution are required to identify the specific relationships between food availability and primate feeding and social ecology."

Another problem with models of primate sociality based on feeding competition is their failure to account for the tremendous behavioral flexibility of primates (Chivers 1991, Sussman et al. 2005, Sussman and Garber 2011). Sussman et al. (2005) suggested that primates are able to use a variety of behavioral strategies to mitigate feeding competition and that competition may not be nearly as important in shaping primate sociality as has traditionally been assumed. One of these strategies is the ability to form subgroups in response to resource scarcity. Subgrouping has been reported for a variety of primate species, although patterns of subgroup formation, ranging, and group membership often differ among taxa (Dunbar and Nathan 1972, Ayres 1981, 1986, Pereira et al. 1988, Symington 1988, Chapman 1990, Kinzey and Cunningham 1994, Norconk and Kinzey 1994, Jamieson 1998, Garber et al. 1999, Dias and Strier 2003, Veiga 2006). While the subgrouping of primates exhibiting highly fluid, fission-fusion social systems (e.g., those of *Pan* and *Ateles*) has received a great deal of attention in the literature, group fissioning in other primates is less well studied. Also, most attempts at correlating group fissioning with ecological variables have been limited to correlations between subgroup size and patch size as defined by the DBH of a single feeding tree. However, patterns of group fissioning are likely highly variable both between primate species and within species during different times of year.

Fission-fusion social systems are probably only one end of a broad continuum of group fissioning patterns that are present in many species of primates (*Papio papio*: Dunbar and Nathan 1972; *Papio hamadryas*: Kummer 1968, Swedell 2002; *Cercocebus albigena*: Waser 1997; *Cacajao calvus*: Ayres 1986, Bowler and Bodmer 2009; *Cebus apella*: Terborgh 1983; *Varecia variegata*: Pereira et al. 1988; *Alouatta palliata*: Chapman 1990, Garber et al. 1999; *Macaca fasicularis*: Jamieson 1998, Sussman et al. 2011; *Lemur fulvus coronatus* and *Lemur sanfordi*: Freed 1998). According to Norconk and Kinzey (1994: 171), “Several investigators have suggested that fission-fusion travel patterns (sensu *Ateles* and *Pan*) have the potential to reduce feeding competition among troop members. We suggest that even slight modifications in the size and composition of foraging parties, such as ‘local’ temporary troop fragmentation, have the same effect, and may be common among frugivorous primates.” Quantifying exactly what is meant by group fissioning and how patterns of group fissioning vary within a species depending on differences in food availability and patch size is important for better understanding this common behavioral response to feeding competition.

In addition, expanding the ways in which a feeding patch is defined is necessary for better characterization of the relationship between patterns of group fissioning and food abundance/distribution. For example, if a feeding patch is an area of several individual feeding trees, increasing group spread is an easily understood strategy frugivorous primates could use to mitigate feeding competition. Frugivores could spread out and feed on fairly dispersed clumps without increasing day range, similar to what Isbell (1991) suggested for folivorous primates. In fact, grouping patterns in several species of frugivorous primates are consistent with this pattern (Chapman 1990, Di Fiore 1997, Freed 1998, Garber et al. 1999, Wrangham 2000). Nevertheless, the traditional measure (DBH of a single feeding tree) for quantifying feeding patch remains pervasive in the literature.

Assessing the relationship between resource quality and distribution and grouping and ranging patterns is also fundamental in human behavioral ecology (Birdsell 1986, Smith 1983, Kelly 1995, Marlowe 2010). Many groups of hunter-gatherers have highly fluid social structures and adjust foraging party size in response to seasonal changes in resource abundance. Researchers have long used optimal foraging theory to explain variation in hunter-gatherer ranging behavior and grouping patterns (Winterhalder 1981, Smith 1981, 1983, Kelly 1995, Winterhalder 1996, Marlowe 2010). Models based on optimal foraging theory have similarly been used to reconstruct the foraging ecology and social structure of early humans (Birdsell 1986, Bluminschine 1992, Kelly 1995, Winterhalder and Smith 2000, Winterhalder 2001). Yet human ecologists attempting to define patch distrubtion and quality and group cohesiveness have experienced many of the same methodological problems described above. Therefore, establishing more accurate ways of quantifying these variables has important implications beyond primate behavioral ecology.

Introduction to the Pithecines

Together, bearded sakis (genus *Chiropotes*), titi monkeys (genus *Callicebus*), white-faced sakis (genus *Pithecia*), and uakaris (genus *Cacajao*) comprise the family Pitheciinea (Rosenberger 2011). *Chiropotes, Pithecia*, and *Cacajao* are united and distinguished from *Callicebus* by their dental adaptations for seed eating (Kay et al. 2008, Norconk 2011). They have been characterized as “sclerocarpic” forgers due to their preference for thick-husked, “mechanically protected” fruit (Kinzey 1992, Norconk et al. 2009). The fruits of their preferred plant families, like Lecythidaceae, Chrysobalanaceae, and Sapotaceae, often have tough exocarp but relatively soft seeds (Kinzey and Norconk 1990, 1993, Boubli 1999, Peetz 2001, Barnett et al. 2005, Bowler 2007, Norconk 2007, Boubli and de Lima 2009). Sakis and uakaris have laterally splayed canines and procumbent incisors, which they use to extract seeds from husks (Kinzey 1992, Ledogar 2009). Their seed crushing adaptations include flat molars and very robust mandibles (Figure 1.1).

All of the Pitheciini are highly frugivorous, with fruit making up 60% to over 95% of their diets (van Roosmalen et al. 1988, Soini 1986, Ayers 1989, Kinzey and Norconk 1993, Peres 1993, Setz 1993, Norconk 1996, Homburg 1997, Aquino 1998, Boubli 1999, Defler 1999, Peetz 2001, Barnett et al. 2005, Palminteri et al. 2005, Veiga et al. 2006, Veiga and Ferrari 2006, Bowler 2007, Norconk 2007, Boubli et al. 2010; Table 1.1). Seeds make up a large portion of fruit consumed (40-87.2%). This extremely high reliance on seeds makes them virtually unique in the primate world and Norconk et al. (2006) have argued that sakis/uakaris are the most specialized primate seed predators based on dietary and morphological traits. Bearded sakis and uakaris appear to consume a higher percentage of seeds than any other primates (Norconk 2011, Norconk and Veres 2011). Along with and likely because of this high reliance on seeds, the Pitheciini generally have very diverse diets, with most plant species making up less than 1% of annual feeding time. They show a preference for slowly maturing fruit and seeds available in the dry season. This may account for their ability to live in oligotrophic species-poor forests or flooded forests (Boubli et al. 2008). The ability to consume a diet composed primarily of seeds appears to somewhat insulate the pitheciines from seasonal shortages of food resources (Ayers 1989, Kinzey and Norconk 1993, Peetz 2001, Bowler 2007, Norconk 2007, Norconk and Veres 2011). Seeds have a much longer temporal availability than ripe fruit and are an important source of protein, lipids, and fiber (Kinzey and Norconk 1993). This is especially true for bearded sakis and uakaris, which travel large distances to locate widely dispersed seed patches.

Until recently the Pitheciines were among the least studied Neotropical primates. Bearded sakis, sakis, and uakaris are notoriously difficult to study for many reasons. All of the Pitheciines are extremely fast moving and, in addition, bearded sakis have large home ranges, long day ranges, and spend most of their time in the upper parts of the canopy (Walker 1996, Walker and Ayers 1996, Vie et al. 2001, Norconk 2007, Boyle et al. 2009). In the last decade, studies throughout the Guiana Shield, Brazil, Colombia, Peru, and Venezuela have greatly expanded our understanding of these species (Aquino 1998, Boubli 1999, Defler 1999, Peetz 2001, Barnett et al. 2005, Palminteri et al. 2005, Veiga et al. 2006, Veiga and Ferrari 2006, Bowler 2007, Norconk 2007,Boubli et al. 2010). However, much of their behavior is still poorly described, and long-term studies in continuous, non-fragmented habitats are rare (Ayers 1989, Boyle 2008, Gregory 2011). This is especially true for the genus *Chiropotes*, which is almost completely unstudied in continuous forest (Table 1.2).

Introduction to Bearded Sakis, (*Chiropotes* spp.)

Chiropotes are small primates ranging in body size from 2.5 to 3.7 kg (Smith and Jungers 1997). Males are slightly larger than females but sexual dichromotism is absent. They are distinguished by their characteristic beards and bulbous temporal swellings, both of which are more prominent in males (Figure 1.2). Bearded sakis are found both north and south of the Amazon River but are restricted to areas east of the Caroni River in Venezuela (Hershkovitz 1985, Ferrari and Lopes 1996, Norconk et al. 1996, Walker 1996, Shaffer 2006; Figure 1.3). Nevertheless, bearded sakis show a somewhat patchy distribution in eastern Amazonia, possibly due to riverine and habitat barriers (de Granville 1982, Lehman 1999, Bongers et al. 2001, Norconk 2007). *Chiropotes* and

Pithecia pithecia are sympatric throughout much of their geographic ranges, although *P. pithecia* is more widely distributed (perhaps because of their more flexible habitat requirements). Hershkovitz (1985) identified two species of *Chiropotes, C. satanas*, with three subspecies, and *C. albinasus*. Bonvicion et al. (2003) revised this taxonomy using genetic data and pelage color. They recommended elevating all of the subspecies of *C. satanas* to species status and classifying the most westerly group as a fifth species. This is currently the most accepted taxonomy of the genus, although the systematics of the western bearded sakis may require further revision (Norconk 2011).

Habitat and Locomotion

Chiropotes has traditionally been thought to be strict in its habitat requirements, restricted to closed canopy, undisturbed, terra-firma, lowland rainforest (van Roosmalen 1981, Hershkovitz 1985, 1987). Data from a number of sites throughout eastern Amazonia is now showing that the genus is much more flexible in habitat requirements than previously thought. Bearded saki populations have been studied in fragmented habitats, island environments, dry forests, and seasonally inundated forests. Researchers have specifically addressed the ability of *Chiropotes* to subsist in forest fragments of various sizes, some as small as 10 ha (Kinzey and Norconk 1993, Peetz 2001, Port-Carvalho and Ferrari 2004, Norconk 2006, Veiga 2006, Boyle 2008, Silva and Ferrari 2009). Researchers in these studies have shown that the incredibly diverse diet and flexibility of bearded sakis in ranging and grouping patterns allows them to persist in highly disturbed environments.

In all habitats, bearded sakis spend most of their time in the upper parts of the canopy. They are arboreal quadrupeds but are also adept leapers (Fleagle and Meldrum 1988, Walker 1996). Unlike *Pithecia*, *Chiropotes* leaps from a pronograde position and lands in the terminal branches of a neighboring tree rather than on larger vertical supports. Although rare, *Chiropotes* does exhibit suspensory postures, especially during feeding and play. During these postures, bearded sakis hang from their hindlimbs and use their non-prehensile tails to support themselves.

Diet and Ranging Behavior

Bearded sakis are reported to be highly granivorous in all studies, with seeds making up as much as 75% of the diet (van Roosmalen et al. 1988, Ayers 1989, Norconk 1996, Peetz 2001, Boyle 2008, Gregory and Norconk 2011, Gregory 2011). Seeds from the Sapotaceae and Lecythidacae families are generally preferred, although *Chiropotes* shows a tremendously diverse diet and most plant species make up less than 1% of the annual diet. Bearded sakis also consume fruit pulp, both unripe and ripe. Preferred fruit resources are often slowly maturing species and *Chiropotes* will frequently utilize the same plant species in a variety of states of maturity (Norconk 2011).

Insects form a small part of the bearded saki annual diet but can be very important seasonally (Ayres and Nessimian 1982, Mittermeier et al. 1983, Frazao 1991, Peetz 2001, Veiga and Ferrari 2006). For example, in Venezuela, insects made up over 10% of *Chiropotes sagulatus* feeding time in some dry season months (Peetz 2001). Bearded sakis target social insects like caterpillars that can be found in high concentrations during certain parts of the year. Flowers are an important part of the bearded saki diet in some studies but are rarely eaten in others (Norconk 1996, Peetz 2001, Veiga 2006). Although they do so infrequently, bearded sakis also consume leaves and pith.

Along with uakaris, bearded sakis have among the largest home and day ranges of any neotropical primates, although range estimates are hampered by the lack of data from groups in continuous forest. Almost all studies of *Chiropotes* have been conducted on islands or in fragmented habitats (Bobadilla and Ferrari 2000, Peetz 2001, Setz et al. 2008, Boyle 2008, Boyle et al. 2009). Nevertheless, day ranges average 3-4 km but can be as large as 5 km. Home ranges in continuous habitats range from 250 to over 500 Ha (van Roosmalen 1981, Ayers 1986, Boyle 2008, Gregory 2011). Sakis show seasonal differences in ranging behavior in some studies. Peetz (2001) reported a decrease in daily path lengths during the dry season for *Chiropotes sagulatus* in Venzeuela. Gregory (2011) found that travel in bearded sakis in Suriname remained relatively consistent throughout the year, although feeding party size decreased in the long dry season. It is unclear why sakis range so far, although a possible explanation is the need to minimize the effects of the toxins from any one type of seed (Kinzey and Norconk 1993, Norconk 1996, Norconk pers. comm.). This is consistent with their reliance on many food species each day.

Social Structure, and Social Organization

While social behavior is relatively rare in bearded sakis, they do show high levels of male affiliation, with males commonly huddling and grooming each other (Peetz 2001, Veiga and Silva 2005, Veiga 2006). One of the most common bearded saki social behaviors consists of a ritualized pattern of lining up and huddling in groups of 2 to 8 animals (Peetz 2001). These huddles commonly consist of adult males. Veiga (2006) found that 90% of male interactions were affiliative and Peetz (2001) found that bearded saki males frequently play with and groom infants and juveniles.

Bearded sakis live in large, multi-male multi-female groups ranging in size from 8 individuals (in fragmented habitats) to 50 or more in continuous forest (van Roosmalen et al. 1981, Ayers 1989, Norconk and Kinzey 1994, Ferrari and Lopes 1996, Ferrari et al. 1999, Peetz 2001, Boyle 2008, Pinto 2008, Silva and Ferrari 2009, Gregory 2011). *Chiropotes* is highly flexible in their social organization, with groups at many sites frequently breaking up into subgroups. While all observers of *Chiropotes* have reported a certain amount of group fissioning, the specific pattern of subgrouping sakis exhibit appears to differ across studies. Norconk and Kinzey (1994) found *Chiropotes satanas* groups in Suriname to travel cohesively between "feeding patches," then fission, with subgroups up to 75 m apart. They contrasted this behavior with that of sympatric *Ateles* groups, which exhibited the typical fission-fusion pattern characteristic of the genus. The authors attributed this difference to the more clumped distribution of the trees used by sakis for feeding.

In his comparison of the feeding ecology of *Cacajao calvus* and *Chiropotes albinasus*, Ayres (1981, 1989) reported that groups of *Chiropotes* generally foraged as a cohesive unit. He found that "group splitting is not infrequent, but the separation of individuals never exceeds a few hundred meters" (Ayers 1989: 711). Even when feeding in trees with small canopy areas, groups remained relatively cohesive, with animals waiting in order to feed and individuals removing food and eating it in adjacent trees. Ayers (1989) proposed that the ability of *Chiropotes* to eat fruit in several stages of development allowed it to exploit larger food clumps than *Ateles* and led to its more cohesive pattern of foraging.

In contrast, Frazao (1992) suggested a more regular pattern of fissions and fusions in a study of *Chiropotes satanas* in Brazil. Group fragmentation occurred throughout the day, during both travel and in feeding patches, with group spread reaching up to 300 m during travel. Like subgroups of *Ateles* and *Pan*, the composition and size of bearded saki subgroups varied.

Similarly, Veiga et al. (2006) found that groups of *Chiropotes albinasus* and *Chiropotes satanas* were almost continuously fragmenting into two or more subgroups. They also found a high degree of variability in subgroup composition. The authors concluded that group fusion was influenced by the availability and distribution of *Simarouba amara*, a patchily distributed food species exploited for immature seeds. Pinto (2008) also reported nearly constant subgrouping among *Chiropotes albinasus* in Brazil.

In one of the only long term studies of *Chiropotes* ranging behavior, Peetz (2001) found *Chiropotes satanas* used both patterns. The group in her study exhibited a foraging pattern of intensively exploiting a small area with several feeding trees for up to five consecutive days then traveling long distances to another food "patch." When traveling between highly dispersed food patches, individuals generally traveled in single file, and group spread rarely exceeded 100 m. When the group stayed in the same area for more than a day, group spread increased and animals were separated by up to 1 ha. This foraging pattern is consistent with Terborgh's (1983) shifting patch model and the predictions of optimal foraging theory. Similar patterns of home range use have been reported for several species of primate (*Cebus albifrons*: Terborgh 1983; *Brachyteles* *arachnoides*: Strier 1986; *Cacajao calvus calvus*: Ayres 1986). Peetz (2001) found that saki daily path lengths were shortest during periods of fruit abundance while sakis increased daily path length when fruit became scarce.

However, her study was conducted in dry forest, which is unrepresentative of most of the geographic range of *Chiropotes*, on an island smaller than most estimates for *Chiropotes* home range size (van Roosmalen et al. 1981, Ayers 1981, Frazao 1992, Norconk and Kinzey 1994, Pinto 2008, Gregory 2011). In addition, the island was inhabited by only one group of *Chiropotes* and only two other species of primate (*Alouatta seniculus* and *Cebus olivaceus*). Peetz attributed the ranging pattern cited above to the lack of potential competitors with sakis, thus allowing feeding patches to support more intensive exploitation before becoming depleted. Nevertheless, Peetz (2001: 21) warned,

> The results must be considered taking account of several limitations of the study: the use of space was restricted by the island's edge; neighboring groups of bearded sakis were not present on the island, therefore excluding the possibility of interactions between groups; immigration and emigration were not possible; nothing is known about *C. s. chiropotes* home range sizes or habitat choice prior to the conversion of the river basin ecosystem. Nor is it known whether the bearded sakis confined to the island were originally members of the same social group. Isolation effects might have an influence on social behavior patterns.

These studies suggest that members of the genus *Chiropotes* may exhibit highly flexible pattern of subgrouping, with cohesiveness fluctuating considerably across different study sites and seasonally within the same study site. Therefore, they are an ideal primate with which to test the relationship between group fragmentation, food patch size, and seasonality. Yet few long term studies of the ranging behavior of this genus have been conducted, especially in continuous forest.

Specific Objectives

In this dissertation, I present data from a study of the activity patterns, feeding ecology and patch use, and ranging behavior of northern bearded sakis (*Chiropotes sagulatus*) in Guyana. The primary objectives of this study were to:

(1) document the behavioral ecology and natural history of bearded sakis in a habitat representative of most of their geographic range. Prior to this research, almost all studies of bearded sakis have been conducted in fragmented habitats where ranging was limited, neighboring conspecific groups were not present, and a complete community of sympatric primates and predators was lacking. These studies have provided invaluable insight into many of the adaptations of the genus *Chiropotes*. However, it is impossible to fully understand the bearded saki niche without long-term studies in the habitat type in which they have evolved. In this study I attempt to partially fill this void in knowledge.

(2) assess the influence of intragroup feeding competition on primate behavior and how seasonal changes in resource availability affect primate behavioral ecology. Many researchers in primatology have sought to understand the relationship between changes in resource abundance and primate behavior. Most of these authors have assumed intragroup feeding competition to be a pervasive force dictating how primates respond behaviorally when resources

become scarce. By collecting data on changes in activity, feeding, food patch use, ranging behavior, and group cohesiveness, I seek to better understand how bearded sakis mitigate intragroup feeding competition.

(3) create better methods for quantifying food patch quality and how it relates to group cohesiveness in primates. Using a novel GIS – based method, I attempt to better quantify how food patches and group cohesiveness are defined, as well as how to assess the relationship between them.

In order to complete these research objectives, I constructed several specific hypotheses concerning the relationship between changes in resource distribution and bearded saki behavior.

Research Question 1. How do bearded sakis change their activity patterns in response to seasonal changes in ecological conditions?

Optimal foraging theory predicts that when resources in the environment become scarcer, the foraging efficiency of primates in that environment (i.e., net energy return per foraging effort) decreases (Charnov 1967, Schoener 1971, Robinson 1986). Therefore, primates must alter their foraging strategy to compensate for this reduced efficiency. In terms of activity patterns, primates can either increase foraging effort (i.e., time spent feeding and traveling) to locate and process more patchily distributed resources or minimize energy expenditure and reduce metabolic needs (i.e., decrease foraging effort and increase resting). Researchers have found that primates employ both strategies but have failed to find a general pattern that characterizes how primates adjust activity patterns in response to resource scarcity (Robinson 1986, Strier 1987, Isbell and Young 1993, Di Fiore 1997).

Hypothesis 1 – The bearded saki activity budget (specifically time spent feeding, traveling, and resting) will show significant seasonal variation and this variation will be correlated with seasonal changes in the availability of their food resources.

Research Question 2. How do bearded sakis adjust their feeding ecology in response to changes in resource abundance?

Optimal foraging theory predicts that primates should concentrate on preferred resources when overall resource abundance is high but increase dietary breadth to incorporate less preferred resources when overall resource abundance is low (Charnov 1967, Schoener 1971). Several researchers have suggested that Pithecines and other specialized seed predators are buffered against seasonal changes in resource abundance because of their ability to exploit a variety of seeds (Norconk et al. 1998, Norconk and Veres 2011). Because of their unique dental adaptations for seed eating, Pitheciines are able to increase dietary breadth to include a variety of plant species not available to other primates. These researchers have suggested that the highly specialized dental mophology of the Pitheciines has been selected for because these specializations allow them to deal with the detrimental effects of resource scarcity.

Hypothesis 2 – Bearded sakis will increase dietary breadth when resources become scarce and will rely more heavily on seeds (i.e., the resources they are highly specialized to exploit) during these periods.

Research Question 3. How do bearded sakis adjust group cohesiveness and food patch use in response to changes in food patch quality and monthly resource abundance? Using optimal foraging theory, researchers have developed several predictions about how intragroup feeding competition dictates primate ranging behavior and patch use (Schoener 1971, Chapman 1988, 1990, 1995, Symington 1988, Strier 1989, Wrangham 2000). Using the ecological constraints model, these researchers argue that intragroup feeding competition should be lower in high quality food patches and higher in low quality food patches. Higher quality patches contain more total energy and are depleted at a slower rate than lower quality patches. Therefore, primates should be able to feed longer in high quality patches before the costs of staying in the patch become higher than the costs of traveling to the next one. In addition, if primates increase group spread to mitigate intragroup feeding competition, group spread should be higher in lower quality food patches. Also, primates should be less cohesive during periods of resource scarcity, when intragroup feeding competition should be at its highest.

Hypothesis 3 – Bearded sakis will spend more time feeding in higher quality food patches

Hypothesis 4 – Bearded sakis will increase group spread when feeding in lower quality patches

Hypothesis 5 – Bearded sakis will increase group spread during feeding and decrease group spread during traveling

Hypothesis 6 – Bearded sakis will be less cohesive during periods of resource scarcity.

Research Question 4. How do bearded sakis adjust their ranging behavior in response to seasonal variation in resource abundance?

The ECM predicts that primates should increase daily path lengths when resources become scarce and patch quality decreases. When resources become scarce, patch quality should decrease and patches will become more widely scattered. As lower quality patches contain fewer available nutrients, primates must visit more of them to obtain the same amount of nutrients. In addition, because the distances between patches increase as they become more scattered, primates must travel further each day.

Hypothesis 7 – Bearded sakis will increase daily path length during months of resource scarcity or when feeding on lower quality patches.

Organization of the dissertation

In Chapter 2, I describe the methodology used in this study. While specific methodology is detailed in each subsequent chapter, Chapter 2 contains a description of behavioral data collection methods, research schedule, and general description of data analyses. In Chapter 3, I introduce the study site for this research. I describe previous research in Guyana and provide justification for why I chose the Upper Essequibo Conservation Concession for this study. I then describe the study site, including the other primates, the forest structure, and seasonal patterns of rainfall and resource abundance. In

Chapter 4, I present data on the activity patterns and social behavior of bearded sakis. I test whether intermonthly variation in activity patterns is related to seasonal changes in resource availability and describe bearded saki social interactions and intergroup encounters. In Chapter 5, I provide a detailed examination of bearded saki feeding ecology. I describe the bearded saki diet in terms of plant parts and plant species and test how sakis adjust feeding behavior in response to seasonal ecological changes. In addition, I introduce a new method for defining food patches and describe the characteristics of bearded saki patches.

In Chapter 6, I discuss bearded saki ranging behavior and group cohesiveness. I describe saki home and day ranges and see how ranging varies seasonally. I then test how group cohesiveness relates to food patch quality and seasonal changes in resource abundance. Finally, in Chapter 7, I synthesize the data presented in the previous chapters to describe the bearded saki ecological niche. I compare bearded saki behavioral ecology to that of other primates and present important areas for future research revealed by this study.

Table 1.1. Comparison of weight, group size, diet, home range, day range for Guinean *Pithecia*, Western Amazonian *Pithecia*, *Chiropotes* and *Cacajao*. Data for *Chiropotes* do not include the results of this study.

Genus	Male Wt (kg)	Female Wt (kg)	Group Size	%Seed*	%Fruit*	%Flowers*	%Leaves*	%Insects*	Home Range Size (ha)	Day Range (km)
Pithecia pithecia	1.8	1.5	2-12	26-60	28-31	2-16	4-18	2-4	10-20	1.5-2.0
Amazonian *Pithecia*	2.0-3.0	1.3-1.9	2-8	40-80	15-55	0.5-7	1.5-9.5	NA	10-200	??
Chiropotes	2.9-3.7	2.5	10-44+	35-75	5-54	0-19	0-7	0-4	200-560	1.5-3
Cacajao	3.5	2.9	20-150+	46-67	20-50	Up to 5	Up to 4	Up to 2	500-1000+	2.5-5

* Percentage of feeding time

Pithecia pithecia references: Setz 1993, Norconk 1996, Homburg 1997, Norconk 2007
Amazonian *Pithecia* references: Soini 1986, Peres 1993, Palminteri et al. 2005, Norconk 2007
Chiropotes references: Peetz 2001, van Roosmalen et al. 1988, Kinzey and Norconk 1993, Norconk 1996,Veiga 2006, Veiga and Ferrari 2006, Norconk 2007, Gregory 2011
Cacajao references: Ayers, 1986,1989, Aquino 1998, Boubli 1999, Defler 1999, Barnett et al. 2005, Bowler 2007, Norconk 2007, Boubli et al. 2010

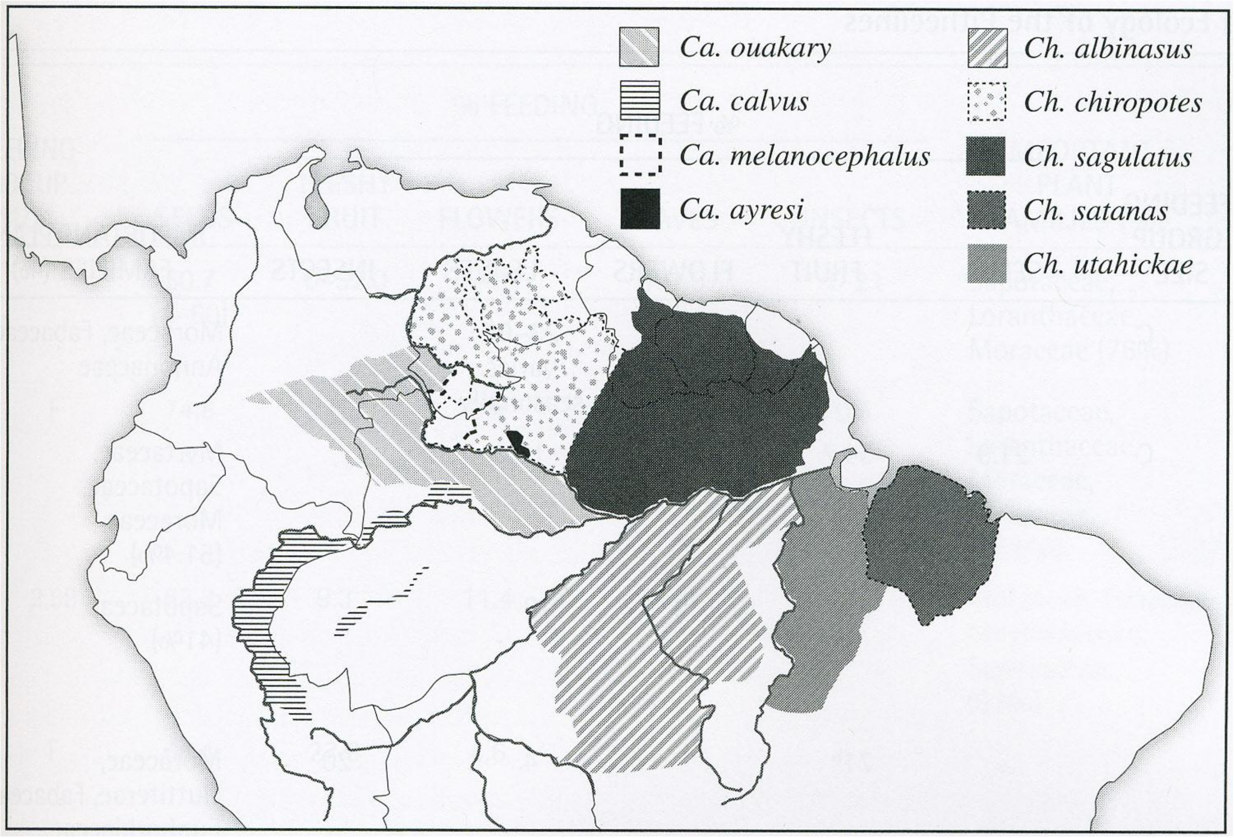
Table 1.2. Previous long-term studies of the genus *Chiropotes*.

Study	Species	Location	Duration	Forest Type
Ayers 1981, 1989	*C. albinasus*	Brazil	Concurrent observations during a 12 month study of *Cacajao calvus*	Continuous
Norconk 1996	*C. chiropotes*	Venezuela	6 months	Island
Peetz 2001	*C. chiropotes*	Venezuela	12 months	Island
Veiga 2006, Veiga et al. 2006	*C. satanas*	Brazil	Monitoring since 2005	Fragmented
Boyle 2008	*C. sagulatus*	Brazil	6 months	Fragmented and continuous
Pinto 2008	*C. albinasus*	Brazil	15 months	Continuous
Silva and Ferrari 2009	*C. satanas*	Brazil	6 months	Fragmented
Gregory 2011	*C. sagulatus*	Suriname	12 months	Continuous

Figure 1.1. Skull and dentition of *Chiropotes sagulatus*, showing adaptations for seed eating. Notice especially the robust mandible with expanded attachment for the masseter muscle, flaring canines, and procumbent incisors. Photos by Jessica Joganic.

Figure 1.2. Bearded saki (*Chiropotes satanas*) male showing temporal swellings and prominent beard (Photo by Stephen Ferrari)

Figure 1.3. Geographic distribution of the genus *Chiropotes* (*Ch.*) and the genus Cacajao (*Ca*) (Modified from Norconk 2011).



CHAPTER 2: METHODOLOGY

Introduction

In this chapter, I describe the methodology used in this study of bearded sakis (*Chiropotes sagulatus*) in Guyana. I present detailed methods for collecting activity data, feeding data, and ranging and group cohesiveness data in their respective chapters. Here I provide a summary of behavioral data collection procedures, research schedule, and general data analyses. I begin by describing the habituation process, establishment of base camp and a trail system, and phenological data collection. I then discuss behavioral data collection, sampling protocol, and my research schedule. Finally, I briefly describe general methods for data analysis used in subsequent chapters.

Establishment of a Trail System and Habituation

This study began in early November 2007 in the Upper Essequibo Conservation Concession in south-central Guyana (see Chapter 3 for study site description). The study site contained several thatched roof, open air structures that had been used and abandoned by a British Broadcasting Corporation documentary film crew. The first two months of the study were dedicated to establishing a trail system and phenological transects and to locating and habituating the study group.

The BBC team had also cut a basic trail that looped around the base camp for approximately 1 km. Upon arrival at the study site, my team of research assistants, which consisted of between two and four amerindians from the villages of Apoteri and Rewa for the duration of the study period, began to establish a more extensive trail system. We first cut a 2 km trail to an east – west running transect that had been established by the Guyana Forestry

Commission. This allowed us to begin searching for the bearded saki group that had been reported in the general vicinity of the base camp.

The rest of the trail system was created by following the bearded saki group for as long as we could throughout the day and returning the following day to cut trails in the area. This method ensured that trails ran through areas that the sakis actually used, although it made for a much less uniform trail system than a grid method. Over the course of the first four months of the study, the trail system was expanded to include over 23 km of trails (Figure 2.1). As this represented only a fraction of the bearded saki home range, most observation of the study group was conducted off-trail. The closed canopy and fairly sparse shrub layer of the forest at the study site made moving through the forest off-trail relatively easy.

The habituation process consisted of simply trying to locate the study group and then following them for as long as possible. Because of the extremely large home range of bearded sakis in continuous forest, habituation for the genus had been suggested to be very difficult (Marilyn Norconk pers. comm., Liza Veiga pers. comm.). Fortunately, the most important food species of the study group (*Manilkara bidentata*) had just begun fruiting when I arrived at the study site. There is a high concentration of large *M. bidentata* trees in the immediate vicinity of the Guyana Forestry Commission transect so the bearded saki group was often very easy to locate. This helped the habituation process tremendously and was especially fortuitous because *M. bidentata* only fruits once every three or four years (Polak 1992). In addition, the lack of regular subgrouping in the study group during this part of the year also aided the habituation process.

During habituation, I assessed group size, approximate age-sex composition, and established an ethogram (see Appendix I). In addition, I estimated the study group home range area to determine appropriate locations for botanical transects. Deciding when a group is sufficiently habituated is notoriously difficult for primate researchers (Lehner 2000, Williamson and Feistner 2003, Campbell et al. 2011). For this study, I ended habituation and began behavioral data collection when the study group no longer acknowledged the presence of the research team. During the habituation process, the group almost never traveled below the upper reaches of the canopy, and when they did, they were extremely skittish. Once they no longer voiced alarm calls at us, rarely looked at us, and did not appear to restrict their use of vertical space, I determined habituation to be complete. This process took approximately 1.5 months and I commenced behavioral data collection in the beginning of January 2008.

Measurements of Resource Availability and Feeding Trees

Using the approximate home range of the study group as a guide, I established 31 botanical transects (5 X 50 m). Detailed discussion of how I chose the size of transects and the methods for monitoring transects are provided in Chapter 3. I monitored each transect once a month for the presence of ripe fruit, immature fruit, or flowers. I then used the relative monthly phenology scores to construct indices of the abundance of different plant parts. In addition, I measured the DBH and height for all transect trees, and identified as many as possible with the aid of a trained tree spotter and a botanist. This allowed for a general characterization of forest structure and species abundance throughout the study group home range.

As defining food patches was an important part of this study, I recorded the location and phenology score (see Chapter 5) for every tree from which I observed the bearded saki group feeding. I took fruit and leaf samples, when possible, for later identification when plant species was unknown. In addition, I measured as many feeding trees as possible for dbh, height, crown width, crown depth, and crown shape. I then used these measurements to quantify bearded saki food patches using geographic information systems (GIS).

Behavioral Data Collection and Research Schedule

Behavioral data were collected using instantaneous scan sampling at five minute intervals with the first observed activity of each visible group member recorded as an individual activity record (Hall 1965, Crook and Aldridge-Blake 1968, Altmann 1974). Scans lasted for three minutes and effort was taken to ensure that no animal was sampled more than once during a scan. Activity and vertical stratification were recorded for all visible animals during scans. When at least one individual was observed feeding, the plant species and food item were recorded and the location of the feeding tree was marked. Scan sampling was chosen over alternative behavioral observation methods for several reasons. First, bearded sakis are virtually impossible to distinguish individually; researchers who have previously studied bearded saki species have been entirely unable to identify individuals. As focal animal sampling requires that the observer be able to distinguish individuals to make certain all group members are equally sampled (Aldridge-Blake 1970, Martin and Bateson 1986), this strategy is not an option when studying bearded sakis. In addition, scan sampling allows for comparisons with previous research of bearded sakis. Finally, scan sampling allows for an assessment of group synchrony in behavior and facilitates calculation of group spread, as the observer’s focus is on all visible animals rather than an individual.

To assess vertical stratification, I divided the forest into four layers: (1) understory, (2) lower canopy, (3) middle canopy, and (4) upper canopy/emergent layer (Sussman and Tattersall 1981, Strier 1986; Figure 2.2). The actual height of these layers varied in different areas of the forest because of differences in forest structure and habitat type. Therefore, these layers were determined relative to surrounding vegetation and do not reflect actual distances from the ground.

As daily ranging behavior was an important focus of this study, most of the data collected were recorded during all-day follows. All day follows were conducted between three and six days per month, with the exception of July and August (during the rainy season), and consisted of following the study group from sleeping tree to sleeping tree. Table 2.1 shows the number of all day follows and the number of hours of behavioral observation collected each month. Each all day follow consisted of 12 hours of behavioral observation (6 am to 6 pm). The study group was occasionally active before and after these times, but observation records were too few to include in analyses. Nevertheless, any travel during these times was included in day range estimates.

In order to ensure that bearded sakis were followed from sleeping tree to sleeping tree, all day follows were only conducted after the location of the study group had been determined the night before. The study group was then followed for as many days in a row as possible. Unfortunately, this was usually just two and occasionally three. The wide ranging, rapid travel, and lack of long resting periods of the study group often led to exhaustion of the research team after only a few days. In addition, when the study group ended the day at the outer edges of their home range, reaching them before they left their sleeping tree the next morning was sometimes impossible.

The large home range of the bearded sakis also made locating the group extremely difficult at times. In general, for every full day follow, five days or more were spent searching for the group. Therefore, the number of full-day follows and behavioral observation hours was less than anticipated. Nevertheless, the 44 all-day follows recorded in this study were twice as many as any other study of bearded sakis in continuous forest (Ayers 1986, Norconk and Kinzey 1994, Boyle 2008, Gregory 2011).

Ranging and Group Spread Data Collection

To assess daily path lengths, the location of the approximate middle of the study group was recorded with a GPS unit during every five minute scan. The cumulative distance between five minute locations was then used to calculate the approximate distance the group traveled during the day.

To calculate group spread, two field assistants recorded the locations of the approximate extent of the group on each side using GPS units. These assistants would stay on either end of the periphery of the group, following the individuals that were furthest from the core of the group. Two-way radios were used by team members to communicate with one another as group spread exceeded 1.3 km on some occasions. These three GPS locations (one in the approximate middle of the group and two on either side of the group) were then used to calculate a linear group spread distance at five minute intervals. This distance was simply the greatest distance between any two of the tree points (representing an estimate of the extent of group spread). This allowed for a much more accurate assessment of group spread than visual estimation.

Data Analysis

Detailed descriptions of methods of data analysis are given in Chapters 3-6. All statistical data analysis was conducted in the SPSS 20.0 statistical software package (IBM Corporation). All data were tested to see if they were normally distributed using one-sample Kolmogorov-Smirnov tests. Non-normal data were log-transformed and re-tested for normalcy. Because almost all behavioral data violated the requirements for parametric tests, nonparametric tests were used unless otherwise indicated. For ranging and group cohesiveness data, log transformations produced normally distributed data. Therefore, these transformed data were analyzed using parametric tests. The alpha level for all statistical tests was set *a priori* at 0.05.

While every effort was made to have an equal number of observation records during different months and hours of the day, there was considerable monthly variation in the number of all day follows and, therefore, behavioral observation records. Accordingly, to assess intermonthly variation in bearded saki behavior, I first calculated percentage of activity or feeding for each hour of the day, then averaged these percentages within each month to determine monthly activity or monthly consumption of different plant parts/species. To account for the small sample size of behavioral data, and because the theoretical distribution from which these data are drawn is unknown, I used bootstrapping to obtain confidence intervals and standard deviations (Efron 1982, Krebs 2000). Bootstrapping consisted of 1000 iterations. To assure maximum accuracy in bootstrapped estimators, bias corrected and accelerated (BCa) boostraps were preformed in all cases (Efron 1982).

To characterize the general species composition of the study site, absolute and relative densities were calculated for all trees in botanical transects. Absolute density was defined as average number of individual trees of a species per hectare (Myers and Shelton 1980, Lehner 2000, Peetz 2001). Relative density was defined as the number of individuals of a species divided by the total number of individual trees (Curtis and McIntosh 1951, Lehner 1996, Peetz 2001). To assess monthly changes in resource abundance, a resource abundance index (RAI) of different plant parts (phenological abudance) was calculated.

Monthly variation in activity patterns, feeding behavior, and ranging behavior was assessed using G-tests for goodness of fit (Sokal and Rohlf 1981). The G-test for goodness of fit is a likelihood ratio test that tests whether observed numbers are significantly different from expected. All G-tests for goodness of fit were calculated using the Williams' correction to obtain more conservative p-values. The relationships between activity, diet, and ranging behavior and monthly changes in food abundance were assessed using Pearson's product-moment correlations. Feeding data were analyzed using several indices of selectivity and dietary diversity, including selection ratios (Clutton-Brock 1975), Strauss' index of selectivity (Strauss 1979), the Shannon-Wiener index of diversity (Pielu 1966), and the Pielu eveness index (Pielu 1966).

GIS Analysis

Because of their ability to simultaneously analyze large quantities of spatial data, GIS represent a powerful tool for addressing primate behavioral ecology research questions that include a spatial component. While GIS analysis has become increasingly common in the primate literature, most research involving GIS has been large scale and populational (Irwin et al. 2005, Lehman et al. 2006, Bergl et al. 2007, Boyle 2008, Buckingham and Shanee 2009, Pinto et al. 2009). Few researchers have applied GIS to analyze the day-to-day foraging patterns of primates.

GIS were used in this study to estimate the home range size and daily path lengths of the study group, to quantify bearded saki feeding patches, and to assess the relationship between saki ranging behavior and group cohesiveness and patch quality. All GIS analysis was conducted in Arc GIS 9.3 (ESRI Corporation). A detailed description of GIS analysis is provided in Chapter 6.

The home range size of the study group was estimated using four methods: (1) minimum convex polygon, (2) grid cell, (3) fixed kernel analysis, and (4) adaptive kernel analysis. To quantify food patches, grids of different sizes were superimposed over saki feeding trees. Each grid cell that contained at least one feeding tree was thus defined as a food patch. The physical characteristics of each feeding tree within the grid cell were used to calculate the quality of that patch. The quality of these patches was then compared to the group spread values of the study group when they occupied the patches to assess the relationship between group cohesiveness and patch quality. The use of different sized grid maps allowed for a definition of patch size that extended beyond the dbh of a single feeding tree. In addition, this methodology allowed me to combine maps of the different sized grids to simultaneously analyze the relationship between group spread and feeding patch quality on several spatial scales. Choosing the size of the grid/s used to quantify patches in a *post hoc* manner allowed for a more accurate depiction of patches in relation to how they were actually used and perceived by the primates themselves in accordance with Pruetz (1999: 53), who stated that “describing patch size relative to social group size or relative to the individual and providing data on the absolute sizes of these patches would more effectively reveal the affects of food availability on primate behavior than if either of these methods were considered alone.”

Lack of Wet Season Data

One of the primary deficiencies of this study is the lack of data obtained during the long wet season. No behavioral or ranging data were collected in the months of July and August. The primary reason for this was the extensive flooding of the Essequibo River during this period, which covered a large portion of the bearded saki home range with up to five meters of water (see Chapter 3). Consequently, following the study group on foot was impossible and attempts to follow them in canoes were unsuccessful because of the monkeys’ rapid travel.

In addition, locating the study group was exceedingly difficult during heavy rain. One of the primary methods for finding the bearded sakis was to walk slowly while listening for contact calls, branch shaking, and fruit falling. Because of the size and noisiness of the study group, it was almost always heard before it was seen. However, the sound of rain falling on leaves made hearing any of these noises impossible. As it rained almost every day during the long wet season, locating the group during this period was extremely difficult.

Finally, the wet season also posed logistical problems, paramount of which was the closure of the Georgetown-Lethem road, the primary avenue for obtaining supplies (see below). This road became impassable for weeks at a time during the long wet season, making getting supplies and even traveling to the study site impossible at times.

Study Logistics

A detailed description of the study site and base camp is provided in Chapter 3. To get to the base camp, I first traveled by bus from the capital of Georgetown to Annai on the Georgetown-Lethem road (a 12 to 16 hour journey depending on road conditions; Figure 2.3). This road bisects the country and provides the only means of transportation to the interior besides aircraft. Upon reaching Annai, I traveled by motorized boat to the village of Apoteri, the nearest village to the UECC (a 4 to 8 hour journey depending on river level). Apoteri was used as a satellite base, as Conservation International (CI) has a small facility there with a radio and basic supplies. The journey by boat from Apoteri to base camp within the Concession took between seven and sixteen hours depending on river level.

Because of the time and cost (e.g., boat fuel) involved in traveling between base camp and Apoteri (and especially between base camp and Georgetown), trips away from the study site were limited as much as possible. Supplies were obtained by having them sent from the CI office in Lethem to Annai by bus and then having them put on the first boat traveling from Annai to Apoteri. Field assistants rotated shifts at base camp, allowing them to see their families and attend to other activities in the village. Resupplying was timed to coincide with these shift changes, allowing me to remain at base camp while supplies were transported from Apoteri to base camp. For safety reasons, at least one boat was kept at base camp as long as it was occupied. While this was the general plan, innumerable logistical problems involved in coordinating activities in a country where the answer to any question involving a time component is “just now” meant that I often needed to deviate from the plan.

Table 2.1. All day follows and hours of behavioral observation per month.

Month	All day follows	Hours of observation
January 2008	4	58
February 2008	6	72
March 2008	5	60
April 2008	4	58
May 2008	5	60
June 2008	4	48
September 2008	3	44
October 2008	4	56
November 2008	5	60
December 2008	4	48
Total	**44**	**564**

Figure 2.1. Map showing the base camp and trail system used in this study.

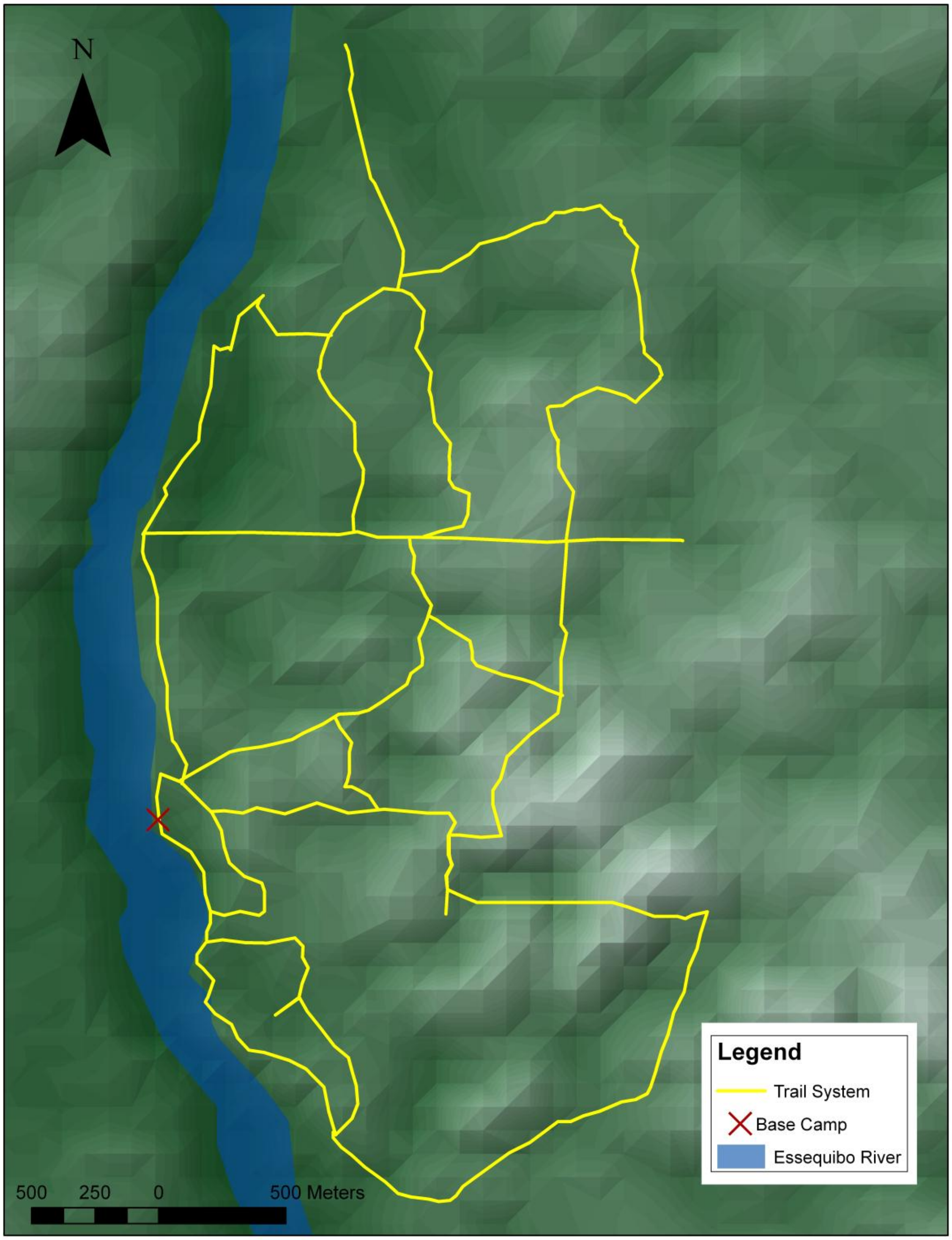


Figure 2.2. Diagram showing the layers used for assessment of vertical stratification.

Figure 2.3. Map of Guyana showing how the study site was reached. Land travel is represented in black and boat travel is represented in blue.

CHAPTER – 3 INTRODUCTION TO GUYANA, STUDY SITE, AND FOREST STRUCTURE

Introduction to Guyana

Guyana is a small country of about 750,000 people on the northern coast of South America (Figure 3.1). Unlike most of the countries in Latin America, Guyana retains over 80% of its original forest (ter Steege 1993, Huber et al. 1995). These forests are among the least distributed in the tropical world and support eight sympatric species of primates in many areas. Due to extensive botanical research for more than 100 years, the vegetation of Guyana is well documented (Schomburk 1876, Tate 1939, Fanshawe 1952, Hammon et al. 1996, 1998, Boggan et al. 1997, Hout 1999). Researchers have recognized five main biogeographic regions of Guyana based primarily on soil type and dominant vegetation (Fanshawe 1952, Boggan et al. 1997, Lehman 1999). These include: (1) the low-lying coastal plain with some seasonally flooded forest, (2) the dry evergreen, wallaba (*Eperua* sp.) dominated, white sands region, (3) the expansive interior rain forest, (4) the highly species diverse highlands, and (5) the Rupununi Savannas, dominated by lowland shrubs and grasses.

The topography of Guyana is heavily influenced by the ancient rock of the Guiana Shield, upon which the country rests. The Guiana Shield is a 1.7 billion year old Precambrian base that represents the remaining exposed section of Gondwanaland (Gibbs and Baron 1993). The formation underlies Guyana, Suriname, French Guiana, and parts of Venezuela, Brazil, and Colombia. The lowlands of the Guiana Shield consist of red, clayey, and ferrallitic soils interspersed with white sand (Gibbs and Baron 1993). Much of the southern area of Guyana, including the study site for this research, is peneplain or low-relief plain. This relatively flat, featureless plain is characterized by an extremely high concentration of meandering rivers and creeks.

Guyana's tropical rainforests are unique in their high levels of endemism and the fact that large parts are dominated by a few or one species (Fanshawe 1952, Granville 1988, ter Steege 1998, Lehman 1999). These rainforests have been divided into five primary and 34 specific vegetative types based primarily on dominant tree species (Huber et al. 1995, Lehman 1999, ter Steege 1996) (Figure 3.2). Mora forest is dominated by stands of *Mora excelsa* and found along low-lying creeks and rivers. Morabukea forest is found on lower slopes above Mora forest and dominated by *Mora gonggrijpii*. Highly species diverse mixed forest is found on slopes with good drainage. Greenheart forest is dominated by *Chlorocardium rodiei* and occurs on steep hills composed of brown soils. Finally, wallaba forest is found on white sand soils of higher elevations and is dominated by stands of *Eperua falcata*. While mixed forest appears to harbor the highest primate species diversity, the habitat preferences of Guyana's primates are not well documented (Lehman 1999).

Guyana's primates have not attracted the same scientific interest as the country's flora. Of the few studies on Guyanese primates, all but one have been surveys and most lasted only a few months (Muckenhirn et al. 1975, Sussman and Phillips-Conroy 1995, Sauther et al. 1998, Lehman 1999, 2004, Barnett et al. 2000). The most extensive surveys on Guyanese primates were conducted by Lehman (1999, 2000, 2004) in the mid 1990s. Lehman covered 1,725 km of transects in 16 sites throughout Guyana to ascertain the biogeographic processes that led to the present distribution of Guyanese primates. Using GIS and satellite photographs, Lehman produced detailed maps of species distributions for 8 primates. Most recently, Wright (2004) conducted a long term study of food mechanics and food processing behavior in *Cebus apella* in the Iwokrama Reserve in central Guyana. Therefore, while the geographic ranges of Guyana's primates are well documented, their behavioral ecology is almost completely unstudied.

Conservation Efforts

Unfortunately, Guyana’s forests came under siege from a variety of threats in the mid-1990s. After decades of crumbling infrastructure, the desire for immediate economic growth led the government to encourage an influx of foreign logging and mining companies, many with a history of questionable environmental practices (Colchester 1993, 1997, Sizer 1996). By 1996, of the 9.1 million ha of “State Forests,” administered by the Guyana Forestry Commission, 7.1 million ha had been allocated to concessionaires through “timber sales agreements” (Colchester 1997). This represents 43% of Guyana’s total forest area. Fortunately, steep terrain, major rivers interrupted by rapids and waterfalls, lack of marketable timber species, and the lack of suitable roads make timber extraction in the far interior difficult. Nevertheless, logging represents a significant threat to Guyana’s forests.

Mining also poses a considerable threat. Guyana has some of the largest gold and bauxite mines in South America and both exports make up a significant portion of the country’s GNP (Roopnaraine 1996, Sizer 1996). In addition to these large, internationally owned mining operations, small scale mining is rampant across the country. The most destructive type of small scale mining incorporates “missile-dredges,” huge vacuum cleaners that are mounted on river dredges (Roopnaraine 1996, Colchester 1997). These machines pump water into alluvial deposits and suck them up to process the minerals. They can dig as far as seventy meters into river banks and cause tremendous environmental damage. The relatively low costs of these dredges means highly destructive mining is available to large numbers of Guyanese. As of 1995, 40,000 to 60,000 people were involved in small-scale gold and diamond mining in Guyana (Colchester 1997). This number may be even higher today, as improvements to the Georgetown-Lethem road that bisects Guyana have increased the number of Brazilian gold miners entering Guyanese territory (Eustace Alexander pers. comm., David Singh pers. comm.). While mining has yet to reach the upper parts of the Essequibo River, the rising price of metals means mining in previously ignored areas may now be profitable. Mining is even more prevalent in Suriname, where several primate study sites have been virtually shut down to researchers because of mining operations (Norconk 2007, Norconk pers. comm.).

In the past decade, the Guyanese government has increasingly shown a commitment to sustainable management of biodiversity and has sought advice from international researchers in ecology (CI 2008, 2011, David Singh pers. comm.). While Guyana has only one tiny National Park, the government has been working with conservation organizations (especially CI) to create an extensive protected areas system. Figure 3.3 shows the paucity of nationally protected areas in Guyana compared to the other countries in the Guiana Shield. Currently, there are several large, privately managed protected areas. The largest of these is the unique Konashen Community-Owned Conservation Area (COCA), a 1000 km^2 area that is titled to and managed by the WaiWai indigenous people of Southern Guyana. The land is managed in a partnership between the WaiWai and CI, with a sustainable use plan developed by both parties (CI 2008).

The second largest protected area in Guyana is the Iwokrama Rain Forest Reserve, a 365,000 ha area managed by an international consortium. The forest in the reserve is divided into a sustainable utilization area, where reduced impact logging is practiced and research on the effects of logging on forest structure are conducted, and a strictly protected wilderness preserve. The third largest of these protected areas is the UECC, the study site for this research.

Previous Research

I conducted reconnaissance of six potential study sites throughout Guyana from June – July 2005. The objective of this research was to identify a site with a large community of primates in relatively undisturbed, lowland rainforest. The feasibility of the aforementioned research questions was assessed for each site. Surveys and interviews with local people were conducted to determine the primate species present and their relative abundance at each site. Sites were chosen based on the results of previous researchers in Guyana and consultation with Guyanese researchers (Sussman and Phillips-Conroy 1995, Lehman 1999, Godfrey Bourne, pers. comm., Eustace Alexander, pers. comm.). This research indicated that CI's Upper Essequibo Conservation Concession (UECC) was the best site for long-term study of *Chiropotes*.

In Table 3.1, I show the sighting rates for the surveys conducted in the UECC in July 2005 (Shaffer 2006). Surveys consisted of walking preestablished transect lines (used by the Guyana Forestry Commission to assess marketable timber) using standard transect methodology (Brockelman and Ali 1987) and boat surveys along the Essequibo River and several creeks. In addition, I interviewed local people in the village of Apoteri who had traveled to the Concession.

I surveyed approximately 167 km during the study period (88 km during land surveys and 79 km during boat surveys). I observed 22 primate groups (11 during land surveys and 11 during boat surveys) representing 8 species. The total sighting rate was 1.32 groups/10 km. The most frequently encountered primate *was Alouatta seniculus macoconnelli*, which accounted for 27% of groups observed. *Chiropotes sagulatus* (18% of total groups) and *Cebus apella apella* (14% of total groups) were also commonly observed. I only sighted one group of *Pithecia pithecia*

pithecia. Estimates of primate group sizes are also shown in Table 3.1. These results were consistent with estimates of primate abundance provided by local people.

Despite the small sample size, individual species and total sighting rates were similar to those reported from other sites in Guyana (Muckenhirn et al. 1975, Gillman and Johnston 1994, Sussman and Phillips-Conroy 1995, Lehman 1999). The largest difference between these previous surveys and my UECC study was the high frequency of sightings of *Chiropotes sagulatus* in the concession. *Chiropotes* represented 18% of groups observed and was ranked by local people as the most common primate. In previous surveys, *Chiropotes* accounted for 1.8%, 8%, 15%, and 2% of groups seen.

The results of this survey suggested that the concession was an excellent site for future research on Guyana's primates, especially *Chiropotes sagulatus*. *Chiropotes* groups were seen in a variety of habitats and were relatively easy to follow. In addition, the continuous, undisturbed forest, extremely low human population density, and lack of conservation threats in the UECC provided a great deal of optimism for the success of conservation efforts.

After the conclusion of this preliminary research, the Director of Protected Areas Planning for CI-Guyana, Eustace Alexander, encouraged me to conduct my dissertation research in the Concession and CI-Guyana agreed to provide logistic support.

Upper Essequibo Conservation Concession

The UECC is a large (81,000 ha) protected area located between 3° 40' – 3° 20' S and 58° 25' – 58° 5' W on the Essequibo River (Figure 3.4). CI purchased a 30 year lease for the land from Guyana's government in 2002 and pays royalties on the Concession's marketable timber without extracting it (Eustace Alexander, pers. comm.). The UECC is approximately 84 km upriver from Apoteri, a village of approximately 250 Macushi and Wapishana Amerindians and the nearest human settlement. These indigenous people practice subsistence agriculture (primarily bitter manioc [*Manihot esculenta*]) and subsistence hunting and fishing. Conservation International allows the local people, who occasionally venture into the area to hunt terrestrial game and fish, to continue their activities. During the 15 month period that I spent in the concession, I only observed 3 such excursions. All of these excursions targeted the black pacu (*Colossoma macropomum*), a locally abundant fish. It took approximately four days for these fishermen to reach the Concession border from Apoteri in their non-motorized dugout canoes. Given the difficulty of these expeditions and the abundance of game around Apoteri, it is safe to assume that the UECC is under extremely low hunting pressure from humans.

Much of the Macushi and Wapishana hunting is opportunistic, with the primary hunting strategy consisting of quietly walking through the forest and shooting any game encountered with bow and arrows (Henfrey 2002, pers. obs.). The most commonly hunted species include the paca (*Agouti paca*), two species of peccary (*Tayassu tajacu* and *T. pecari*), agouti (*Dasyprocta agouti*), currasow (*Crax alector*), and tapir (*Tapirus terrestris*). There is no evidence that indigenous people in the villages closest to the Concession hunt primates for food and they even use the phrase "they'll eat anything, even monkeys" (pers. obs.) to belittle the WaiWai people in southern Guyana. This is perplexing, as the Macushi were considered expert monkey hunters by late-19th and early-20th century explorers (Waterton 1825, Schomburgk 1876, Im Thurn 1883, Schomburgk 1923, Roth 1924). In addition, primates are a considerable source of protein for subsistence hunters throughout Amazonia. While it is possible that local people were reluctant to admit that they hunted primates to a primate researcher, there are several factors indicating that primate hunting was not commonly practiced.

First, I established an excellent rapport with many people in Apoteri and Rewa and spent many days in each village. Had primate hunting been common, I almost certainly would have been aware of it. Second, several of the local people admitted to me that they had shot a primate or two; in a couple of cases just for fun or to practice their aim (*Alouatta seniculus*), and in another case to obtain infants to keep as pets (*Cebus apella*). They appeared genuinely revolted when I asked whether or not they ate the monkeys they had shot. Third, the hunting kit of the Macushi and Wapishana is no longer specialized for primate hunting. In the past, the Macushi were masters of the blowgun and the curare poison that is used on blowgun darts (Roth 1924). This is the weapon of choice for primate hunting throughout Amazonia, as its silence allows the taking of more than one primate individual and the curare acts as a muscle relaxant, relaxing the prehensile tail of atelines and facilitating them falling to the forest floor (Yost and Kelley 1987). The Macushi no longer use the blowgun or know how to make curare, and no one in Apoteri or Rewa that I interviewed remembered anyone using them. Fourth, the Macushi and Wapishana exhibit a tremendous knowledge of the ecology of the species they hunt, including diet, ranging behavior, and activity patterns. Yet they showed a surprisingly low level of knowledge about the local primate species. Finally, the monkeys in the Concession and in the forest around Apoteri did not react as if they were under regular hunting pressure. While some of the species were quite shy (especially *Alouatta seniculus*), they did not flee rapidly upon seeing humans and many of the primates in the area surrounding Apoteri acted as if they were habituated (likely because they see villagers on a regular basis).

Prior to the primate surveys that I conducted in 2005, previous research in the Concession was limited to botanical surveys by the Guyana Forestry Commission to assess timber royalties. Since then, the Concession has attracted a botanist, a mammalogist, and several researchers documenting fish diversity (Eustace Alexander pers comm.). These studies were limited to a couple of weeks in duration.

Most of the forest throughout the UECC is broadly classified as seasonal mixed rainforest (see below). In addition, the concession encompasses a variety of forest types characteristic of lowland rainforests in Guyana, including mora forest (dominated by *Mora excelsa*), greenheart forest (dominated by *Chlorocardium rodiei*), wallaba forest (dominated by *Eperua falcata*), and other types of mixed forest (Huber et al. 1995). The forest throughout the reserve is completely undisturbed and is contiguous with undisturbed forest outside of the reserve for hundreds of kilometers (Figure 3.5). Elevation varies from 80-300 m. There are marked seasonal differences in rainfall, with two wet seasons and two dry seasons (Eustace Alexander pers. comm., see below). The primary rainy season runs from May to mid-August, when much of the annual rainfall occurs. The long dry season, characterized by monthly rainfall of less than 200 mm, lasts from mid-August until November or December. Much of the forest immediately adjacent to the Essequibo River floods during the wet season, with forests being inundated for up to four months (see below).

Base camp and Study site

Base camp for this research was a site on the west bank of the Essequibo river at 3° 31’40”N 58° 14’ 10”W (elevation 110 m). This specific site was chosen because of the temporary thatched shelters that had been constructed for a British Broadcasting Corporation documentary in September 2007 (Figure 3.6). In addition, surveys conducted in 2005 and interviews with local people worked with the documentary team confirmed that bearded sakis were commonly seen in the immediate area. Finally, the terrain in the vicinity of the base camp was relatively flat, an important consideration given the difficulty of following bearded saki groups.

Forest surrounding the base camp consisted of a variety of habitat types, including Mora, mixed, swamp, and greenheart forests. In Figure 3.7, I show the approximate distribution of these forest types throughout the home range of the bearded saki study group. This distribution map was created using transect data, the locations of bearded saki feeding trees, and a digital elevation model of the Concession. Habitat designations are not included in further analyses as they are very general estimates. They are presented here as a qualitative and heuristic way of representing the heterogeneity of the forest within the study group home range.

The most common forest type in the area surrounding base camp was mixed rainforest, which occurs on well-drained soils throughout central and southern Guyana. Mixed forests are characterized by large numbers of plant species in the same area, although the canopy is usually dominated by a few species. The canopy is closed and tall (30-45 m), although not as tall as mora forest. *Swartzia leiocalycina* (Wamara) is locally dominant. Other common canopy species include *Catostemma fragrans* (Sand baromalli*), Geissospermum sericeum* (Manyokinaballi), *Licania densiflora* (Marishiballi), *Goupia glabra* (Kabukalli), and *Ocotea canaliculata* (White silverballi). The understory is fairly open, with the shrub *Rheedia benthamiana* (Asashi) and palm *Attalea regia* (Kokorite) common species.

One subtype of mixed forest is greenheart forest, dominated by *Chlorocardium rodiei* (Greenheart). This forest type was only found in a small area in the central part of the study group home range. The canopy was relatively open, with a height of 25-30 m. Other species encountered in this forest were *Eschweilera sagotiana* (Black kakaralli), *Licania alba* (Konoko), and *Licania laxiflora* (Kauta). Interestingly, this particular forest patch represents the southern-most range of the Guyana endemic Greenheart (Eustace Alexander, pers. comm.).

Mora forest is found on alluvial silt along the Essequibo and riverine flats throughout the UECC. As its name suggests, this forest type is dominated by *Mora excelsa*, with almost all canopy trees being mora. Mora forest surrounding base camp was very tall (canopy height 35-45 m, emergents reaching 50+ m) and many of the canopy trees were extensively buttressed (Figure 3.8). The canopy was extremely dense, with a particularly sparse understory. Other common species in this forest type were *Eperua falcata* (Crabwood), *Eschweilera sagotiana* (Black kakarelli), *Clathrotropis brachypetala* (Aromata), and *Couratari gloriosa* (Wadara). This forest type is seasonally inundated from the middle of June to the end of August (Figure 3.9).

Marsh or swamp forest is also seasonally inundated, and the marsh forest adjacent to base camp was flooded between May and early September. This forest occurred in low lying areas adjacent to the Essequibo River and immediately around creeks. Marsh forest is characterized by a low canopy (10-17 m) and a low density of trees with dbh greater than 30 cm. Common tree species include *Abarema jupunba* (Huruasa), *Pradosia schomburgkiana* (Liquorice tree), *Pterocarpus officinalis* (Swamp corkwood), *Eschweilera corrugata* (Wina kakaralli), and *Gustavia augusta* (Kakaralli). In addition, palms, especially *Euterpe edulis* (Manicole), *Attalea regia* (Kokorite), and *Jessenia bataua* (Turu), are frequent.

The bearded sakis in this study utilized all of these forest types, and exploited many of the most common trees in each for food (see Chapter 5).

Primate Species

The forest surrounding the study base camp harbored all eight species of Guyana's primates. All eight were observed within the home range of the bearded saki study group. In fact, there were several days when all eight were seen during the course of a single all-day follow. These primates are briefly described below, in order of the frequency in which they were encountered.

Alouatta seniculus macoconnelli

Howlers are one of the larger neotropical primates (5-8 kg) and are named for their raucous calls that are thought to function as an intergroup spacing mechanism (Neville et al. 1988). Red howlers have a number of morphological and behavioral adaptations for consuming leaves (primarily young leaves), although they also incorporate a high percentage of ripe fruit in their diet (Gaulin and Gaulin 1982, Julliot and Sabatier 1993, Simmon and Sabatier 1996). They have small home and day ranges (4-25 ha and around 600 m, respectively) and appear to show a high degree of intraspecific variation in group size and social structure (Neville et al. 1988, Terborgh 1983, Gillman and Johnston 1994, Crockett 1997). Red howlers inhabit a variety of habitat types, including montane forest, dry forest, and disturbed and fragmented habitats. While they are among the most studied South American primates, few of these studies have been conducted in continuous rainforest.

Red howler monkeys were frequently encountered in all habitat types throughout the range of the study group. The bearded saki study group would often encounter howlers in the trees in which the sakis fed or traveled, although howlers were rarely observed feeding from the same species as bearded sakis. These encounters were never agonistic and the primates usually did not even acknowledge one another. Due to their skittishness, howlers were rarely observed feeding. However, they were the only other primate observed eating wamara (*Swartzia leiocalycina*), the second most important bearded saki food species. Like the sakis, howlers opened immature wamara pods to expose and consume the seed.

Ateles paniscus paniscus

Black spider monkeys are the largest primate in Guyana with a mean male body size of 9 kg (Smith and Jungers 1997). They prefer undisturbed, closed canopy rainforest and are generally found in the upper levels of the canopy (Fleagle and Mittermeier 1980, van Roosmalen and Klein 1988). They are highly frugivorous, with 75-90% of the diet consisting of ripe fruit (Mittermeier and van Roosmalen 1981, van Roosmalen 1987, Symington 1988, Kinzey and Norconk 1990). Spider monkeys are thought to be important seed dispersers in tropical rainforest, especially for species with fruits too large for birds, bats, and smaller primates (van Roosmalen 1985, Kinzey and Norconk 1990). They have large home ranges that may exceed 250 ha and day ranges between 500 m and 5 km (van Roosmalen and Klein 1988). The genus *Ateles* is characterized by a highly fluid, fission-fusion social structure, where the main group breaks into small subgroups throughout the day (Terborgh 1983, van Roosmalen 1985). The size of these subgroups is reported to be related to the size, quality, and distribution of feeding patches.

At this study site, mean foraging party size observed for spider monkeys was 2.5 individuals. Much of the variation in daily path length is thought to be related to subgroup size (van Roosmalen and Klein 1988, Gillman and Johnston 1994).

Black spider monkeys were also commonly encountered during this study and were occasionally observed feeding from the same species (and even the same trees in some cases) as the bearded saki study group. When spider monkeys entered trees in which the study group was feeding, the sakis would generally move away, although the two species would occasionally feed together. On one occasion, a lone spider monkey attempted to displace eight individuals of the study group from a Kokritiballi feeding tree. These individuals responded by mobbing the spider monkey (repeatedly running at the spider monkey as if it was a predator) and eventually displaced it from the tree. Most encounters between the two species, however, consisted of them simply passing by one another during travel.

Cebus apella apella

Brown capuchins are medium sized primates slightly larger than bearded sakis (mean male body mass of 3.6 kg; Smith and Jungers 1997). They occupy a wide variety of habitat types but prefer the understory and lower canopy. While primarily frugivorous, brown capuchins show a high degree of dietary flexibility, exploiting seeds, pith, nectar, insects, and young leaves. They live in small multimale-multifemale groups that range in size from about 5–16 animals (Robinson and Janson 1986, Gillman and Johnston 1994, Jack 2011). These groups often form polyspecific associations with squirrel monkeys (*Saimiri sciureus*). Brown capuchin home range sizes range from 125 ha to over 250 ha depending on study site. Their daily path lengths are seasonally variable, with larger paths (2.6 km) reported during periods of fruit scarcity and shorter paths (1.6 km) when fruit is more abundant (Robinson and Janson 1986).

Brown capuchins were frequently encountered in most areas of the study site, almost always in association with *Saimiri sciureus*. These mixed species groups of capuchins and squirrel monkeys would occasionally forage with the bearded saki study group, sometimes for up to 2 hours. These encounters are discussed more fully in Chapters 5 and 7. Despite the close contact between individuals of all three species during these episodes, agonism was very rare. In fact, bearded sakis were often observed traveling past capuchins on the same branches, sometimes even jumping over them, without agonism. Brown capuchins were observed feeding from the same species as bearded sakis most frequently. These species included *Geissospermum sericeum, Manilkara bidentata,* and *Pieruella spp*., some of the most important bearded saki food species.

Saimiri sciureus sciureus

Squirrel monkeys are small (mean body mass 800 g) primates that exploit a variety of habitat types and are generally found in the understory (Fleagle and Mittermeier 1980, Boinski 1995, Peres 1997). They are primarily insectivorous, devoting around 80% of their annual feeding time to insects. Squirrel monkeys are extractive insectivores and primarily target cryptic, immobile prey like caterpillars and larvae. They supplement their diet with ripe fruit, exudates, flowers, nectar, and vertebrate prey (Terborgh 1983, Janson and Boinski 1992). Squirrel monkeys form large, multimale-multifemale groups of 20 to over 100 individuals (Baldwin and Baldwin 1981, Terborgh 1983, Boinski 1991, 1994, 1999). Home range estimates for *Saimiri* vary considerably across study sites, from 30 ha to over 250 ha (Klein and Klein 1975, Terborgh 1983, Robinson and Janson 1986). Their day ranges are 1-1.5 km and appear to exhibit little seasonal variation (Robinson and Janson 1986, Boinski 1991). Squirrel monkeys at the study site were almost always observed in mixed-species associations with *Cebus apella*.

Saguinus midas midas

The golden handed tamarin is the smallest primate in Guyana, with a body size of approximately 500 g (Smith and Jungers 1997). While generally found in terra firme rain forest, they appear to prefer edge habitats, such as forest edges, swamps, and forest gaps (Mittermeier and van Roosmalen 1981, Kessler 1995, Day and Elwood 1999). *Saguinus midas* is poorly studied but they appear to be primarily frugivorous (Kessler 1995, Day and Elwood 1999). They also consume insects, animal prey, and flowers. Unlike many other species of tamarin, golden-handed tamarins studied in French Guiana did not feed on exudates (Kessler 1996). Anecdotal evidence suggests that exudates are an important part of the tamarin diet at this study site, however (see below).

Although I often saw groups of *Saguinus midas* when not following the bearded sakis, the study group rarely encountered them. When they did, the sakis almost completely ignored the tamarins, treating them as they would small birds (i.e., occasionally glancing at them when they vocalized or moved abruptly but otherwise paying them no attention). Tamarins were observed frequently feeding on a tree species utilized by the bearded sakis (*Parkia nitida*) but only exploited the exudates while sakis fed from the seeds. This appears to be an extremely important resource for *Saguinus midas*, as tamarins were observed feeding from one huge hiponi tree virtually every day for two months. This tree was only a few hundred meters from base camp so I usually walked by it on my way to find the study group in the morning and after returning from observing the sakis in the evening. On many days during a two month period, I encountered tamarins feeding from the tree on both passes.

Pithecia pithecia pithecia

White-faced sakis are the smallest of the Pitheciinae, with mean adult body sizes of 1.5-1.8 kg (Hershkovitz 1986, Smith and Jungers 1997). Sakis are arboreal quadrapeds but spend a significant amount of their time clinging and leaping on vertical supports (Fleagle and Mittermeier 1980, Fleagle and Meldrum 1988, Walker 1998). They spend most of their time in the lower levels of the canopy and understory and can spend several hours a day on ground. Jumping and leaping are their primary locomotive modes of travel. They can travel very quickly in quick spurts, so much so that white-faced sakis are known as “flying jack” or “breezy monkey” in Guyana.

Like all of the pitheciines, *Pithecia* rely heavily on seeds, with the percentage of time eating seeds varying from around 40% to over 80% in different studies (Kinzey and Norconk 1993, Norconk 2004, Cunningham and Janson 2006, Frisoli et al. 2007). Sakis generally show a preference for immature seeds and preferred plant families such as Sapotaceae, Lecythidaceae and Fabaceae. Most of the rest of the diet of *Pithecia* is made up of ripe fruit, which becomes the most important food source when widely available in most studies. *Pithecia* appear to be more selective than *Chiropotes* in their preference for fruit in only one stage of maturity, generally exploiting different tree species for flowers, ripe fruit, and seeds (Norconk 1996).

Leaves are also an important part of the diet of *Pithecia*, making up 10% of feeding time in several studies (Norconk 2011). Flowers and insects, while a relatively small percentage of saki feeding time, may be important seasonal resources in many habitats. Wasps and grasshoppers eaten by white-faced sakis are among the highest resources in crude protein that they ingest (Norconk 1996).

While still large, *Pithecia* home and day ranges are much smaller than *Cacajao* and *Chiropotes*. Home range estimates range from 10-100 ha (Norconk et al. 2003, Norconk 2006, Norconk 2007, Setz et al. 2008). Day ranges average 1-2 km in *Pithecia pithecia* and range from 500-2800 m (Vie et al. 2001, Cunningham 2003, Norconk 2006, Setz et al. 2008).

Pithecia is characterized by short daily activity periods (8-10 hrs) (Vie et al. 2001, Norconk 2007, Setz et al. 2008). White-faced sakis were long thought to form pair-bonded groups with one male, one female, and dependant offspring (Buchanan et al. 1981, Hershkovitz 1985, Poyas and Bartlett 2009). This is consistent with census data from several populations, showing 2-5 individuals per group (Mittermeier 1977, Oliveira et al. 1985, Soini 1986, Kessler 1998, Ferrari et al. 1999, Heyman et al. 2002). Several other surveys, however, (Shaffer pers. obs., Lehman 2001, Norconk 2006) show larger group sizes, ranging up to 14 individuals. While the specific social structure of *Pithecia* remains unclear, Norconk (2007: 135) has characterized their group sizes as “small but flexible and responsive to variables such as population density, food distribution and sympatry with *Chiropotes* and *Cacajao*”.

White-faced sakis were rarely observed at the study site (12 observations), although they were encountered in all of the habitat types described above. When they were observed, they would usually either flee extremely rapidly out of site or disappear into dense vegetation. I always observed white-faced sakis in the understory or lower part of the canopy, usually at a height of between 15 and 25 m. Their group sizes were generally small (2-5 individuals) although I observed groups of 11 and 14 individuals during the short dry season.

I only encountered white-faced sakis once while following the bearded saki study group, although the study group either did not see the white-faced sakis or completely ignored them. I observed white-faced sakis feeding on three occasions. On two of these, they fed from species that were also exploited by the study group (*Eschweilera corrugata* and *Gustavia augusta*). The other species they fed from was an unidentified liana that was not seen being consumed by the study group.

Cebus olivaceus olivaceus

Wedge-capped capuchins are slightly smaller than brown capuchins (mean male body mass 3.3 kg; Smith and Jungers 1997). They are found in a variety of habitat types but appear to prefer evergreen rain forest (Robinson 1986, Miller 1996). They are primarily frugivorous (about 50% of feeding time) but also incorporate a high percentage of insects in their diet (35% of feeding time; Robinson 1986, Miller 1996, 1997). They supplement their diet with leaves.

Wedge-capped capuchins form smaller groups than brown capuchins, with mean group sizes ranging from 4 to 15 individuals (Robinson and Janson 1986, Gillman and Johnston 1994). They have large home ranges (250+ ha) and seasonally variable day ranges (1-3.6 km, longer daily paths during periods of resource scarcity).

During the 15 month study period, I only observed groups of wedge-capped capuchins on five occasions. These groups were very shy (much more so than *Cebus apella*) and moved away fairly quickly upon discovering my presence. I did not observe bearded sakis interacting with wedge-capped capuchins.

Predators and other Animals

The forests of Guyana and the UECC in particular, are unique in the abundance of large animals that have become rare in most of the rest of Amazonia. Mammals such as tapirs, white-lipped and collared peccaries, giant river otters, giant anteaters, and reptiles like the giant Amazonian river turtle, black caiman, and giant anaconda were frequently encountered at the study site. In addition, animals that are extremely rarely encountered in South American rainforests, like the harpy eagle, jaguar, ocelot, and jaguarundi, were each encountered on multiple occasions. The abundance of these animals, combined with the undisturbed nature of the forest at the UECC, shows that it harbors a complete and healthy ecological community, something that is virtually unknown in Amazonia today.

Of all the animals inhabiting the study site, including the other primates, the species that appeared to have the greatest dietary overlap with bearded sakis were the larger Psittacines, especially mealy parrots (*Amazona farinose*), and three species of macaws (*Ara ararauna, A. macao,* and *A. chloroptera*). While other primates were rarely seen feeding from plant species eaten by the study group, the psittacines were observed feeding on bearded saki foods almost every day of the study period. For many of the study groups’ food species, especially those with dry fruits and indehiscent pods, the psittacines were the only other animals seen exploiting them.

Macaws were often observed feeding from the same tree crowns as the study group, especially in larger trees. This is not surprising, given the convergent adaptations of the psittacines and the pithecines for seed eating, and other researchers have noticed this dietary overlap (Norconk et al. 1997). It is possible, therefore, that sakis share an ecological guild with psittacines rather than the other sympatric primates.

Several of these animals are potential predators for the small bearded sakis, including eagles (harpy eagle, crown eagle), felids (jaguar and ocelot), large arboreal constrictors (boa constrictor and rainbow boa), and the tayra, a medium sized mustelid. Several attempted predation events were observed during the course of the study and several factors suggest bearded sakis may be under a high degree of predation pressure at this site (see Chapter 4).

Rainfall and temperature

Mean monthly rainfall was recorded at base camp with a rain gauge and temperature was taken each day using a Six's thermometer. Mean monthly rainfall and mean monthly high temperature are shown in Figure 3.10. Total annual rainfall from December 2007 to November 2008 was 259 cm and mean high temperature during this period was 31.7℃. While temperature did not vary much throughout the year, rainfall was highly seasonal. As expected, there were two peaks in rainfall representing the short rainy season or "Christmas rains" (mid-December to mid-January) and the long rainy season (mid-May to the end of August). Almost 60% of the annual rainfall occurred during the long rainy season, while mean monthly rainfall during the dry season months was generally less than 20 cm. October was the driest month, with only 5 cm of rainfall. During the short-dry season, it was not uncommon for several days to pass with no rain.

Forest structure and resource availability

Characterizing forest species composition and resource availability is necessary for understanding the relationship between primate behavior and ecological variables (Ganzhorn 2003, Vogel and Dominy 2011). To assess the species composition and productivity of the forest throughout the bearded saki home range, I established 31 5 X 50 meter botanical transects (Figure 3.11). Transect locations were chosen by overlaying a 50 meter grid over the estimated bearded saki home range and using a random number generator to chose 60 of them (non-adjacent) at random. The eastern edge of each grid (running north-south for 50 meters) was then used as a transect. While I had initially intended to monitor all 60 transects, the difficulties of and time spent locating the study group, combined with the huge area covered by the transects, made this impossible. I therefore selected thirty-one transects at random from the 60.

2 X 50 meters was the originally intended size for transects based on Gentry (1993). Smaller sized “Gentry transects” were chosen because this allowed me to establish more of them than if I had chosen larger plot sizes. By having more, smaller sized transects, I was able to better capture the habitat heterogeneity. In addition, Gentry transects are relatively easy to establish and have been shown to provide relatively good resolution for characterizing habitat structure (Gentry 1993, 1995, Southward and Henderson 2000). However, shortly after transects were established it became apparent that the enormous size of the bearded saki home range necessitated larger plot sizes. As establishing more transects would have been extremely time consuming, and the established transects provided decent coverage of the home range area, transects were simply enlarged to 5 X 50 meters. While this was certainly not an ideal method for sampling the forest structure, for the purposes of this study a general estimate of plant species diversity and forest productivity was sufficient. Transects were not meant to document total

species diversity at the study site. Rather, they were established to show the most common plant species and plant families, as well as their approximate abundance.

Transects were established in January 2008. All trees over 10 cm diameter at breast height were measured (dbh and height), marked for identification, and assessed for the presence of fruit and flowers. Abundance of plant parts was rated on a relative scale of 0 – 4 with scores indicating the percentage of total crown volume that contained fruit (or flowers). A score of (0) indicated no fruit, (1) indicated < 25%, (2) indicated 25% - 49%, (3) indicated 50% - 74%, and (4) indicated 75% - 100%. Abundance was recorded for immature fruit, mature fruit, and flowers. Because previously studied groups of bearded sakis had rarely been observed eating leaves, young leaf abundance was not recorded. All transects were monitored once per month throughout the duration of the study period with the exception of the month of August (when forest flooding and logistical issues made monitoring impossible). Phenological monitoring was conducted during the middle days of the month (10th – 20th) to assure records were approximately one month apart.

Using these phenological data, I calculated monthly forest productivity by multiplying basal trunk area by phenology score for each tree that had either fruit or flowers in a given month. Basal area was defined as the cross sectional area of the truck at breast height:

$$\pi \left({}^{Dbh}/_{2}\right)^2$$

I then added these scores and divided them by total monitored basal area to obtain an average Resource Availability Index (RAI) for each month.

The 31 5 X 50 meter transects provided a sample of 0.775 ha of the bearded saki home range. A total of 443 trees were present in the transects, giving an estimated tree density of 572 individuals per hectare. These trees represented more than 119 species, at least 75 genera, and at least 30 plant families. In Table 3.2, I show the plant families represented by transect trees. In Tables 3.3 and 3.4, I show the top ten most abundant tree species in terms of percent of total basal area and number of individuals, respectively. A species and family list for all 443 transect trees is shown in Appendix II. The sizes of transect trees were highly variable, but more than 55% were between 10 and 20 cm dbh (Figure 3.12). Mean dbh was 23.71 cm (std = 17.55, min = 10, max = 181) and mean height was 16.08 m (std = 8.40, min = 4 m, max = 46 m).

The abundance of immature fruit, mature fruit, and flowers all varied considerably throughout the year. G-tests with Williams correction showed RAI scores for each of these resources varied significantly across months (Immature Fruit $G = 142.06$, $p < 0.001$, Mature Fruit $G = 210.11$, $p < 0.001$, Total Fruit $G = 248.41$, $p < 0.001$, Flowers $G = 142.06$, $p < 0.001$). Immature fruit abundance peaked in April and was lowest in September and October. Mature fruit abundance peaked in May and was lowest in February, September, and October. Flower abundance showed two peaks, one in February, and the other from September to November. Using a Spearman's rank correlation, flower abundance was not significantly correlated with total fruit abundance (rho, $\rho = -0.35$, $p = 0.328$) but was significantly negatively correlated with mature fruit abundance ($\rho = -0.75$, $p = 0.013$) (Figure 3.13). Flowers were negatively correlated with rainfall but this relationship was not significant ($\rho = -0.46$, $p = 0.187$). Mature fruit abundance was positively correlated with monthly rainfall but this relationship was also not statistically significant ($\rho = 0.52$, $p = 0.128$; Figure 3.14). Neither immature fruit abundance ($\rho = -0.15$, $p = 0.676$) nor total fruit abundance ($\rho = 0.24$, $p = 0.511$) were significantly correlated with monthly rainfall. However, the months where total fruit abundance was lowest were also the driest months of the year (September and October). Both mature and immature fruit were extremely scarce during these months, although flowers were at their highest abundance.

Despite the small size of the area surveyed in this study, these results are remarkably similar to phenology data from over 50 years of monitoring in northern Guyana (ter Steege and Persaud 1991). This similarity indicates that transects accurately represented seasonal changes in phenology at the study site. ter Steege and Persaud (1991) reported that flowering patterns in Guyana coincide with peak sunshine during the two dry seasons. In contrast, fruiting peaks occur in the late dry seasons, prior to months with maximum rainfall, to both aid in germination and facilitate dispersal of hydrochorous (water dispersed) fruits. Both of these patterns were observed in this study.

These data reveal several notable characteristics of the forest at this study site that differ from those of forests in western Amazonia. Perhaps the most notable is the abundance of legumes (plant familiey Fabaceae, subfamilies Papilionaceae, Caesalpiniaceae, Mimoceae) and species of the Lecythidaceae. An abundance of plant species from these families is characteristic of forests of the Guiana Shield and distinguishes them from forests in western Amazonia, where the Moraceae and Bombacaceae are more dominant (ter Steege et al. 2000, ter Steege et al. 2006). This has important implications for the feeding ecology of seed predators and is discussed in Chapters 5 and 7.

Another notable characteristic of the forest at the study site is the lack of asynchronous fruiting species. Asynchronous fruiting species like figs (*Ficus* spp.) exhibit considerable intraspecific variation in seasonal fruiting patterns such that individuals of the same species fruit at different times throughout the year (Grochov 1988). These species are often considered “keystone resources” because they are available to frugivores throughout the year even during the periods of the year when most species are not fruiting (Stevenson 2005, Chapman et al. 2005). Only a few species at this study site (e.g., *Pouteria cuspidata*, *Licania densiflora*) were observed fruiting throughout the year. These results are consistent with previous phenological surveys of Guyana’s forests (ter Steege and Persaud 1991, ter Steege et al. 2000). For example, ter Steege and Persaud (1991) reported that 74% of species only fruited during the peak fruiting season. The lack of asynchronous fruiting species poses unique challenges to frugivores at this study site.

Summary

In summary, the forest inhabitated by the study group was very heterogenous, consisting of a variety of habitat types. In contrast to most sites where bearded sakis have been studied, this site was completely undisturbed and contained a full community of sympatric primates, other potential competitors, and predators. Rainfall at the study site was highly seasonal, as was the availability of potential food resources for bearded sakis. Fruit availability peaked in March and April, immediately before the long-wet season. During the short-dry season, from September to mid-December, fruit availability was very low. Fruit species at the study site were mostly synchronous fruiters, and Fabaceae, Lecythidaceae, and Sapotaceae were the dominant plant families. All of these characteristics have a profound influence on bearded saki activity patterns, feeding and ranging behavior, and group dynamics.

Table 3.1. Sighting rates for primates observed during 2005 surveys in the UECC.

Primate Species	**Boat Surveys (Groups seen)**	**Land Surveys (Groups seen)**	**Total**	**Sighting Rate (Groups /10km)**	**Mean Group Size**
Alouatta seniculus	4	2	6	0.36	4.5
Chiropotes sagulatus	**3**	**1**	**4**	**0.24**	**30+**
Cebus apella	1	2	3	0.18	11.7
Ateles paniscus	0	2	2	0.12	2.5
Cebus olivaceus	2	0	2	0.12	11
Saguinus midas	0	2	2	0.12	5.5
Saimiri sciureus	1	1	2	0.12	-
Pithecia pithecia	0	1	1	0.06	2
Total	11	11	22	1.32	

Table 3.2. The 10 most abundant plant families represented in botanical transects (Fabaceae subfamilies are considered separately.

Family	**% of Basel Area**
Fabaceae: Caesalpiniaceae	12.70%
Lecythidaceae	11.72%
Fabaceae: Papilionaceae	11.48%
Sapotaceae	7.76%
Burseraceae	5.41%
Chrysobalanaceae	5.32%
Moraceae	4.65%
Euphorbiaceae	4.54%
Bombacaceae	3.73%
Fabaceae: Mimosaceae	3.44%

Table 3.3. The 10 most abundant transect tree species at the study site by percentage of total basal area.

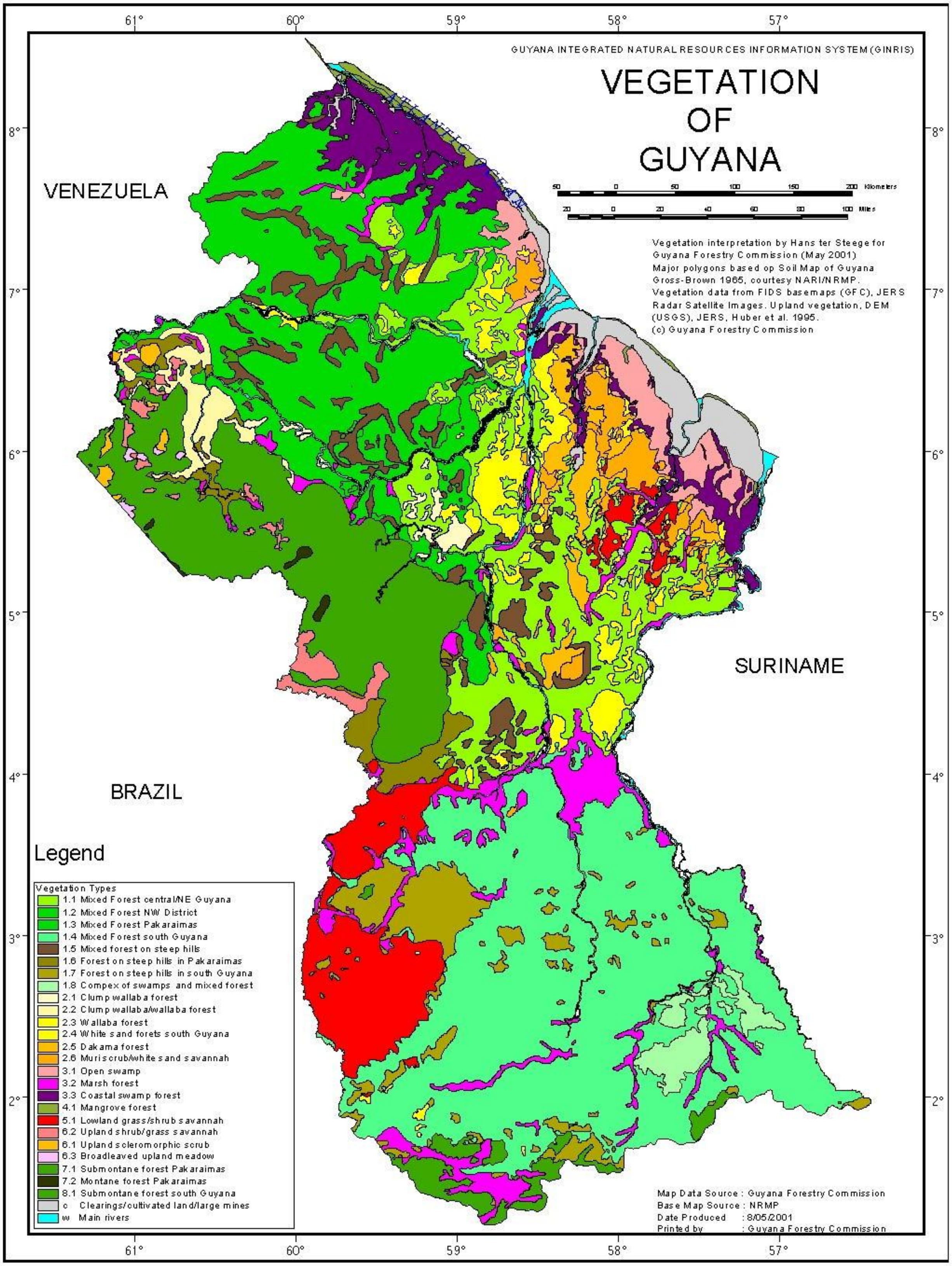
Common Name	**Scientific Name**	**Family**	**# of individuals**	**% total basal area**
Wamara	*Swartzia leiocalycina*	Fabaceae: Papilionaceae	23	6.54%
Wadara	*Couratari guianensis*	Lecythidaceae	14	5.11%
Mora	*Mora excelsa*	Fabaceae: Caesalpiniaceae	14	4.59%
Wallaba	*Eperua falcata*	Fabaceae: Caesalpiniaceae	13	3.90%
Mahicaballi	*Phyllanthus* spp.	Euphorbiaceae	19	3.17%
Hiawaballi	*Tetragastris altissima*	Burseraceae	10	3.15%
Kauta	*Licania alba*	Chrysobalanaceae	14	3.00%
Black Kakerelli	*Eschweilera sagotiana*	Lecythidaceae	13	2.52%
Crabwood	*Carapa guianensis*	Melastomataceae	10	2.48%
Sheu	?	?	12	2.45%

Table 3.4. The 10 most abundant transect tree species by number of individuals.

Common Name	**Scientific Name**	**Family**	**# of transects**	**# of individuals**
Wamara	*Swartzia leiocalycina*	Fabaceae: Papilionaceae	10	23
Mahicaballi	*Phyllanthus* spp.	Euphorbiaceae	11	19
Asepoko	*Pouteria guianensis*	Sapotaceae	10	14
Kauta	*Licania alba*	Chrysobalanaceae	10	14
Manaca	*Oencarpus* spp.	Palmae	8	14
Mora	*Mora excelsa*	Fabaceae: Caesalpiniaceae	7	14
Wadara	*Couratari guianensis*	Lecythidaceae	8	14
Asashi	*Rheedia* spp.	Guttiferae	8	13
Black Kakerelli	*Eschweilera sagotiana*	Lecythidaceae	7	13
Wallaba	*Eperua falcata*	Fabaceae: Caesalpiniaceae	6	13

Figure 3.1. Map of South America showing the location of Guyana and a map of Guyana showing the location of the study site and the villages of Apoteri and Rewa discussed in this Chapter.

Figure 3.2. Vegetation types of Guyana (ter Steege 2001).



Vegetation interpretation by Hans ter Steege for Guyana Forestry Commission (May 2001)
Major polygons based op Soil Map of Guyana Gross-Brown 1965, courtesy NARI/NRMP.
Vegetation data from FIDS basemaps (GFC), JERS Radar Satellite Images. Upland vegetation, DEM (USGS), JERS, Huber et al. 1995.
(c) Guyana Forestry Commission

Map Data Source : Guyana Forestry Commission
Base Map Source : NRMP
Date Produced : 8/05/2001
Printed by : Guyana Forestry Commission

Figure 3.3. Map showing the protected areas of Guyana compared to other countries in the Guiana Shield. The only state managed protected area is Kaiteur National Park.

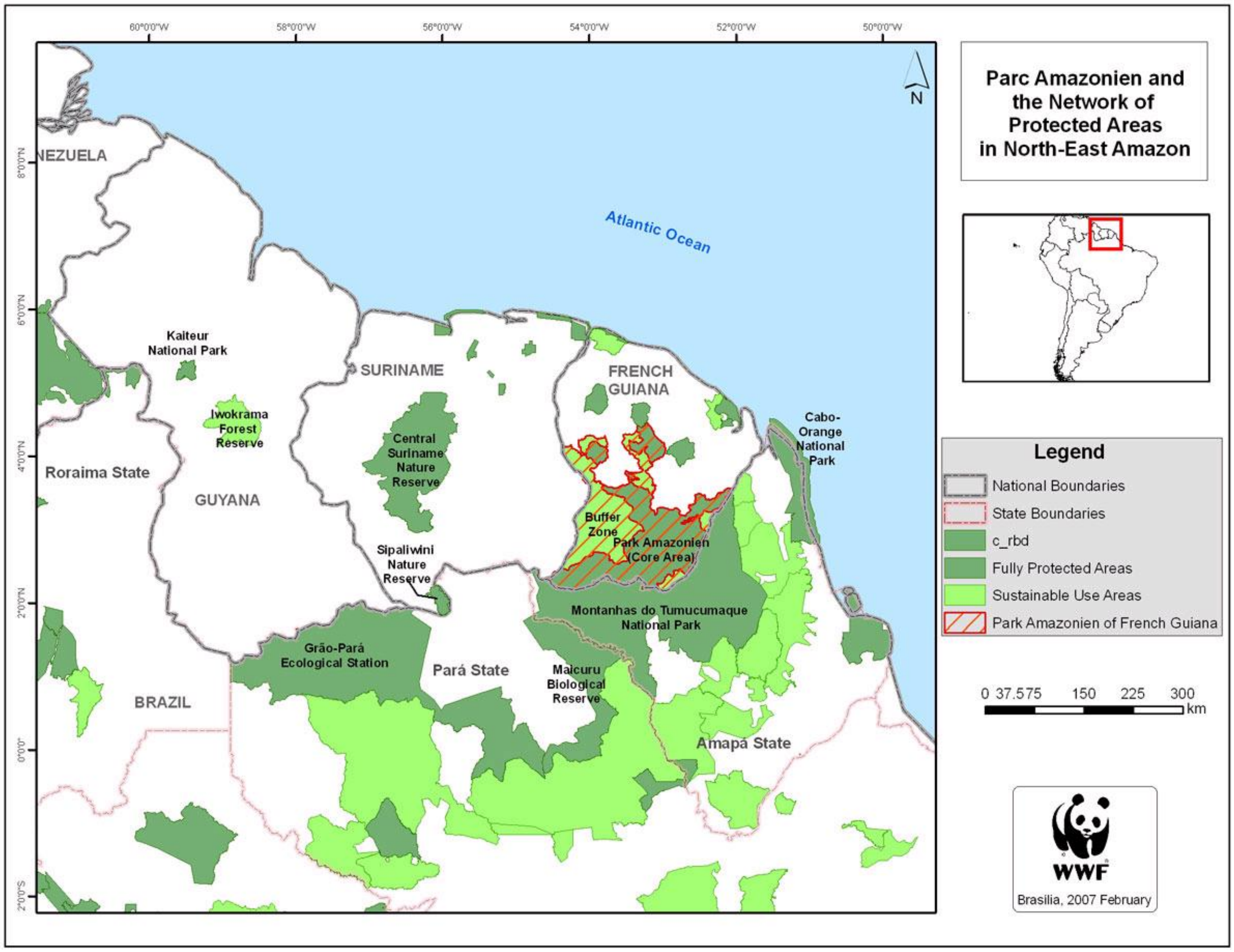


Figure 3.4. Map of the UECC showing the terrain, the base camp for this research and extent of the study group home range within the Concession.

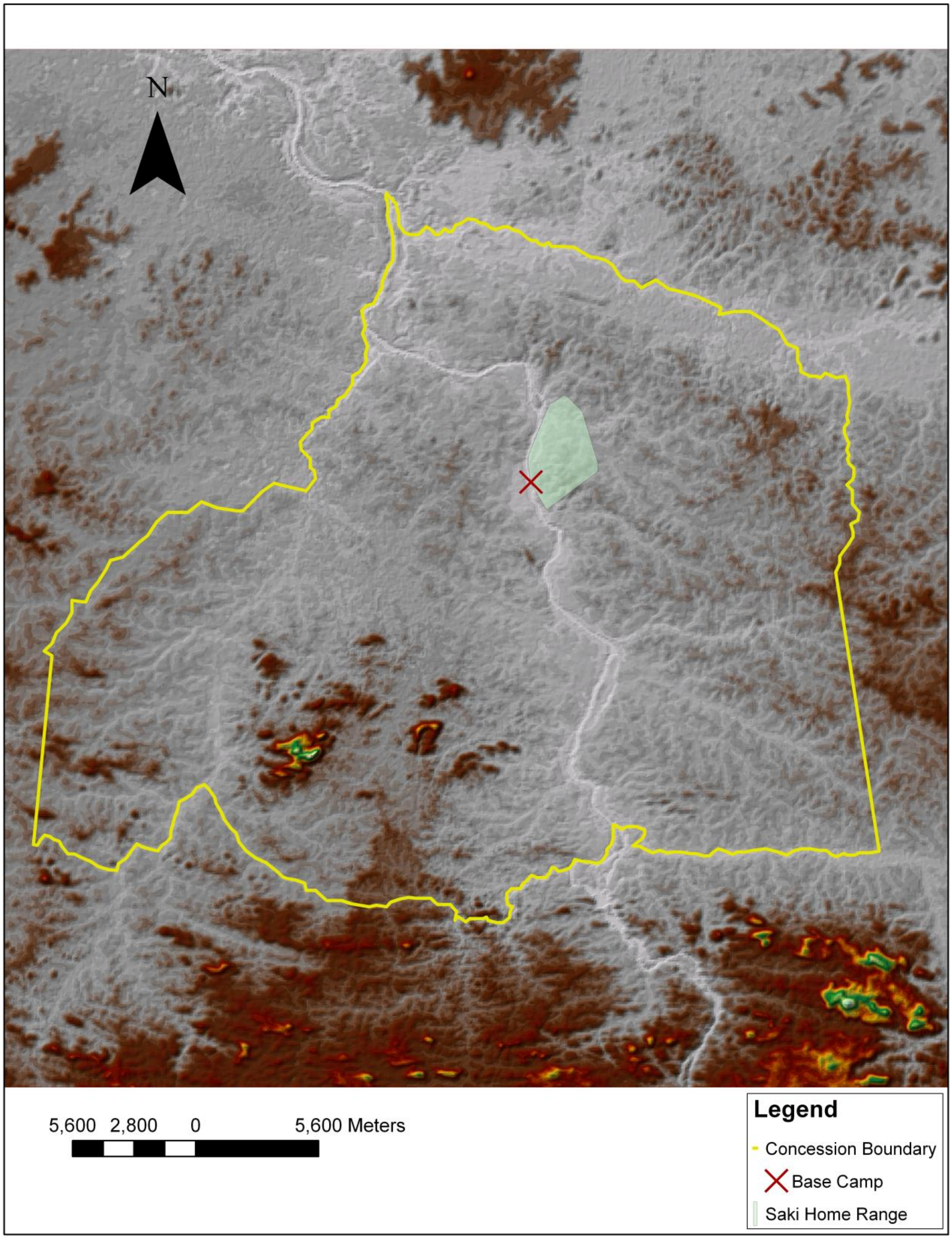


Figure 3.5. Landsat 7+ satellite image of the UECC showing the base camp for this research and the study group home range.

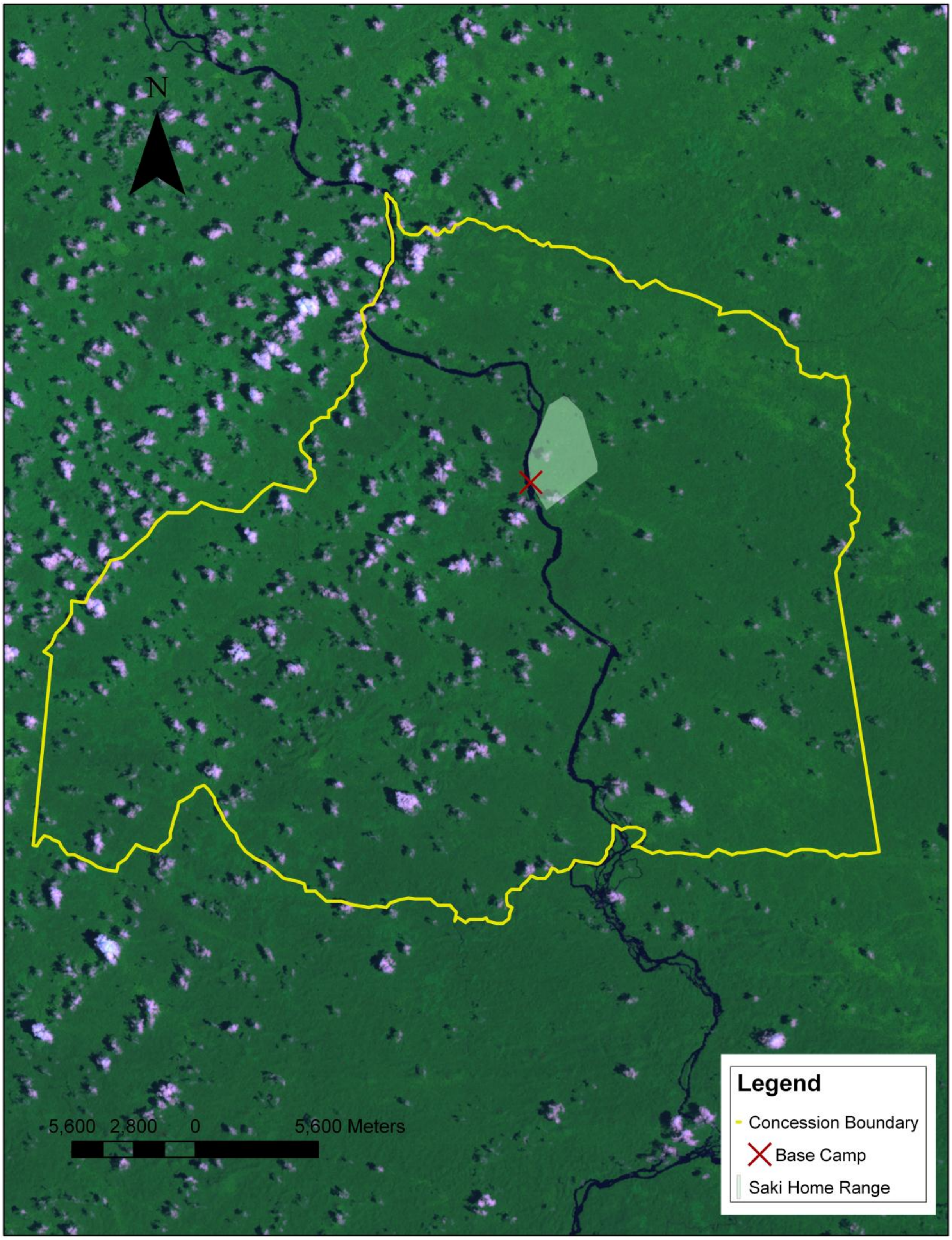


Figure 3.6. Picture of the study base camp.

Figure 3.7. Map of the study site showing the trail system and different forest types.

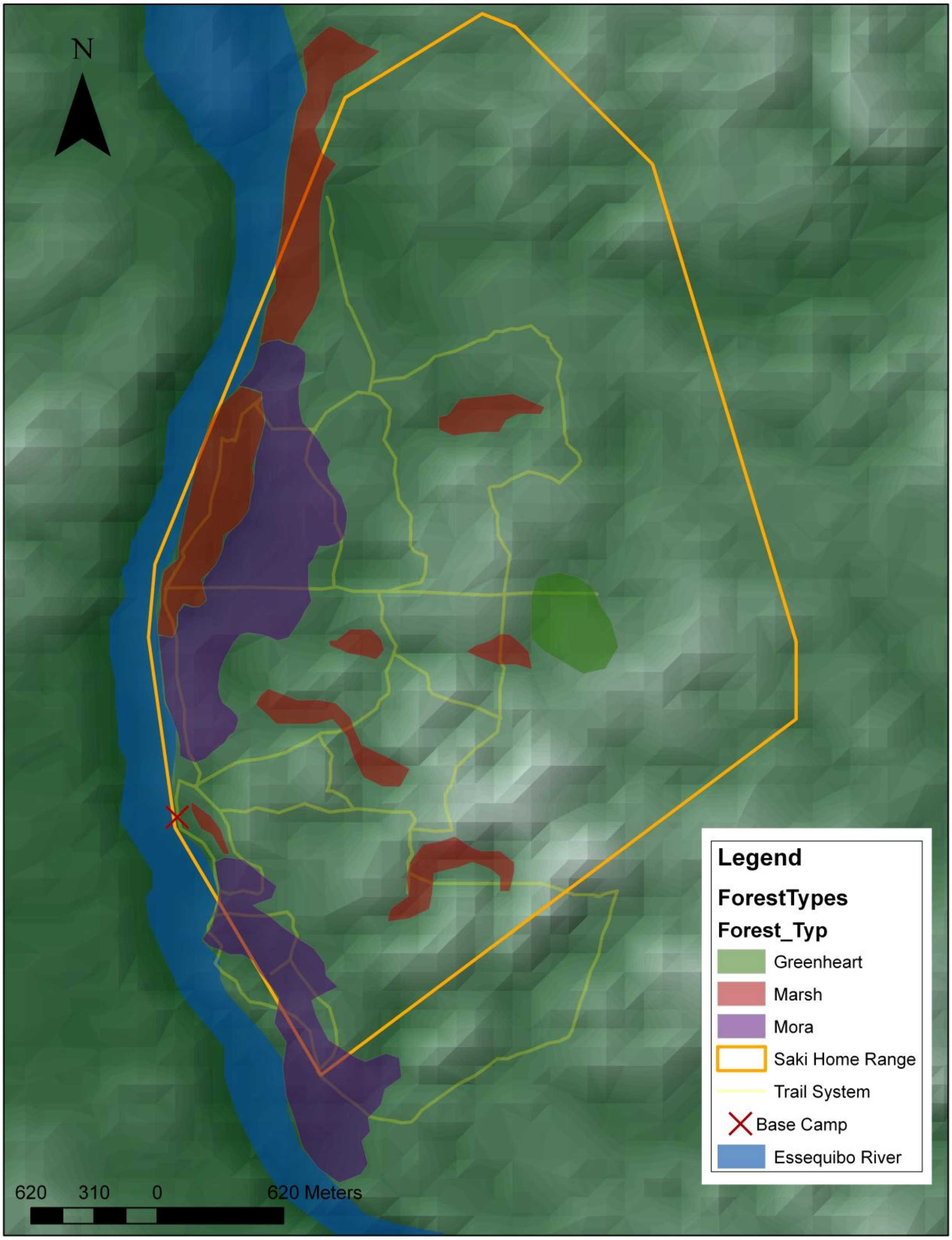


Figure 3.8. A typical *Mora excelsa* canopy tree in Mora forest showing the extensive buttressing and high abundance of mora seedlings characteristic of this forest type.

Figure 3.9. Map of the study site showing the flooding of the Essequibo river during the peak of the long wet season (late July to the middle of August).

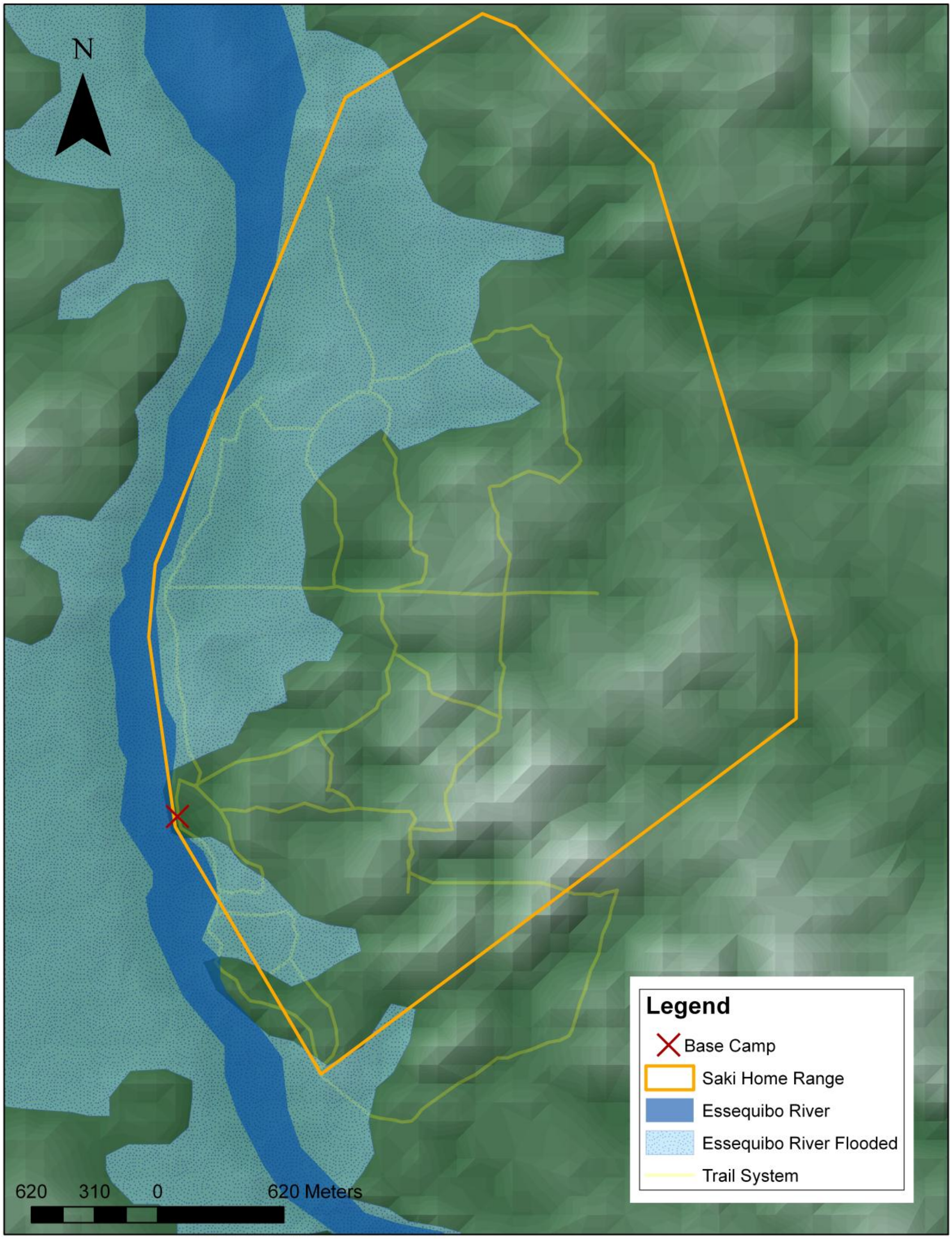


Figure 3.10. Mean monthly rainfall and high temperature at base camp.

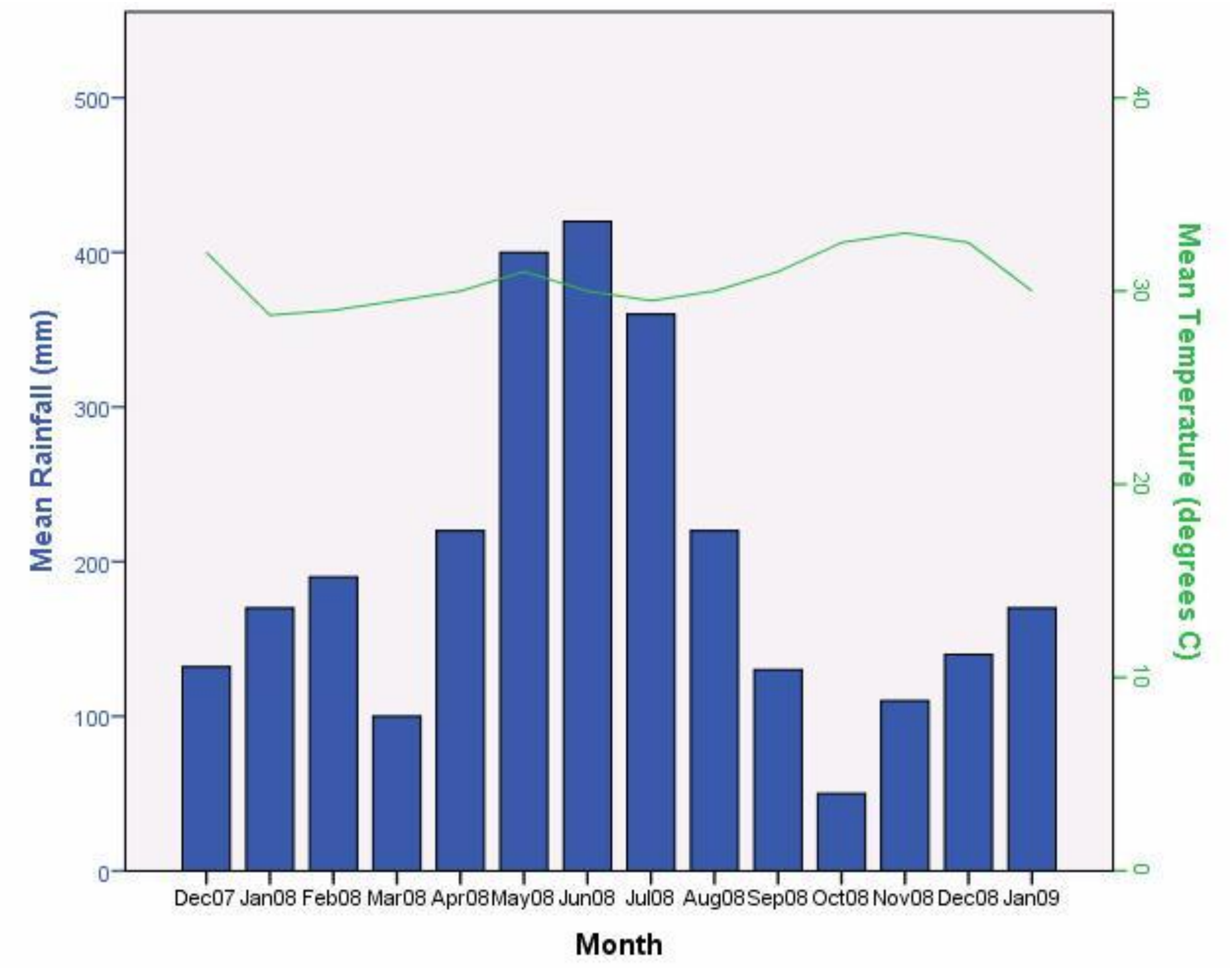


Figure 3.11. Map showing locations of 31 5 X 50 meter transects monitored during the study period.

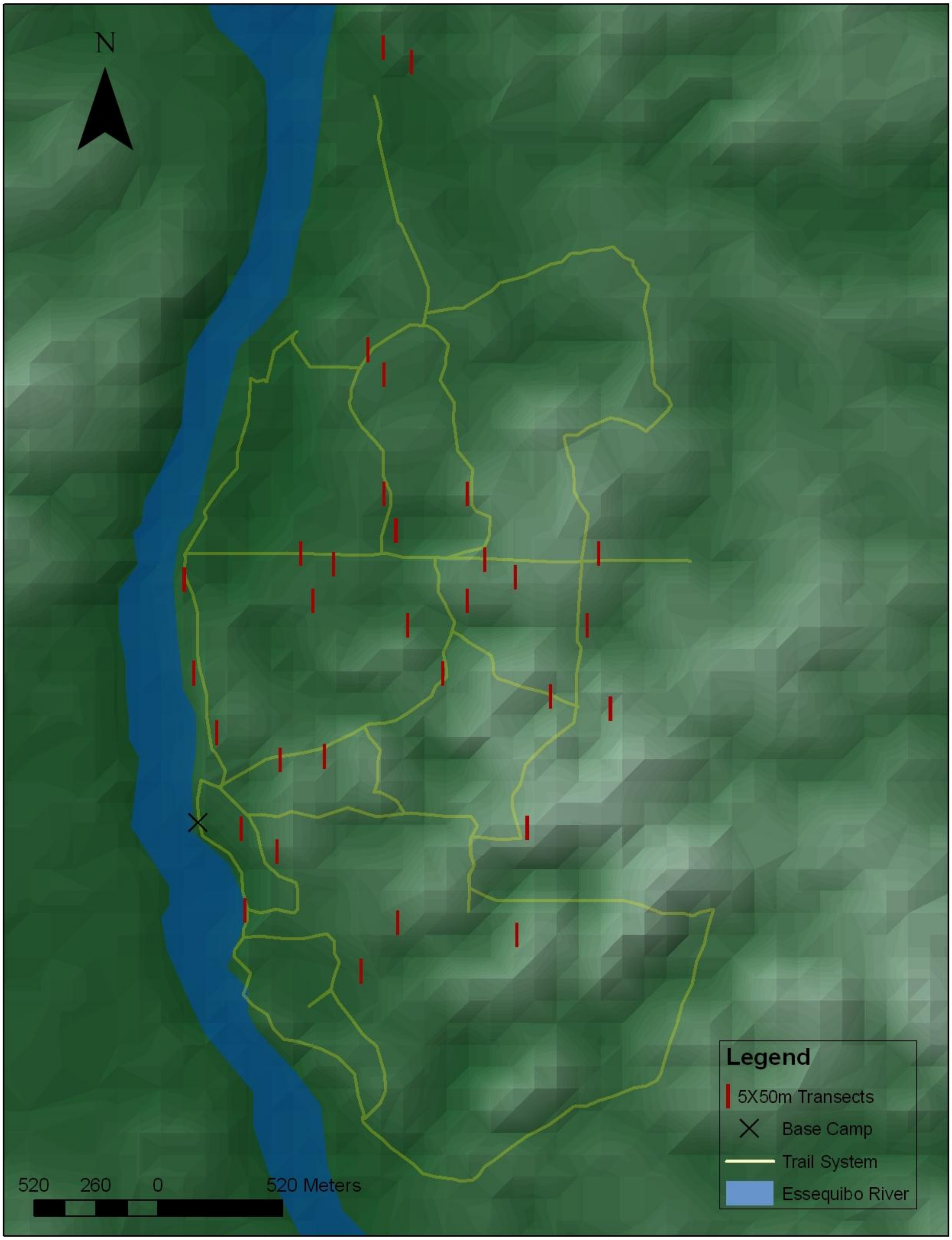


Figure 3.12. Frequency distribution of DBH sizes for transect trees.

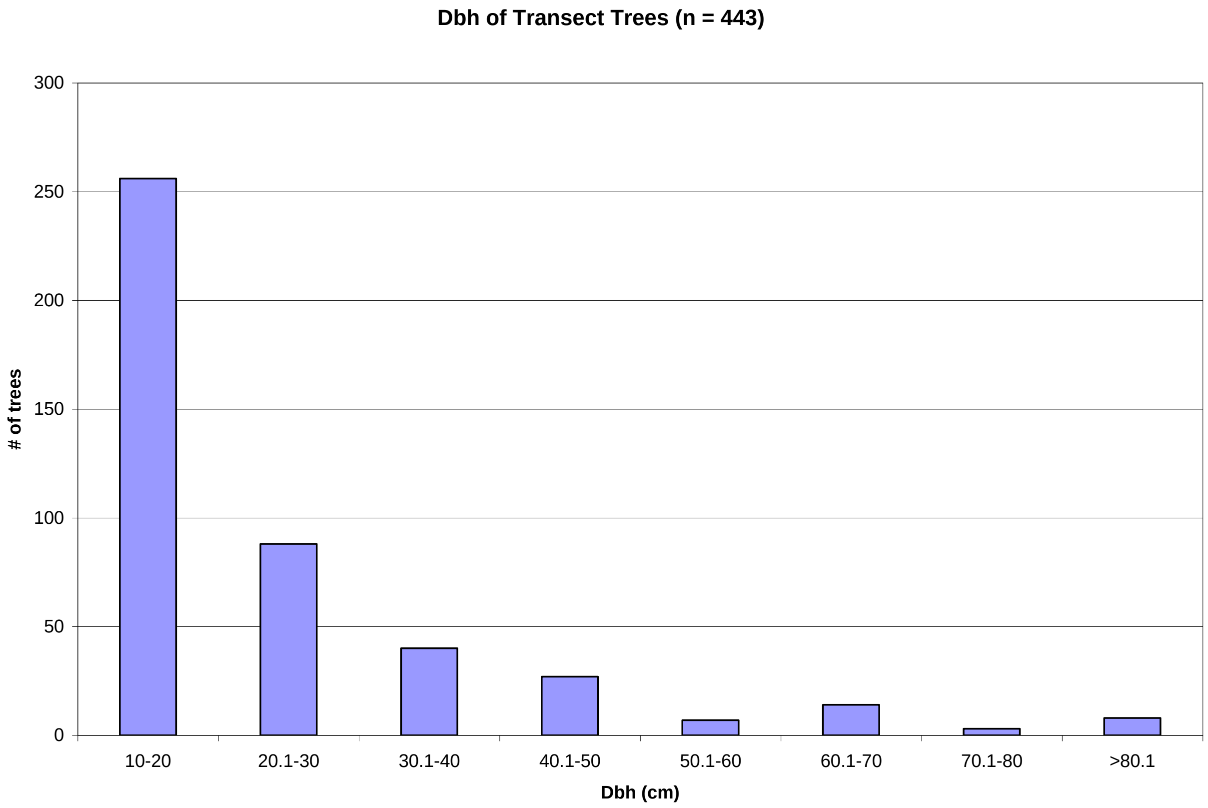


Figure 3.13. Monthly abundance of immature fruits, mature fruits, and flowers based on percentage of total basal area.

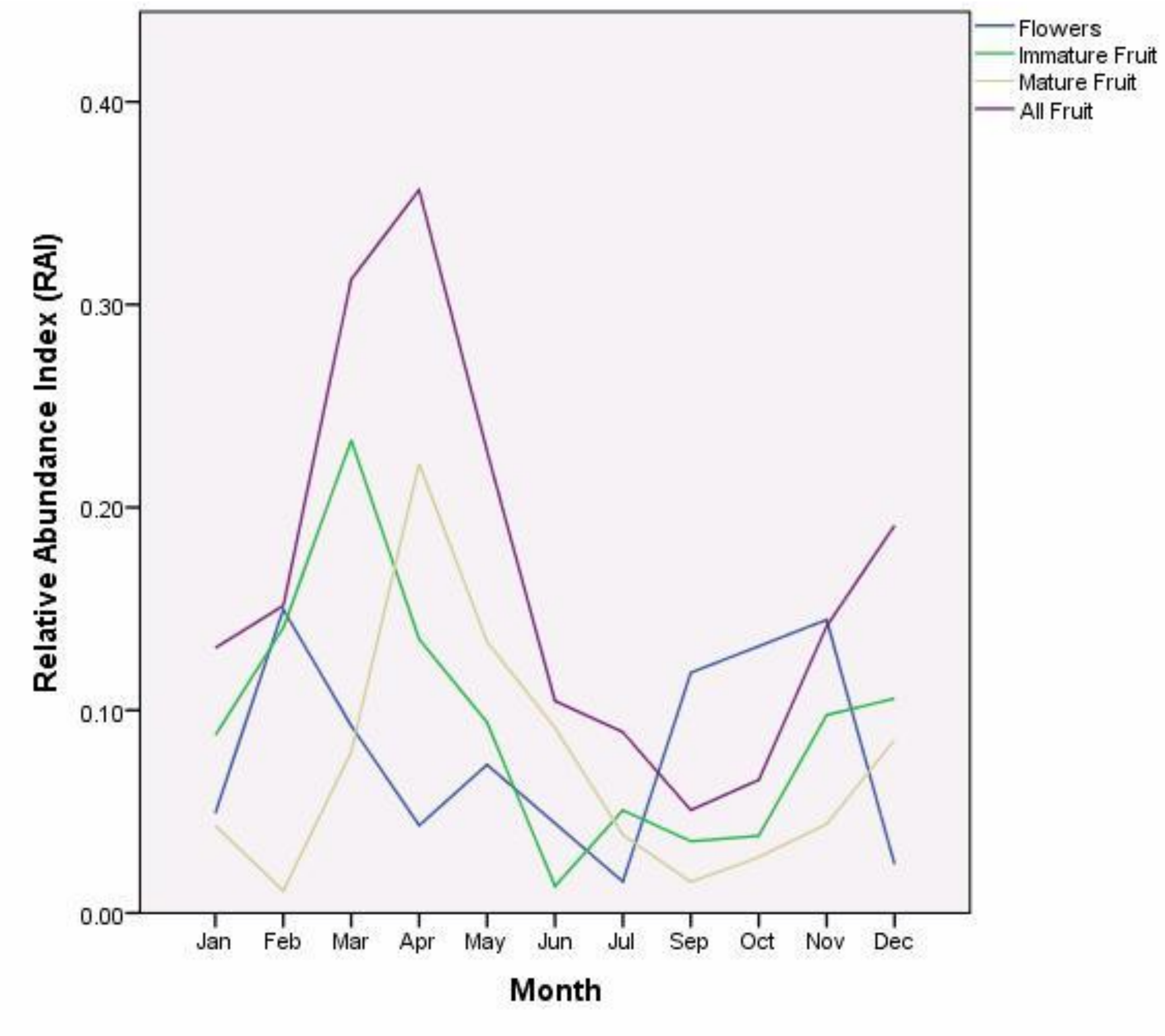
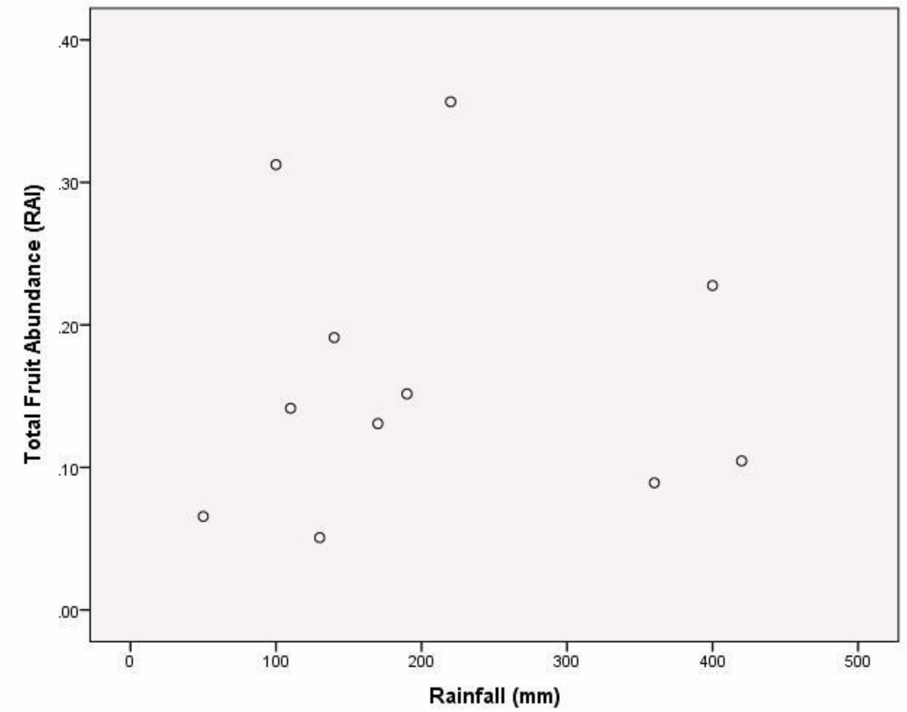
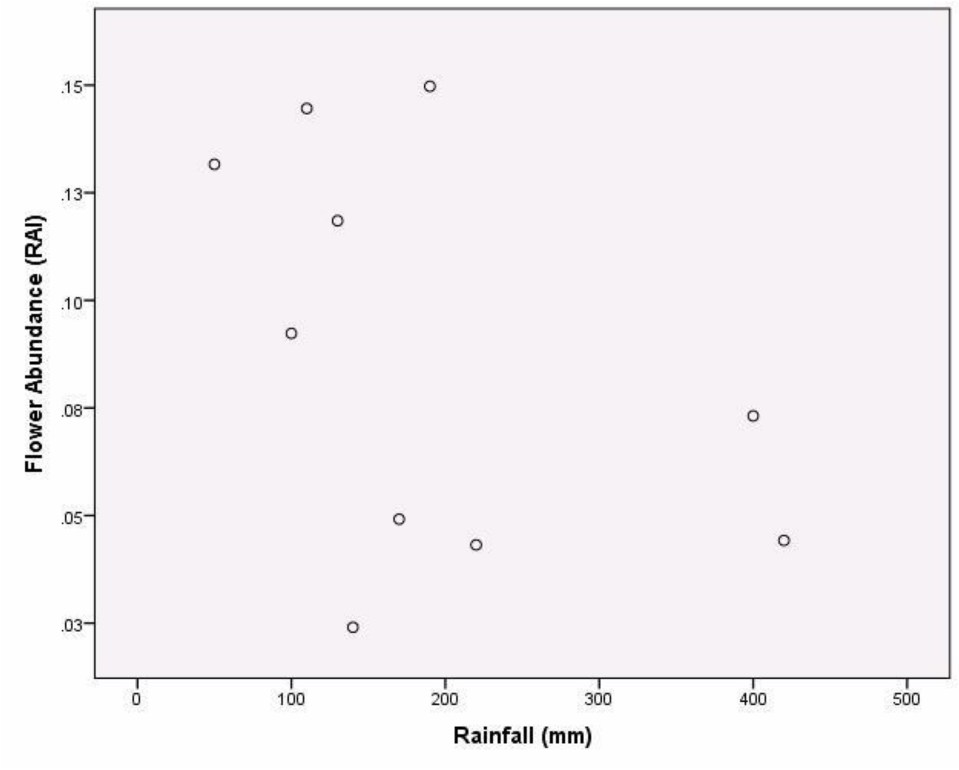


Figure 3.14. (A) Monthly mature fruit abundance and (B) flower abundance compared to monthly rainfall.

(A)



(B)



CHAPTER 4 – ACTIVITY BUDGET, SOCIAL BEHAVIOR, AND INTERGROUP INTERACTIONS

Introduction

Diurnal primates have approximately 12 to 13 hours with which to conduct their daily activities. During these daylight hours, animals must balance the need to procure adequate nutrition with rest and the maintenance of social relationships. The need for sufficient caloric and nutrient intake must be balanced with the time and energy required to travel to feeding patches. Primates must also rest to conserve energy, aid in digestion, and engage in social activities like grooming and huddling to maintain and establish the social relationships required for group living. All of these activities must be performed while remaining vigilant for predators and engaging in anti-predator behaviors when necessary. Many of these activities cannot be conducted simultaneously, requiring animals to decide how best to allocate their time in order to maximize fitness. As ecological conditions often show drastic seasonal variation in primate habitats, evolutionary theory predicts that primate activity budgets should vary in response to these conditions (Schoener 1971, Mangel and Clark 1986).

The assessment of how primates divide their daily activities has been one of the foundations of studies of primate behavioral ecology (Struhsaker 1975, Clutton-Brock 1977, Milton 1980, Terborgh 1983, van Schaik et al. 1983, Goodall 1986, Robinson 1986, Strier 1987, Symington 1988). Much attention has been paid to how primates adjust their activity budgets in response to resource scarcity. Some researchers have suggested that primates allocate more time to foraging when resources are scarce, presumably because they need to increase foraging effort to offset decreased foraging efficiency in poor quality food patches (Schoener 1971, Clutton-Brock and Harvey 1977, Robinson 1986, Isbell 1991, Janson and Goldsmith 1995). This pattern has been observed in several species of primates (Robinson 1986, Altmann and Muruthi 1988, Isbell and Young 1993). Primates in many other studies have shown the opposite pattern, devoting less time to energetically-costly activities like foraging and traveling and more time to resting during periods of resource scarcity (Milton 1980, Strier 1987, Di Fiore 1997). The primates adopting this pattern appear to conserve energy and reduce metabolic needs when resources are scarce and may actually increase foraging effort during periods of resource abundance (Schoener 1971).

Several researchers have attempted to understand seasonal variation in primate activity budgets in the context of intragroup and intergroup feeding competition (van Schaik 1983, Isbell 1991, Wrangham et al. 1993, Janson and Goldsmith 1995). These researchers have suggested that primates living in larger groups will need to allocate more time to foraging and traveling due to the negative effects of higher intragroup feeding competition. Assuming resources are limited, primates living in larger groups will have fewer available nutrients per individual than primates living in smaller groups. As intragroup feeding competition should be highest when resources are most scarce, primates living in large groups should increase foraging effort the most during these periods. This pattern has been reported for several primate species (de Ruiter 1986, Isbell 1991, Miller 1996). Clearly, primates exhibit tremendous diversity in activity patterns and the ways in which they adjust activity seasonally. Understanding how a primate species’ time allocation patterns relate to intragroup social dynamics and ecological conditions is critical for a thorough characterization of that species’ behavioral ecology.

In this chapter, I examine the activity budget of bearded sakis and test:

Research Question 1. How do bearded sakis change their activity patterns in response to seasonal changes in ecological conditions?

As mentioned above, when resources become scarce and intragroup feeding competition is expected to be highest, primates can either increase foraging effort (i.e., time spent feeding and traveling) to locate and process more patchily distributed resources or minimize energy expenditure and reduce metabolic needs (i.e., decrease foraging effort and increase resting). Therefore, I suggest:

Hypothesis 1 – The bearded saki activity budget (specifically time spent feeding, traveling, and resting) will show significant seasonal variation and this variation will be correlated with seasonal changes in the availability of their food resources.

I first discuss the overall saki activity budget and the diurnal variation in time devoted to different activities. I then discuss how the saki activity budget varies throughout the year and whether or not this variation is related to differences in rainfall, temperature, or food availability. I also examine bearded saki social behavior in this chapter, showing the most common social behaviors and the context of social interactions. In addition, I provide a detailed description of three intergroup encounters observed during the course of this study as these represent the first intergroup encounters described for this species. Finally, I compare the activity budget of my study group to those reported for other groups of bearded sakis and those of other primates to better contextualize the foraging strategy of this species.

Methods

Group Census

None of the previous researchers of bearded sakis have been able to recognize individual animals. This is due to their small body size, their rapid travel high in the forest canopy, and their lack of distinctive facial markings or pelage color differences. Despite the large number of contact hours in this study, individual recognition was similarly impossible. Nevertheless, I was able to easily distinguish age-sex classes based on sexual dimorphism in body size, beard length, and temporal swellings. Small body size and several aspects of bearded saki behavioral ecology also made taking accurate censuses of the group difficult. Complete counts of the study group were very rare, as the monkeys' high degree of group spread, fast travel high in the canopy, and the low visibility of the closed canopy forest made accounting for all group members extremely difficult. Counts were only possible when the group traveled relatively cohesively across forest gaps. Age-sex composition is similarly based on estimates obtained during these gap counts.

Data Collection

Data on activity budget were collected using instantaneous scan sampling at five minute intervals (see Chapter 2). Activity categories were established based on those used by previous researchers of bearded sakis and on observations of the study group during the habituation period. The complete ethogram used during this study is given in Appendix 1. Activities were divided into the following categories: feeding, traveling, moving, resting, social resting, social behavior, and other. Moving involved vertical or horizontal movement within a single tree crown that was not food oriented. Unlike travel, movement was typically not synchronous with other group members. Social rest is a species typical behavior of bearded sakis where several individuals rest in extremely close proximity to each other, usually touching. Individuals involved in social resting would clearly seek out other individuals to rest next to. When sakis were observed engaging in social behavior during a scan, the age-sex class of those individuals was recorded when possible.

Many previous researchers of bearded sakis have documented the difficulties in observing their social behavior. These authors have reported that much of bearded saki social behavior and rest is conducted in dense vegetation high in the canopy, which likely serves as an anti-predator response (see below). Combined with the tendency of scan-sampling to overestimate more obvious behaviors like feeding and traveling, this may have led to social behavior being underrepresented in this study.

Data Analysis

I used two methods to analyze activity budget data. First, I used the overall frequency method, treating each individual behavioral record as a separate data point regardless of the scan sample in which it was obtained (Altmann 1974). If scans are sufficiently numerous and unbiased towards any one activity, they should reflect the actual frequencies at which activities occurred. However, Clutton-Brock (1977) observed that this method tends to over-represent conspicuous activities like traveling and feeding. Therefore, I also used the proportion method, where each scan is treated as an independent data point (Altmann 1974, Clutton-Brock 1977). This method involves calculating the proportion of each scan that the activity category represents, then averaging these proportions over the total set of scans. This method is likely more appropriate for this study, as it is necessary when there are highly variable numbers of individuals represented per scan. The mean number of individuals observed during each scan in this study was 16.24 (std = 6.72, min = 3, max = 45).

I used G-tests to detect significant differences in bearded saki activity patterns throughout the day and throughout the year. To assess how seasonal variation in ecological conditions affected bearded saki activity patterns, I compared time budget with monthly food resource availability, monthly rainfall, and monthly temperature using Spearman rank correlations.

Results

Group Composition

The group of bearded sakis that was the focus of this research consisted of a maximum of at least 65 individuals. The group was multi-male and multi-female, with approximate age-sex composition indicated in Figure 4.1. As mentioned above, obtaining accurate group estimates was difficult. Nevertheless, several gap counts produced total number of individuals between 60 and 65, indicating this is a relatively accurate estimate of total group size. Also, censuses conducted in other areas of the UECC produced similar estimates. Therefore, it is likely that the study group (and many other groups in the Concession) had a group size of around 60 individuals for much of the year.

Notably, informal group counts taken during the course of full-day follows showed that the size of the study group was highly variable, especially in the short-dry season (see Chapter 6 for data and discussion of group size variability). While it is possible that the large group of 65+

individuals actually consisted of several groups traveling together, several lines of evidence argue against this point. First, for much of the year, even informal counts showed a group size of over 50 individuals, and these group sizes remained consistent over the course of several days. Second, even during the periods when group size was lowest (i.e., October and November), the study group was occasionally counted at over 50 individuals. Therefore, it is more likely that the group consists of approximately 65 individuals but is highly flexible in social structure (see Chapter 6).

Overall Activity Budget and Diurnal Variation

In Table 4.1, I show the overall bearded saki activity budget, calculated according to both the frequency and proportion methods. Bearded sakis are highly active primates, spending the vast majority of their time feeding or traveling (roughly 40% and 35% of daily activity, respectively). In fact, sakis were so active that these activities were often combined. Sakis would often employ a foraging strategy of traveling quickly through a tree, grabbing a handful of fruits, and then feeding on them intermittently as they continued traveling. Figure 4.2 shows a characteristic example of this behavior. The study group spent relatively little time resting (approximately 20% of the activity budget), and rarely engaged in social behavior (about 1.5%). Comparing yearly time budgets calculated according to the two methods shows that feeding values were slightly higher and resting and social resting values were slightly lower for the frequency method as compared to the proportion method. Thus, it is possible that the overall frequency method was biased towards these more conspicuous activities. Nevertheless, the two methods gave remarkably similar results for yearly activity budget, diurnal activity budget, and monthly activity budget. Therefore, the proportion method was used for the remaining analyses.

Figure 4.3 shows diurnal variation in the time bearded sakis devoted to different activities. All activities except ‘moving’ and ‘social’ showed significant variation by hour (Feeding $G = 46.86$, $p < 0.001$; Traveling $G = 31.35$, $p < 0.001$; Resting $G = 62.86$, $p < 0.001$; Other $G = 20.72$, $p = 0.04$). The study group exhibited two peaks in time spent feeding, one first thing in the morning and the other in the late afternoon. Resting was most common in the middle part of the day, making up almost 30% of the bearded saki time budget from 11AM to 1PM. Social behavior and social resting, although rare compared to other activities, were also more common during the middle part of the day (see below). While “other” behaviors made up a small percentage of activities during all hours, they were more than twice as common from 4 to 6 PM as during any other part of the day. Almost all behaviors classified as “other” were vocalizations. Thus, bearded sakis vocalize much more frequently in the late afternoon and early evening. This was also the part of the day when the widely spaced study group would usually begin to coalesce, indicating vocalizations may be an important way sakis coordinate group cohesiveness (see Chapter 6).

During days when the group did not forage in widely spaced and apparently independently functioning subgroups, they were very rarely spread over more than 1 km. This appeared to be the approximate limit to the distance their vocalizations could be heard (at least to human ears). It may be that the upper limit for bearded saki group spread is dictated by their ability to coordinate activities with vocalizations. Rather than spreading beyond 1 km, the group simply divides into foraging parties that range independently from one another. However, how these foraging parties subsequently coordinate their coalescence is unknown.

Monthly Variation in Activity

Bearded sakis showed a significant amount of monthly variation in the percentage of the day they engaged in most activities except for feeding (Figure 4.4). Although time spent feeding was higher in March, April, and December and lower during the short dry season months of September and October, this variation is not significant across months (G = 2.72, p = 0.974). Resting peaked in January and made up the lowest percentage of the bearded saki time budget in December (G = 45.22, $p < 0.001$). Travel (G = 20.50, p = 0.015) and social behavior (G = 51.66, $p < 0.001$) also showed significant intermonthly variation.

Spearman rank correlations between monthly resource availability and bearded saki activity patterns showed that time spent feeding was highly significantly correlated with total monthly fruit availability (ρ = 0.82, p = 0.004; Figures 4.5 and 4.6). Both resting and social behavior were negatively correlated with total monthly fruit availability but these relationships were not significant (Resting ρ = -0.22, p = 0.533; Social behavior ρ = -0.46, p = 0.187). Traveling was also not significantly correlated with any measure of resource availability (ρ = -0.01, p = 0.987). None of the bearded saki activities showed significant relationships with monthly rainfall or monthly temperature changes (Figure 4.7).

These results support **Hypothesis 1**, and show that bearded saki activity patterns are closely tied to seasonal changes in resource availability, specifically fruit abundance.

Vertical stratification

Overall, the study group spent a majority of its time in the middle canopy (58%) and also frequented the upper canopy and emergent layer (24%) (Figure 4.8). Bearded sakis rarely occupied the understory and were only observed on the ground on a few occasions. In Figure 4.9, I show the amount of time sakis spent in each forest level when engaged in different activities. Bearded sakis showed significant variation in their use of space during feeding ($G = 37.54$, $p < 0.001$) and traveling ($G = 86.82$, $p < 0.001$). During feeding and traveling, sakis spent more time in the upper levels of the canopy. The study group spent more time in the middle canopy during resting and social behavior, although these activities did not show significant variation across the different stratification levels (Resting $G = 5.30$, $p = 0.150$; Social $G = 3.70$, $p = 0.296$). Sakis were observed on the ground on eight occasions, of which three occurred during agonistic interactions (see below), one during a harpy eagle attack, one during play, and three during insect foraging.

In contrast to their preference for the upper canopy during most feeding, when feeding on insects (Figure 4.10), sakis frequented the lower levels of the forest, sifting through dead leaves in understory trees (see Chapter 5). Insect feeding showed significant variation by level ($G = 54.99$, $p < 0.001$). Interestingly, the percentage of time bearded sakis spent in the understory (Level 2) was significantly negatively correlated with overall fruit abundance ($\rho = -0.88$, $p = 0.001$). This was driven by their high degree of insectivory during the short dry season, when fruit was most scarce.

Social Behavior

Bearded sakis spent relatively little time engaged in social behavior and “social” made up the lowest percentage of the study group activity budget besides “other.” Nevertheless, individuals engaged in a wide variety of social behaviors. Figure 4.11 shows the most common social behaviors observed and their proportion of total social behavior. The most common social activity was grooming (39% of social interactions), followed by playing (31%) and huddling (22%). Social behaviors were much more frequently affiliative than agonistic, with affiliative behaviors representing 94% and agonistic behaviors making up only 6% of all social interactions. Most agonistic behavior consisted of minor chases and displacements, and intense agonistic interactions were extremely rare (less than 1% of all social behavior observed). However, three of these interactions involved adult males retreating to the ground to escape a pursuing adult male. During one of these, the individual being chased fell approximately 20 m straight to the ground as he tried desperately to avoid the attacks of another male. Remarkably, the individual appeared uninjured and was able to travel and forage with the group for the rest of the day with no apparent ill effects.

In Figure 4.12, I show how time spent engaged in social behavior varied throughout the day. In general, bearded sakis were more frequently social in the middle part of the day. However, time spent in social interactions peaked between the hours of eight and nine in the morning. Sakis rarely engaged in social behavior in the early morning or late evening.

Interestingly, social activities were much more frequent between adult males than any other age-sex class. Huddling occurred almost exclusively among adult males (with females involved on only four occasions). The behavior consisted of individuals lining up on large substrates in groups of two to six (most commonly groups of two or three). The individuals would rub their bodies together and appeared to synchronize the wagging of their tails, in addition to vocalizing with soft whistles that were not heard at any other time. Huddling was quite different from social resting in that individuals involved in huddles were much more active in their contact with each other and huddles were relatively short in duration (mean duration of 3 minutes). Social rest often lasted for 20 minutes or more and appeared to be as frequent among females as males.

Grooming also was most common among adult males, with male-male dyads representing 55% of all grooming bouts in which the sex of the animals could be identified. Males also interacted with juveniles frequently. 7% of grooming dyads involved a male grooming a juvenile. In addition, while almost all play interactions involved juveniles, 10% also involved at least one adult male. On one occasion, an adult male was observed playing with another adult male.

Copulations represented approximately 1% of social interactions (8 observations). Copulations were usually preceded by grooming between the copulating pair and generally lasted approximately 30 to 60 seconds. During three of these copulations, the adult male emitted a strange cough-like vocalization that was not heard any other time during the study. One copulation was interrupted by another adult male, who chased the copulating male down a tree and across the ground. While no physical contact was made, the interaction was clearly agonistic.

Due to the large size of the study group and the difficulty of distinguishing individual animals, it was difficult to ascertain how group composition changed throughout the study period. However, informal censuses indicated that bearded sakis have a birthing peak in April and May. Females with infants were more commonly observed during this period than any other. This was also the period of maximum fruit abundance.

Intergroup Interactions

One context when intense agonistic behavior was observed was during intergroup encounters. Because of their extremely large home ranges, and the fact that they have rarely been studied in continuous forest where other groups of bearded sakis have been present, almost nothing was known about bearded saki intergroup interactions prior to this study. During the 15-month study period (including habituation), I observed two such interactions between the study group and a neighboring group of bearded sakis. They both followed a similar pattern so only one is reported in depth here. During a full day follow in February, the study group began to alarm call intensely and many individuals were observed staring off to the northeast. Several study group adult males moved to the northeast periphery of the group as a neighboring group came into view, traveling from the northeast. The neighboring group individuals were also alarm-calling intensely, although the focus of their alarm calling appeared to alternate between the study group and the researchers, as they were unhabituated. As the neighboring group approached within 25 m, approximately five males from the study group ran towards the neighboring group. This instigated about 20 minutes of chasing, interspersed by a few fights where physical contact appeared to be made between adult males. Approximately ten individuals were involved in this agonistic behavior, and the animals retreated to the ground repeatedly during the encounter. During one of the intergroup encounters, an individual fell from a height of at least 25 m while being chased and appeared to be injured. After remaining on the ground for 5 minutes, he staggered around the understory but eventually returned to group activities. I was unable to assess whether he suffered any further ill effects from the fall.

During both intergroup interactions, adult females and juveniles appeared to move towards the middle of the group while adult males appeared to move toward the periphery. Females were not involved in any of the agonistic behavior and did not appear to be targets of agonism at any point, despite occasionally being in close proximity to the males that were chasing each other.

Anti-predator behavior

During the course of the 12 month study period, I directly observed four attempted predation incidents on the bearded saki study group. In addition to these, there were several other incidents where the group reacted as if an attempted predation by an avian predator occurred, although no predator was actually observed. Three of the observed predation incidents involved avian predators (two harpy eagles, one where the bird could not be identified) while the fourth involved a tayra. Bearded saki anti-predator behaviors were similar in all cases and involved intense alarm calling and all of the individuals leaping into dense understory vegetation. Alarm calls appeared to be emitted by all adult animals and were nearly constant for as much as 30 minutes after the attempted predation. During one incident, a harpy eagle landed in the middle canopy and remained there, staring at a group of sakis bunkered down in dense vegetation, for six minutes. Four adult males began to mob the eagle, running toward it synchronously then retreating back into the dense vegetation. The eagle then flew away empty handed. Bearded sakis also employed mobbing when attacked by the tayra and were similarly successful at displacing the predator.

None of the predation incidents was observed to be successful, although a field assistant reported that he thought he glimpsed a saki carried off by an avian predator. After this incident, the group seemed particularly disturbed and continued alarm calling intermittently for over an hour. Thus, it is plausible that this particular attack was successful.

All of these predation events appeared to affect bearded saki activity patterns drastically. The entire study group remained in dense vegetation for at least 30 minutes (and up to two hours after the harpy eagle attack described above). Daily path lengths during these days were among the lowest recorded for the study group, and individuals appeared especially skittish throughout the remainder the day, even alarm calling intensely when macaws flew over (despite the flight patterns and constant vocalizations of macaws that made confusing them with birds of prey highly improbable). Even on days when predation events were not observed, the study group would sometimes employ anti-predator behavior when birds (small hawks, vultures, and occasionally macaws) flew overhead. Given (1) the number of predation events reported above and the fact that predation directed at primates is very rarely observed, (2) that the study group drastically altered their daily behavior when these events occurred, and (3) that sakis were often hyper vigilant for predators, it appears bearded sakis at this study site are under intense predation pressure.

Discussion

The bearded saki activity pattern

Analysis of bearded saki time budgets show that bearded sakis exhibit significant variation in their activity patterns both diurnally and throughout the year. Sakis show the common primate pattern of peaks of activity in the morning and afternoon, with resting more common during the middle parts of the day from 11AM-2PM. This pattern of activity has been reported for a variety of primates and likely relates to the need for primates to replenish nutrient stores immediately after nocturnal rest (Robinson 1986, Altmann and Muruthi 1988, Strier 1986, Isbell and Young 1993, Estrada et al. 1999, Di Fiore and Rodman 2001, Vasey 2005). After extended bouts of morning feeding, primates spend the hottest parts of the day resting. This allows them to devote energy to digestion and avoid exhaustion. After this middle of the day period of relative inactivity, primates generally show a second bout of extended feeding prior to resting for the night. Bearded sakis deviate from this pattern only in their shorter resting bouts compared to most primates.

Bearded sakis appear to change their activity patterns monthly, increasing foraging effort when fruit is most abundant, and decreasing feeding while increasing resting when fruit is most scarce. The fact that the study group did not increase their foraging effort during periods of resource scarcity suggests that intragroup feeding competition was not dictating bearded saki activity patterns. As intragroup feeding competition should increase during periods of resource scarcity, animals should increase feeding effort during these periods to compensate for diminished nutrient returns per animal. As sakis showed the opposite pattern yet still maintained high levels of travel during periods of resource scarcity, this suggests they were not minimizing energy expenditure. Therefore, either intragroup feeding competition is not prevalent or they must rely on other behavioral strategies to mitigate feeding competition (discussed more fully in subsequent chapters).

Intraspecific comparisons

The bearded saki group that was the subject of this study was considerably larger than any group of bearded sakis previously reported. There are several possible explanations for this. First, it is possible that the group was actually more than one group that came together during a period of high resource availability. This explanation is highly unlikely, as the full group of over 50 animals was observed throughout the year (although much less frequently during the short-dry season) and, when the full group was observed, it would usually travel together and maintain its approximate membership for several days.

Another explanation is that this study site was particularly resource rich for bearded sakis and thus supported a higher group size than most sites. This is certainly possible, as the study site clearly contained an abundance of plant species that sakis were able to exploit (see Chapter 4). In addition, the regular flooding of large parts of the study site may have produced richer soil and correspondingly more productive forests. However, censuses I conducted in other parts of the UECC, as well as another forest in central Guyana (Mabura Hill Reserve), suggest bearded saki groups of more than 40 individuals (and quite possible as large as the study group) were common. As these sites varied considerably in habitat types, elevation, and degree of flooding, it seems likely that the study group was not abnormally large, at least for Guyana. Nevertheless, this hypothesis deserves further investigation.

Perhaps the most likely explanation for the large observed group size is that this study is one of the few studies of bearded sakis in undisturbed, continuous forest. Several researchers have found that bearded saki group size in forest fragments is directly related to fragment size (Peetz 2001, Veiga 2006, Silva and Ferrari 2009, Boyle and Smith 2010). The only other researchers studying *Chiropotes* in continuous forest over the course of a year found group sizes of over 40 individuals (Pinto 2008, Gregory 2011). While earlier reports of bearded sakis in continuous forest suggested group sizes of about 30 animals or fewer, it is possible that these researchers observed subgroups. Few of these early researchers followed the same study group throughout the year, so they may have observed seasonal fissions that appear to be a common pattern in bearded sakis (see Chapter 6). Therefore, group sizes of at least 40 but probably more than 50 individuals appear to be typical for *Chiropotes sagulatus*. Interestingly, uakaris (*Cacajao spp*.) show similarly large group sizes, with groups in some populations exceeding 100 animals (possibly even 150+ animals!) during certain parts of the year (Ayers 1989, Boubli 1999, Defler 2001, Barnett et al. 2005, Bowler et al. 2009; see Chapter 6). It is unclear what is driving such large group sizes in these species, although high predation pressure is one intriguing possibility. The relationship between bearded saki group size and ecological variables is discussed more fully in Chapter 7.

The bearded sakis in this study showed activity patterns relatively similar to those of *Chiropotes* in other studies. Almost all of these studies have been conducted in forest fragments or islands, most of which are located in the Tucurui hydroelectric reservoir. Forest fragment sizes, group sizes, and study periods were highly variable in these studies. Nevertheless, all previous research of bearded sakis has shown them to be highly active, with a large percentage of their daily time budget devoted to feeding and traveling and less time devoted to resting and social behavior (Peetz 2001, Santos 2002, Veiga 2005, 2006, Silva and Ferrari 2009, Boyle and Smith 2010).

The primary difference between the results of this study and previous research is the lower percentages of resting for Guyanese bearded sakis. The most likely explanation for this difference is the lower habitat quality and reduced overall resource abundance at fragmented study sites. At several of these sites, researchers found that sakis in smaller, lower quality forest fragments spent a higher percentage of their time resting than saki groups in higher quality, larger fragments (Silva and Ferrari 2009, Boyle and Smith 2010). These authors suggested increased resting likely represented an energy-conservation strategy employed by the saki group in marginal environments. It is not surprising, therefore, that the bearded sakis in this study, living in an undisturbed and highly productive habitat, would spend much less time resting. In addition, bearded saki feeding was strongly correlated with overall fruit availability in this study. In an environment where fruit availability was lower, one would expect them to devote less time to feeding and more time to resting. As bearded sakis appear to show a high degree of seasonal variability in activity patterns, it is also possible that the limited temporal scope of these previous studies led to higher annual estimates of resting.

While early studies of bearded sakis suggested that they only utilized the highest levels of the forest canopy, more recent studies have shown them to be more flexible in their use of vertical space (van Roosmalen 1981, Ayers 1986, Peetz 2001, Veiga 2006, Silva and Ferrari 2009, Gregory 2011). While they spent most of their time in the middle and upper canopy levels, sakis in these studies also spent a considerable amount of time in the understory. Nevertheless, the bearded saki preference for the middle and upper canopy levels is thought to act as a form of niche portioning with sympatric white-faced sakis (*Pithecia pithecia*). Consistent with their use of vertical substrates and ability to employ vertical clinging and leaping locomotion, *Pithecia pithecia* spend a vast majority of their time in the understory and heavily exploit understory resources. The results of this study indicate that, while bearded sakis prefer the canopy, they are able to exploit other forest levels as well, especially in areas of the forest where resources are distributed in lower levels (i.e., palm fruits and insects). The study group was even observed using the ground during insect foraging. Although terrestrial behavior has been reported to be extremely rare in other groups of *Chiropotes*, terrestriality has been observed regularly in *Cacajao* and appears to be common in *Pithecia* (Ayers 1986, Norconk 2007, Barnett et al. in press). It is possible that terrestrial insect foraging is an uncommon but consistent pattern of behavior in bearded sakis.

The social behavior of bearded sakis is poorly understood owing to the difficulties involved in observing and identifying them. Thus, while the percentage of the study group time budget allocated to social behavior is very similar to what has been previously reported for the genus, it may underestimate the amount of time sakis actually spend in social interactions (Silva and Ferrari 2009). Consistent with the results of this study, Veiga and Silva (2005) observed high levels of male affiliation in *Chiropotes satanas*. Huddling was a common social behavior which almost exclusively involved adult males and the most common grooming pair was two males. Males also were observed interacting with juveniles on several occasions, including playing for several minutes. It is not clear what function these high levels of male affiliation serve in bearded sakis but Veiga and Silva suggested they may function to reinforce bonds among related males. As social behavior was not the focus of this study, I was unable to address this hypothesis.

As few studies of the genus *Chiropotes* have been conducted in continuous forest with more than one group of bearded sakis, almost nothing is known about their intergroup interactions (Norconk 2007). The fact that at least one (and most likely two) other bearded saki groups were seen within the home range of the study group shows that bearded sakis have overlapping home ranges and they do not appear to actively defend them. Intergroup interactions are clearly agonistic, and have the potential to be costly, especially to adult males. While no animals were observed to be injured during the two observed interactions, one animal did fall a fairly large distance. Given the extremely large home ranges of bearded sakis, and the fact that intergroup interactions were only observed twice during a 15 month study, it is likely that groups rarely encounter one another. It is also possible that their loud vocalizations that carry well through the forest may have a secondary function as a spacing mechanism, further allowing groups to avoid each other. This appears to be the primary function of the enlarged hyoid bone and resonating calls of howler monkeys and is consistent with the constant calling exhibited by adult male bearded sakis upon observing a neighboring group (Milton 1980).

Interspecific comparisons

One of the most notable differences between the activity budget of bearded sakis and those of other neotropical primates is the incredibly small percentage of the day they spend resting. Only *Cebus*, *Saimiri*, and some species of *Saguinus* show comparably high levels of activity and low levels of resting to those of the study group (Digby et al. 2011, Jack 2011). In addition, Di Fiore (1997) found that woolly monkeys in Ecuador spent approximately 18% of their time resting – much less than the percentage of resting of other *Lagothrix* groups. All of these primates, including Di Fiore’s woolly monkeys, spent considerable amounts of their day engaged in insect foraging. While the bearded sakis in this study did incorporate a high percentage of insects in their diet during some months, percentage of time resting was not correlated with percentage of time spent feeding on insects ($\rho = 0.22$, $p = 0.533$). Other highly frugivorous new world primates, such as *Ateles* and most populations of *Lagothrix*, spend much higher portions of the day resting (Stevenson et al. 1994, Peres 1994, 1996, Defler 1995). The percentage of time that bearded sakis spend feeding is similar to most non-folivorous new world primates, while they spend a considerably higher percentage of the day traveling. This is consistent with the extremely large home range and long daily path lengths that characterize the genus *Chiropotes*. Therefore, it appears that a large amount of time dedicated to traveling (at the expense of resting) is a necessary part of the bearded saki activity pattern. Likely reasons for this are discussed in Chapters 6 and 7.

The most important factor driving monthly variation in bearded saki activity patterns seems to be seasonal variation in overall fruit availability. This is contrary to the predictions of Robinson (1986) and others, who suggested that primates should increase foraging effort during periods of resource scarcity to counteract decreased foraging efficiency. Instead, bearded sakis increase feeding when fruit is more available, and appear to increase resting (although only slightly) when fruit is more scarce. Sakis do change the percentage of time they spend traveling monthly, but it is always high, and they exhibit long daily path lengths throughout the year (see Chapter 6). Therefore, they cannot easily be classified as energy minimizers *sensu Alouatta, Brachyteles, Cercocebus,* and some baboon species (Homewood 1978, Milton 1980, Strier 1989, Gaynor 1994, Menard and Vallet 1997) or energy maximizers *sensu Chlorocebus*, *Papio ursinus,* and *Cebus* (Harrison 1985, Robinson 1986, van Doorn et al. 2010). Although bearded sakis maximize energy uptake when fruit is abundant by increasing feeding, they appear to be required to spend a high percentage of their time traveling to obtain a proper balance of nutrients regardless of resource availability. Di Fiore and Rodman (2001) observed a similar pattern for *Lagothrix lagotricia* and suggested that woolly monkeys may take advantage of periods of resource abundance to lay down fat stores in excess of those required for surivival. Similarly, Ayers (1986) found that uakaris built up fat stores by increasing time spent feeding when immature seeds were at their maximum abundance. Like the bearded sakis in this study, he also found that the uakari birth season coincided with this period of maximum fruit availability. Interestingly, indigenous WaiWai hunters in southern Guyana only hunt bearded sakis during the early part of the wet season, when they report the monkeys are the fattest. While anecdotal, this is consistent with the results of this study and suggests bearded sakis may also be establishing fat stores that will help them through the lean season.

Table 4.1. The bearded saki annual activity budget, showing differences between the frequency and proportion methods of analysis. Total number of scans = 6620.

Activity	Frequency Method (# scans)	Proportion Method (# scans)
Feed	38.15% (2487)	37.16% (2423)
Move	4.10% (267)	4.22% (275)
Travel	34.86% (2273)	35.63% (2323)
Rest	18.45% (1203)	19.40% (1265)
Social Rest	1.17% (76)	1.44% (94)
Social Behavior	1.40% (91)	1.40% (91)
Other	0.70% (46)	0.75% (49)

Figure 4.1. (A) Approximate age-sex composition of the full study group based on complete censuses conducted opportunistically from November 2007 – December 2008. (B) Mean minimum group size based on data from all full-day follows.

(A)

Adult Males	Adult Females	Juveniles	Infants	Total
21	26	10	8	65

(B)

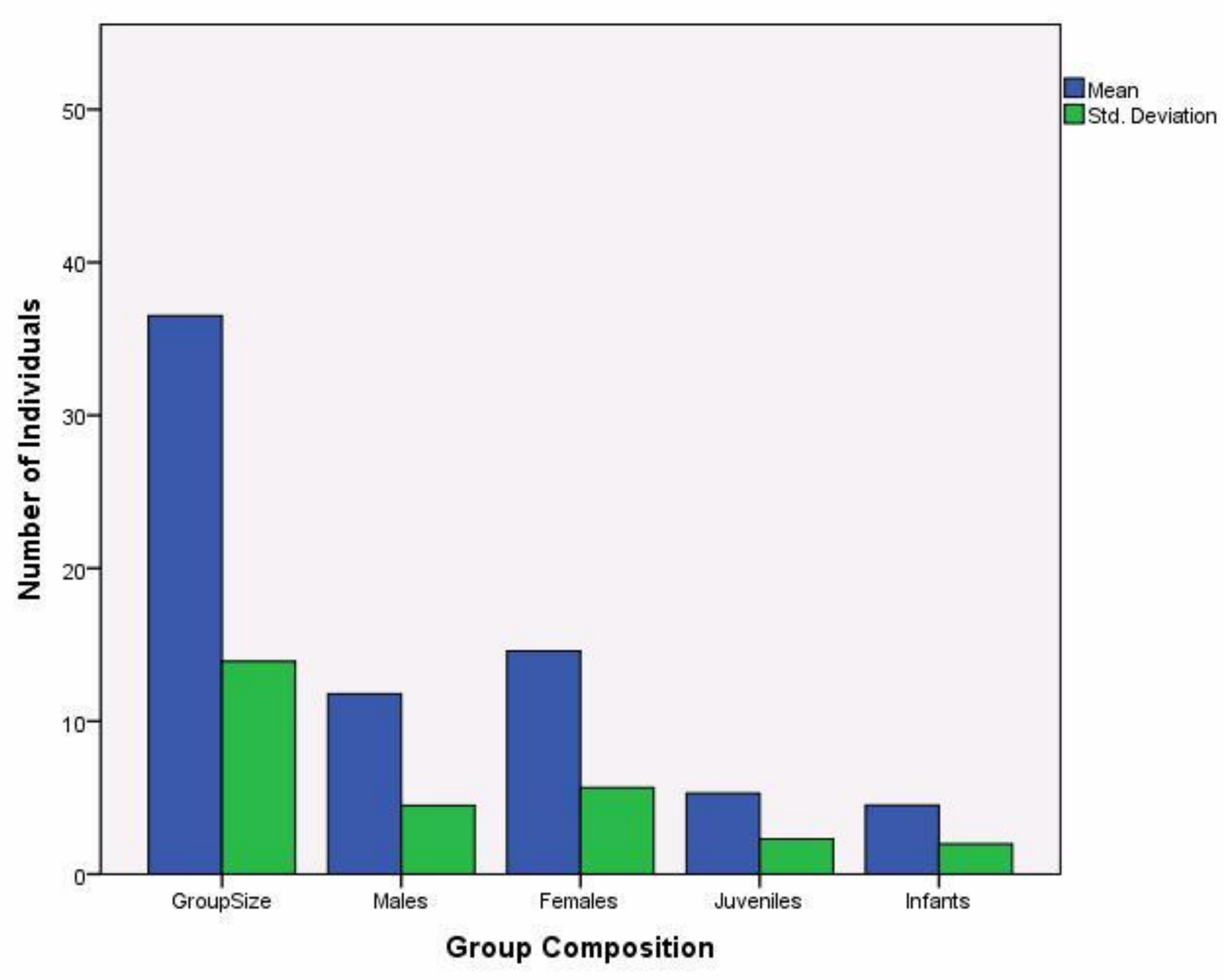


Figure 4.2. A bearded saki individual showing how animals often grabbed several fruits and then moved to another tree. He has just traveled quickly through a bataballi (*Ecclinusa guianensis*) tree, grabbing three fruits as he passed through. He proceeded to feed on these fruits intermittently as he traveled, despite the presumed difficulty of traveling arboreally while three limbs are engaged in holding fruit.

Figure 4.3. Diurnal variation in activity.

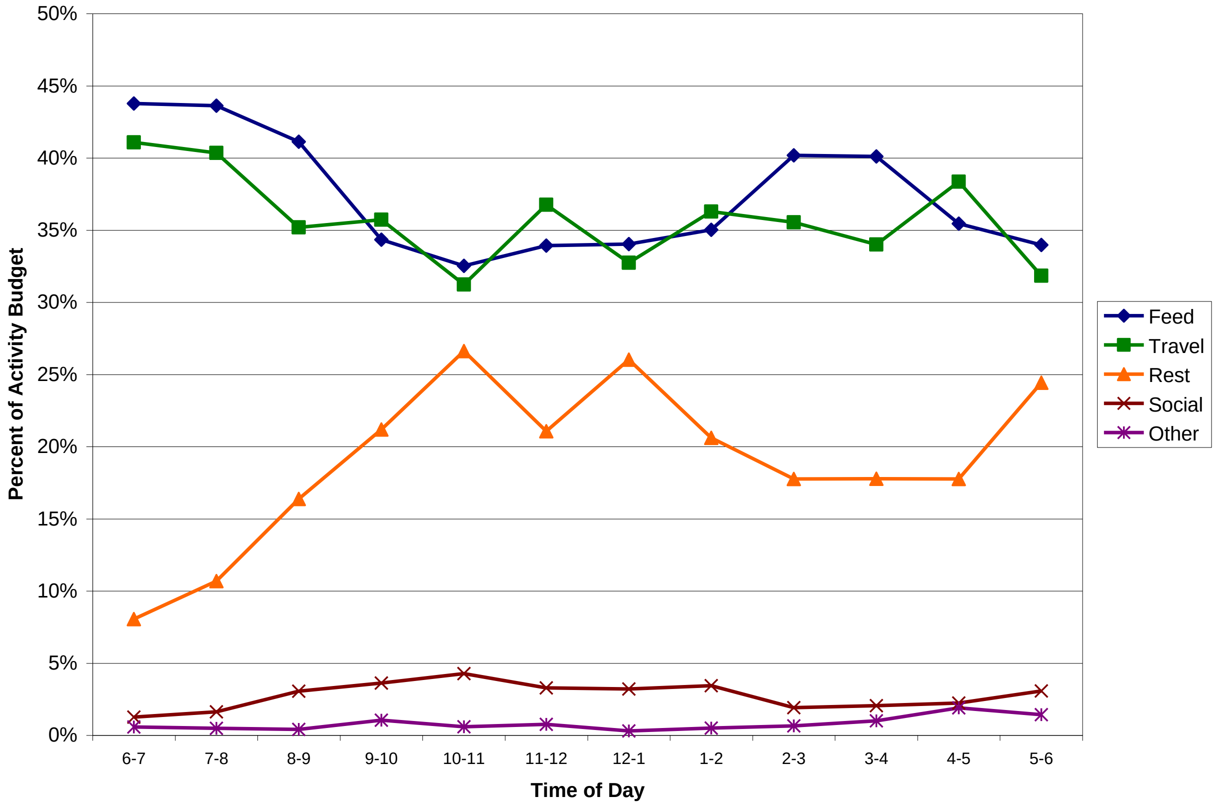


Figure 4.4. Monthly variation in bearded saki activity patterns.

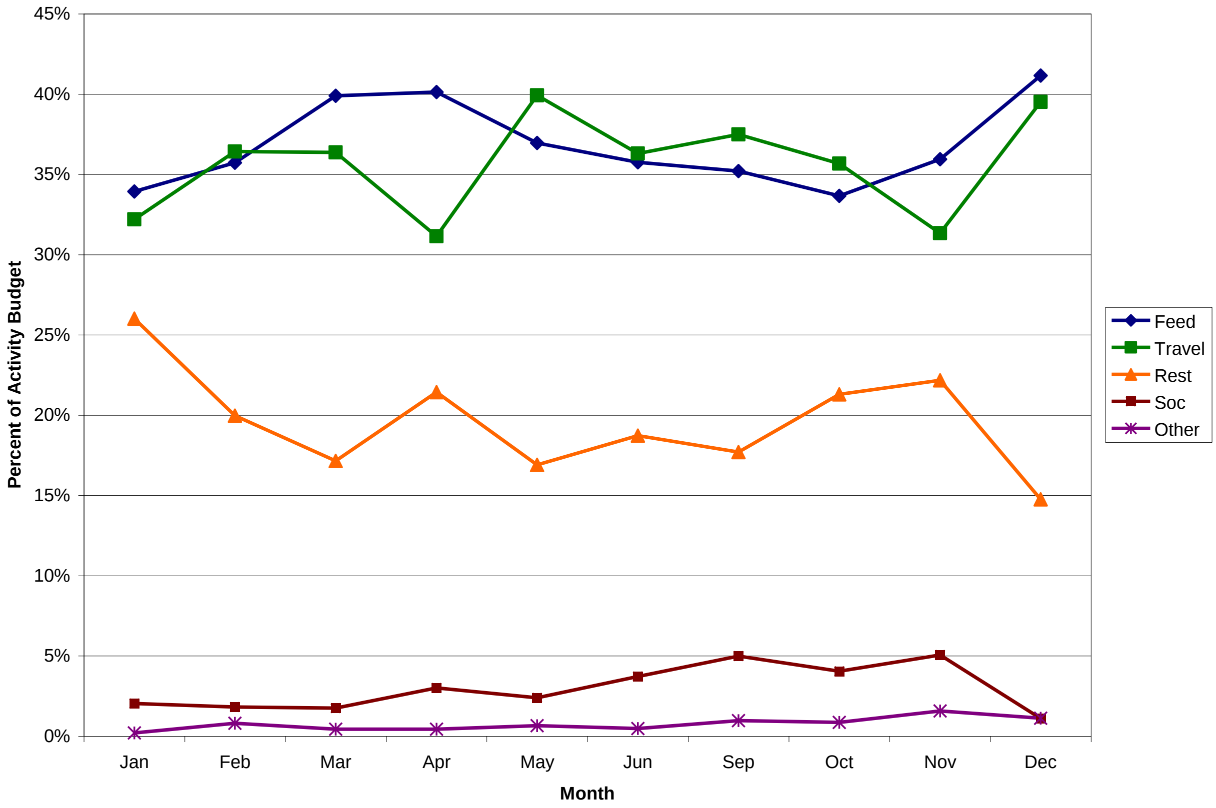


Figure 4.5. Comparison of mean monthly percentage of the bearded saki time budget allocated to feeding and total fruit availability.

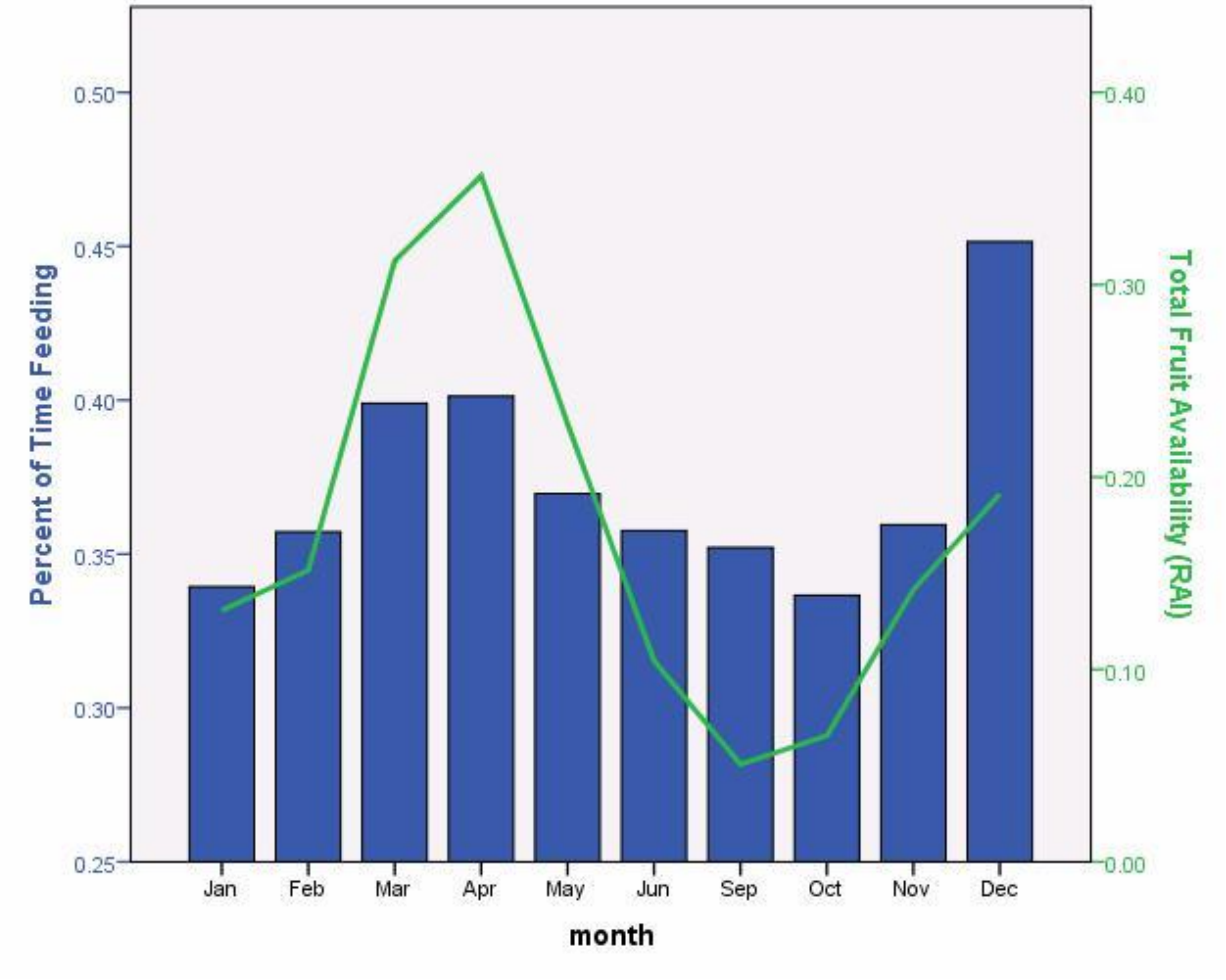
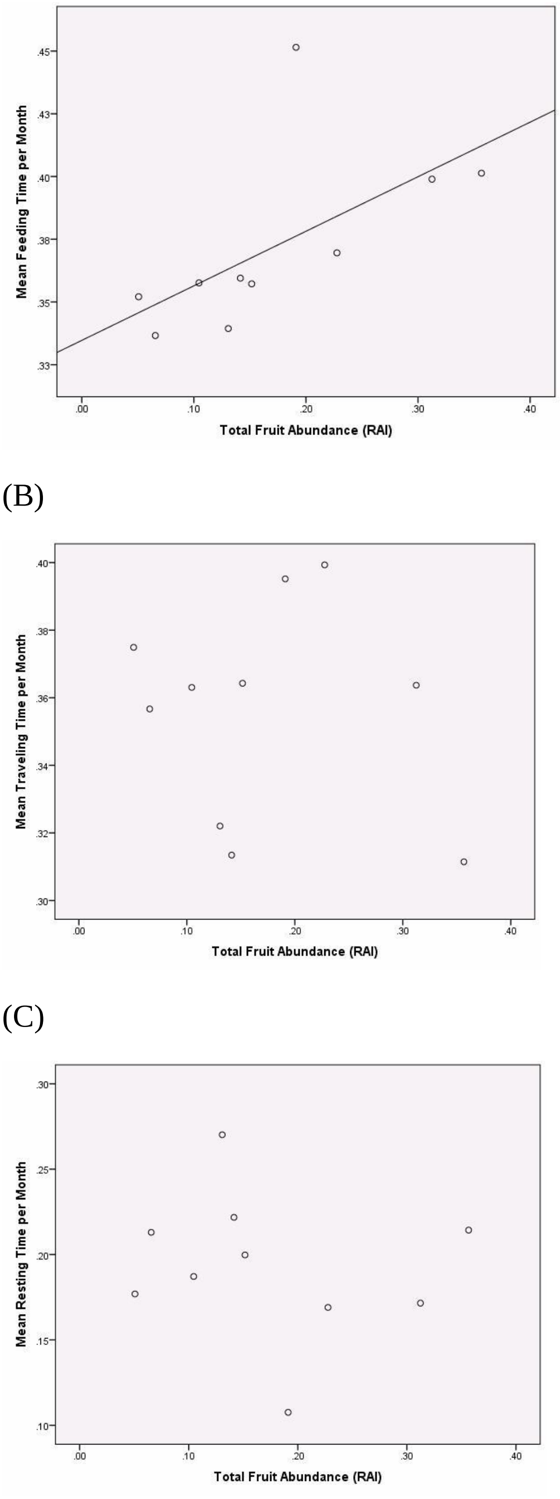


Figure 4.6. Regressions between monthly time spent engaged in different activities and total fruit availability. (A) Feeding, (B) Traveling (C) Resting.

(A)



(B)

(C)

Figure 4.7. Regressions between bearded saki activities and mean monthly rainfall. (A). Feed (B). Travel (C). Rest.

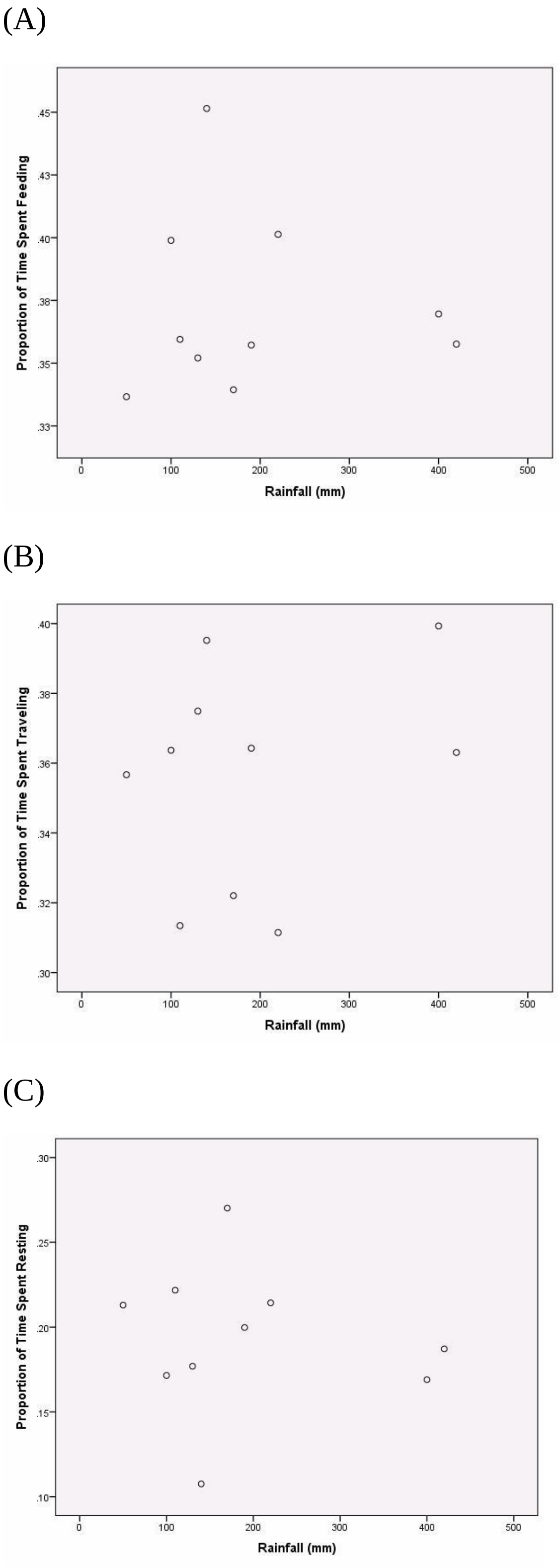


Figure 4.8. Bearded saki vertical stratification.

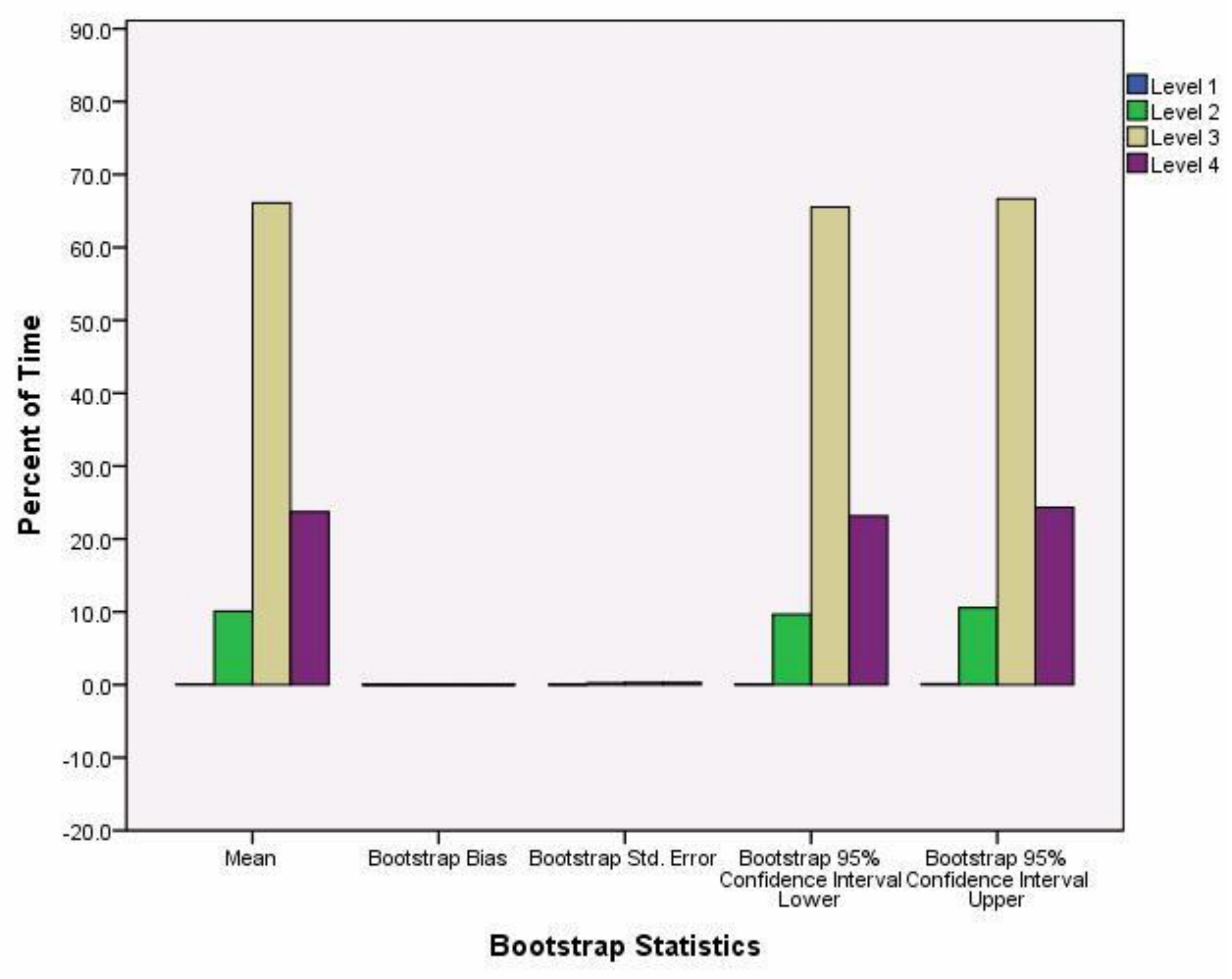


Figure 4.9. Vertical stratification by activity.

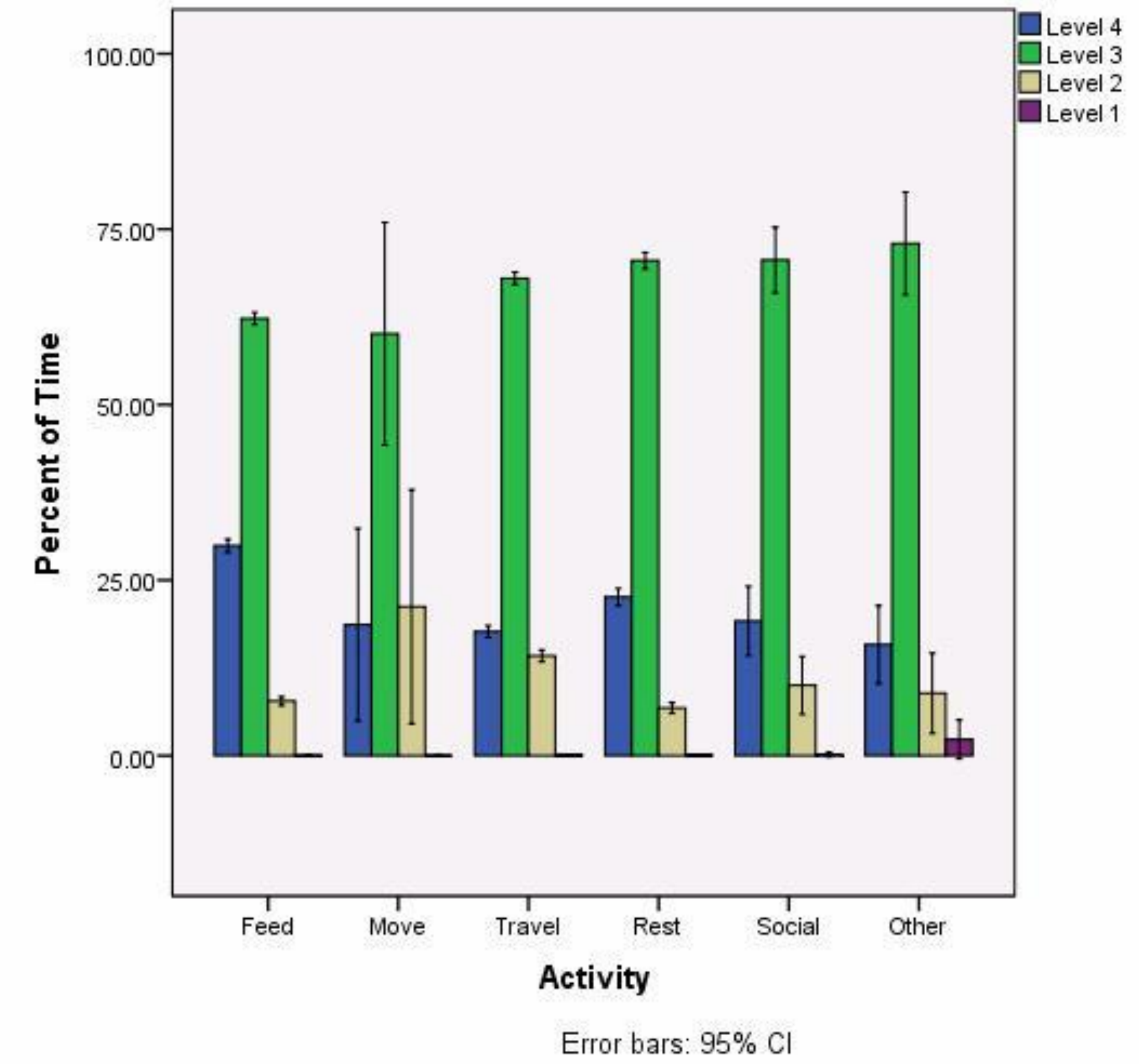


Figure 4.10. Vertical stratification during feeding on different food items.

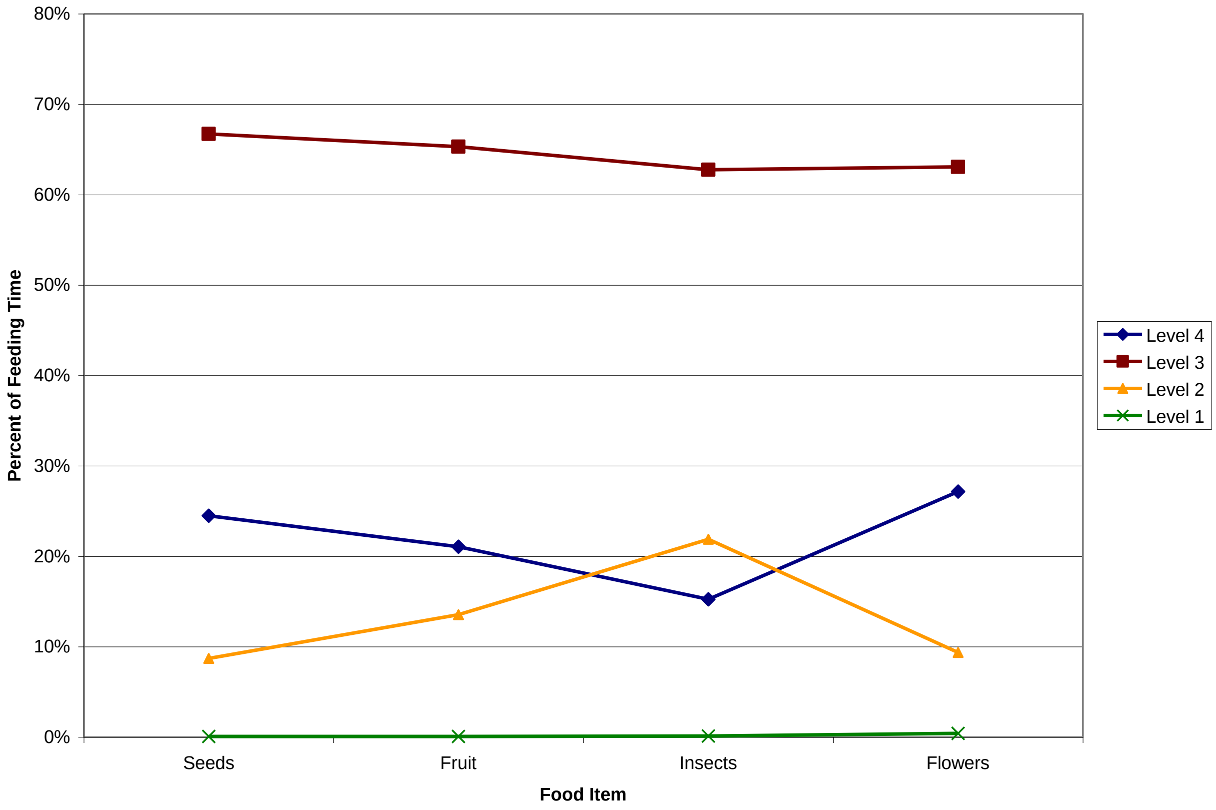


Figure 4.11. The most common bearded saki social behaviors. Percentages are the percentage of total social behavior. Does not include “Social Rest”.

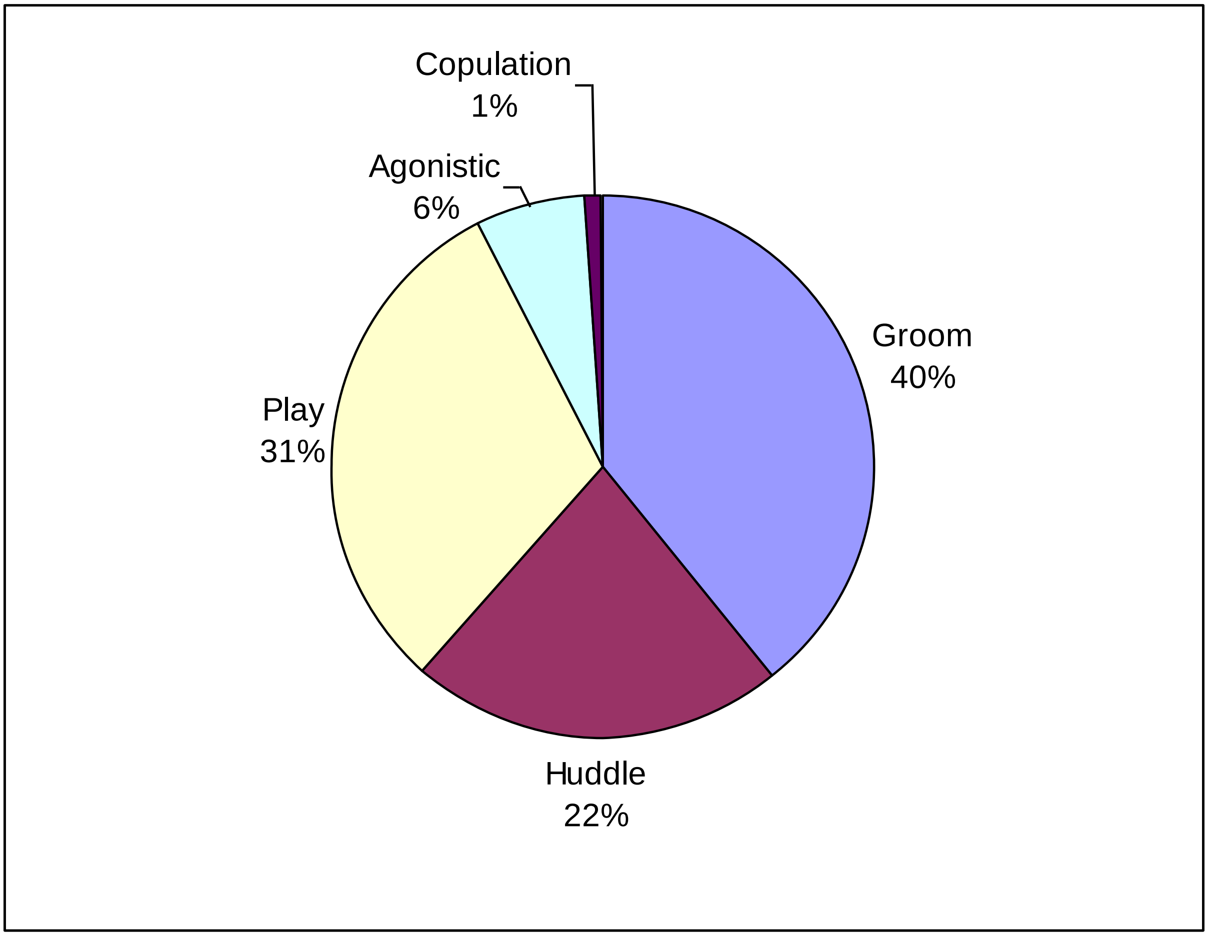
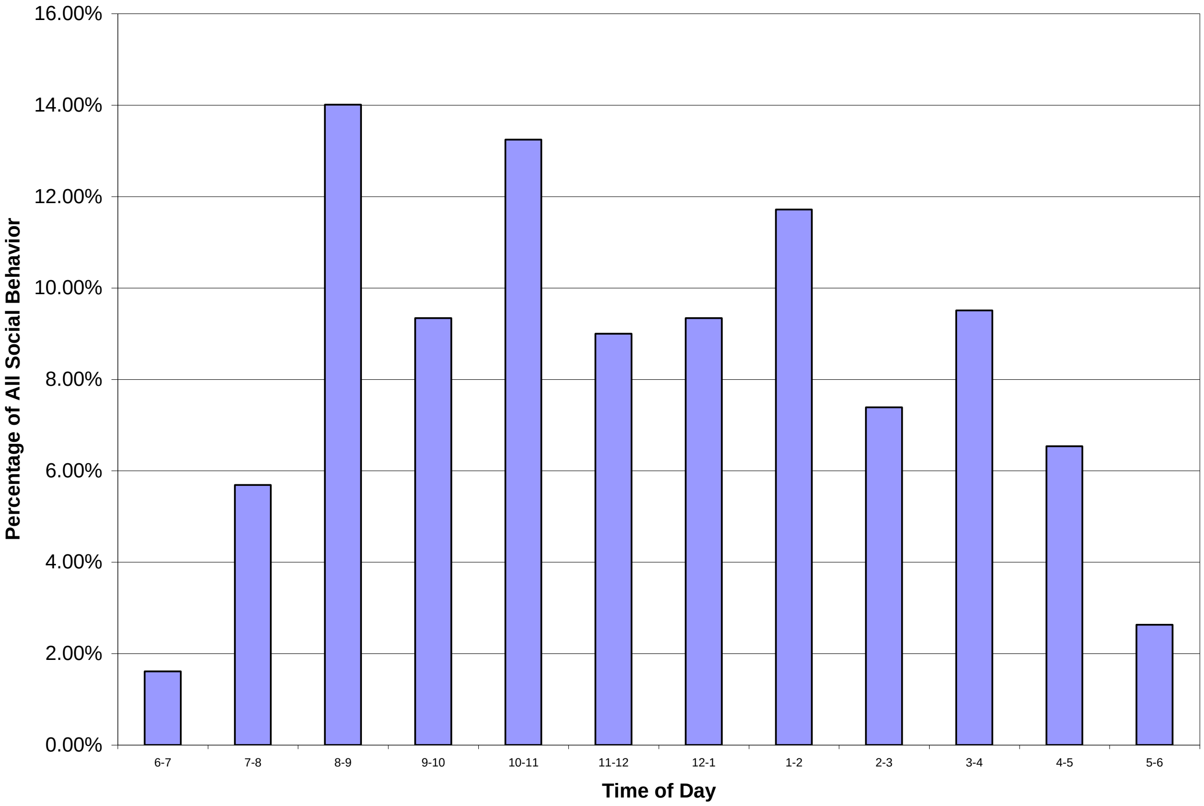


Figure 4.12. Social behavior by time of day.



CHAPTER 5 – DIET AND FEEDING ECOLOGY

Introduction

Foraging and feeding behavior are among the most researched topics in primate behavioral ecology. Identifying the contribution to primate diets of fruit, leaves, flowers, and animal matter and how primates procure and process these items has important implications for understanding ecological and morphological adaptations. While virtually all primates incorporate ripe fruit in their diet, primates vary tremendously in the proportion of fruit, leaves, seeds, flowers, and animal matter that they consume. One of the most important variables dictating the nutrient requirements for a species is body size (Hladik 1978, Sailer et al. 1985, Ford 2005). Researchers have derived predictions for the relative proportions of different food items in primate diets based on allometric theory and the net return for these food items (Bell 1971, Jarman 1974, Richard 1985). The Jarman/Bell principle predicts that primates less than 5 kg in body size incorporate large amounts of insects for their protein requirements. Large primates are thought to depend primarily on leaves for protein and primates in the middle range of body sizes are primarily frugivorous.

Foraging decisions are also influenced by ecological conditions such as the size, spatial distribution, and quality of feeding trees (Leighton and Leighton 1982, Terborgh 1983, Symington 1988, White and Wrangham 1988, Chapman 1988, 1990, Stier 1989, van Schaik 1989, Janson 1992, Pinto et al. 1993, Phillips 1995, Di Fiore 1997, Sterk et al. 1997, Kirkpatrick et al. 1998, Koenig et al. 1998, Stevenson et al. 1998, Pruetz 1999, Chapman and Chapman 2000, Dias and Strier 2003). As primate food items are generally patchily distributed in time and space, these ecological conditions often change seasonally. Primates must adapt their foraging behavior accordingly to optimize foraging efficiency. This may entail changing diet breadth, shifting food item preferences, or changing ranging behavior and activity patterns (Schoener 1971).

Optimal foraging suggests that primates should concentrate on preferred resources when they are abundant and correspondingly demonstrate lower dietary breadth during these periods of resource abundance (Charnov 1967, Schoener 1971, Robinson and Wilson 1998). When preferred resources become scarce, primates should expand dietary breadth and incorporate fewer preferred resources. This pattern has been reported in a variety of primate taxa and has been suggested to be employed by many primate seed predators (Chalmers 1968, Maier 1977, Kay and Hylander 1978, Lucas and Teaford 1994, Fleagle and McGraw 1999, 2002, Poulsen et al. 2001, Cuozzo and Yamashita 2006, Fashing 2007, Kirkpatrick 2007, Norconk and Veres 2011).

Some researchers have suggested that primates may employ a different feeding strategy based on fallback foods (Lambert et al. 2004, Lambert 2007, Marshall and Wrangham 2007, Marshall et al. 2009). Primates relying on this strategy are expected to feed on low-quality, less preferred “fallback” foods when resource abundance declines. While these foods may make up a relatively small proportion of annual feeding time, they are suggested to be critical for maintaining the survival of a species during periods of resource scarcity. Many of the primate morphological and behavioral specializations, therefore, are thought to be related to the processing of these fallback foods. Fallback foods may be nutritionally poor but highly abundant (e.g., leaves, bark) or nutrient rich but less abundant. Some researchers have suggested that seeds are an important fallback food for some primates (Norconk and Veres 2011).

In the last two decades, many primatologists have borrowed from optimal foraging models to focus on how primates maximize foraging efficiency. These models often assume that the abundance and distribution of food items is the primary driver of primate group size (Charnov 1967, Schoener 1971, Leighton and Leighton 1982, Terborgh 1983, Symington 1988, White and Wrangham 1988, Chapman 1988, 1990, Strier 1989, van Schaik 1989, Janson 1992, Pinto et al. 1993, Phillips 1995, Sterk et al. 1997, Kirkpatrick et al. 1998, Koenig et al. 1998, Stevenson et al. 1998, Pruetz 1999, Chapman and Chapman 2000, Dias and Strier 2003). The characteristics of food patches (i.e., how monopolizable or how easily depleted they are) are believed to determine the upper and lower limits for group size and drive intragroup social relationships. These characteristics also determine ranging patterns and group cohesiveness. As food patch characteristics change seasonally or yearly, primate behavior is likely to vary seasonally as well. Therefore, a thorough characterization of the plant species and food items eaten by a primate, as well as the spatial distribution and physical characteristics of these items, is critical for understanding the animals' behavioral ecology.

Unfortunately, the definition and quantification of exactly what constitutes a primate feeding patch has been notoriously problematic for primatologists (Oates 1987, Chapman 1988, Isabirye-Basuta 1988, Isbell et al. 1988, Symington 1988, Byrne et al. 1990, Chapman et al. 1994, Pruetz 1999, Vogel and Janson 2007; see Chapter 1). The traditional definition of a patch as the dbh of a single feeding tree does not allow for an assessment of how entire social groups perceive food resources. This is especially true when individuals in a primate group are spread out and feeding from multiple trees simultaneously. In addition, definitions like "localized aggregation of food items…separated from other such aggregations by regions of markedly lower food density" (Temerin and Cant 1983: 336) are difficult to use operationally. According to Pruetz (1999: 10), “Greater standardization, comparability, and accuracy of measures of food abundance and distribution are required to identify the specific relationships between food availability and primate feeding and social ecology.”

As discussed in Chapter 2, the genus *Chiropotes* is characterized by dental adaptations for a heavily seed-based diet. Previous studies of bearded sakis have shown them to be virtually unique in the primate order in the percentage of feeding time dedicated to seed eating (Ayers 1986, Norconk 1996, Gregory 2011). While primates as taxonomically diverse as sifakas, langurs, mangabeys, and capuchins are all known to ingest seeds and exhibit dental adaptations for seed predation, only the Pitheciini (*Chiropotes, Pithecia*, and *Cacajao*) appear to rely on seeds as their primary food resource throughout the year (Cartmill, 1974, Kinzey 1974, Daegling, 1992, Dumont 1995, Kitko et al. 1996, Shellis et al. 1998, Fashing 2007, Kirkpatrick 2007, Norconk and Veres 2011). This is reinforced by a dental anatomy that is the most derived of all primate seed predators (Norconk and Veres 2011).

Seeds provide a number of nutritional advantages over other food items. Because immature fruit is generally available for much longer than mature fruit, immature seeds tend to be a much less ephemeral resource for primates than mature fruit (Norconk et al. 1994, Norconk et al. 2010, Norconk and Veres 2011). They are also more widely available, as the proportion of trees bearing immature fruit at a given time is much higher than the proportion of trees bearing mature fruit (Janzen 1971, 1978). The ability to exploit this increased availability has led Norconk et al. (1998) to suggest that seed predators are relatively immune to the detrimental effects of seasonal food shortages. In addition, seeds are a valuable resource nutritionally, high in protein and especially lipids (Esau 1977, Janzen 1978, Bell 1984, Norconk et al. 2009).

However, seed eating also provides unique challenges to primates, as plants are heavily invested in preventing their offspring from being consumed and destroyed. Seeds are often high in difficult-to-digest secondary compounds and toxins, like tannins, phenolics, alkaloids, and acid detergent fiber (Esau 1977, Janzen 1978, Bell 1984, Norconk et al. 2009, Norconk and Veres 2011). Seeds are also often mechanically protected, with thick and difficult-to-open husks, woody exocarp, and hard endocarp (Fischer and Chapman 1993, Norconk and Veres 2011). Therefore, specialized seed predators are relatively rare in the primate order. In this chapter, I describe the diet and foraging behavior of northern bearded sakis (*Chiropotes sagulatas*) in Guyana. I focus on:

Research Question 2. How do bearded sakis adjust their feeding ecology in response to changes in resource abundance?

As shown above, optimal foraging theory and the “fallback food” hypothesis predict that primates should concentrate on preferred resources when overall resource abundance is high but increase dietary breadth to incorporate less preferred resources when overall resource abundance is low (Charnov 1967, Schoener 1971). Several researchers have suggested that the ability of Pithecines (and other specialized seed predators) to exploit widely available seeds buffers them against seasonal changes in resource abundance (Norconk et al. 1998, Norconk and Veres 2011).

Therefore, I suggest:

Hypothesis 2 – Bearded sakis will increase dietary breadth when resources become scarce and will rely more heavily on seeds (i.e. the resources they are highly specialized to exploit) during these periods.

I begin by presenting the overall yearly diet of the study group, including plant parts and plant species, and how selective sakis are in terms of plant species preferences. I then describe seasonal differences in diet and how these relate to seasonal differences in food availability. I also detail the spatial distribution and physical characteristics of bearded saki feeding trees and characterize what constitutes a bearded saki feeding patch. Finally, I compare the diet and foraging behavior of my study group with those of both other groups of bearded sakis and other primates to better characterize the bearded saki feeding niche.

Methods

I collected data on feeding behavior concurrently during scan samples (see Chapter 2 for general behavioral data collection methods). For each scan in which I observed animals feeding, I recorded the number of individuals feeding on each plant part category and each plant species.

Plant part categories included mature fruit, immature fruit, mature seeds, immature seeds, flowers, insects, and other. These categories were selected based on previous research of the bearded saki (Ayers 1989, Norconk 1996, Preetz 2001, Boyle 2008). For data analysis, feeding records were analyzed using the proportion method to account for biases related to variation in the number of individuals observed in a scan (see Chapter 4).

All feeding trees used by the study group were tagged, mapped, and assigned a phenology score from 1 – 4 indicating the percentages of branches bearing fruit or flowers (See Chapter 3). Plant species identifications were made using a number of methods. All unknown fruits observed to be eaten by the study group were collected and photographed for later identification. This was facilitated by the extremely messy feeding strategy of the sakis, which generally involved dropping large amounts of fruit and seeds in various states of being masticated. These fruits were then identified using references for plants of the Guiana Shield, especially van Roosmalen (1985), Ribeiro et al. (1999), and Polak (1992), and with the aid of botanists from the Smithsonian Institute's Biodiversity of the Guianan Shield program. Plant species were also identified in the field by one of the research assistants, Henry James, who was previously employed as a trained tree spotter for the Guyana Forestry Service.

I initially aimed to measure all of the feeding trees used by the study group. However, the sheer number of feeding trees utilized by the sakis and the tremendous size of the study group home range made this goal impossible. I was therefore forced to measure a sample of the feeding trees by randomly choosing at least one full-day follow per month and measuring the trees used during that day. This provided a sample of over 1000 trees during 17 full-day follows, representing each month that the study group was observed except April. For each of these trees, the following variables were measured: dbh, height (estimated using a clinometer), crown breadth (measured with a meter tape), crown depth (estimated using a clinometer taking the height to the first branch of the canopy and subtracting from the overall height), and crown shape (using a standard forestry guide of 10 crown shapes; Coder 2000). Crown variables were then used to calculate crown volume for each of these trees using standard forestry formulae for different crown shapes (Coder 2000, Bechtold et al. 2002). Appendix II shows the crown shapes and their respective formulae used in this study. Phenology scores were assigned to all feeding trees based on a five character scale (0 – 1.0) indicating the approximate percentage of branches bearing fruit: (0) indicated no fruit or flowers, (0.25) indicated < 25%, (0.50) indicated 25% - 49%, (0.75) indicated 50% - 74%, and (1.00) indicated 75% - 100%. This scale was modified from a traditional 0 – 4 ordinal scale to produce a more biologically meaningful patch quality score (see below).

As mentioned above, most studies of primate feeding behavior have used dbh as the primary measure of feeding tree, and thus, food patch, size. While dbh has been shown to be strongly correlated with crown volume, this relationship is not 1:1 and can vary widely depending on habitat type and tree species (Dawkins 1962, Francis 1986, Bechtold et al. 2002, Lockhart et al. 2005). By taking both dbh and crown volume measurements, I was able to assess feeding tree size in two ways and compare them for different species.

Data Analysis

To characterize the overall diet of the study group, I calculated the total proportion of food parts consumed and the percent contribution of each plant species to the annual diet. While every effort was made to have an equal number of observation records during different months and hours of the day, there was considerable monthly variation in the number of full-day follows and, therefore, behavioral observation records. Accordingly, to assess intermonthly variation in bearded saki behavior, I first calculated percentage of activity or feeding for each hour of the day, then averaged these percentages within each month to determine monthly activity or monthly consumption of different plant parts/species. I used bootstrapping to obtain confidence intervals and standard deviations (Efron 1982, Krebs 2000). As mentioned previously, bootstrapping consisted of 1000 iterations and bias corrected and accelerated (BCa) boostraps were preformed in all cases to assure maximum accuracy in bootstrapped estimators (Efron 1982).

Many primates are reported to be highly selective in their choice of food species, often eating from species that are relatively rare in their home range. To determine how selective the study group was, I calculated two indices of selectivity, the selection index (or forage ratio) and the Strauss Selectivity index. The forage ratio (w_i) is a commonly used measure of selectivity and is represented by the formula:

$$w_i = o_i/P_i \tag{5.1}$$

where w_i is the forage ratio for species *i*, o_i is the proportion of species *i* in the diet, and P_i is the proportion of species *i* in the environment (Manly et al. 1993, Krebs 1999). Selection indices above 1.0 indicate preference species while values less than 1.0 indicate avoidance. The selection index is the most common measurement of dietary preference used in ecological studies and therefore, is important for comparison with previous research (Krebs 1999). Strauss Selectivity index (L) is calculated according to the formula:

$$L = r_i - p_i \tag{5.2}$$

where r_i is the proportion of species i in the diet and p_i is the proportion of species i in the environment. Values range are normalized to 0 and range from -1 to +1; negative values indicate avoidance of a particular species and positive values indicate preferential selection. While there are many measures of selectivity available to ecologists, the Strauss index is less sensitive to the presence of rare species than other commonly used measures of selectivity (Strauss 1979, Kohler 1982). In addition, it is less susceptible to sampling bias when the sample represents a small part of the environment (Lechowicz 1982). To assess if values of L were significantly different from 0, I used the G-test of independence. The G-test of independence tests the null hypothesis that the proportions of one variable (in this case, proportion of a plant species in the bearded saki diet) are the same as the proportions of a second variable (the relative abundance of the plant species). Bootstrapped means were used for both proportions to account for lack small sample size and uncertainty in the distributional properties of the indices.

To determine whether the physical characteristics of feeding trees played a role in their selection by the study group, I compared the dbh and height of all measured feeding trees to transect trees and tested differences for significance using Mann-Whitney U tests.

To assess monthly variation in the proportion of food items consumed, I used a G-test with Williams' correction for each plant part. I used Spearman rank correlations to test the relationship between the percentage of a plant part in the saki diet and its relative abundance in the environment (based on transect data – see Chapter 3) for each month. To characterize how diverse the bearded saki diet was, I calculated overall dietary diversity using the Shannon-Wiener index (H'):

$$H' = \sum p_i (\ln) p_i \tag{5.3}$$

where p_i is the proportion each food species i consumed compared to the rest of the diet (Pielou 1966). While several indices of dietary diversity are available, I chose the Shannon-Wiener index due to its regular use in studies of primate feeding behavior (Ludwig and Reynolds 1988, Yeager 1996, Di Fiore 1997, Krebs 1999). This facilitated intraspecific and interspecific comparisons in diet breadth. A related measure of dietary diversity commonly used by ecologists is Pielou's index of evenness (Pielou 1966). Evenness (E) measures how similar different species are in abundance (Mulder et al. 2004). For studies of dietary diversity, evenness shows if a few species dominate the diet or if species are fed upon more or less equally (Pielou 1966). I calculated evenness using the formula:

$$E = H'/\ln(s) \tag{5.4}$$

where H' is the Shannon-Wiener index and s is the species richness (the total number of species consumed during the study). The value of E ranges from 0 to 1. When all species are represented in similar proportions in the diet, evenness is 1. When the abundance of different species is widely dissimilar (i.e., some species are very rare and others are very common in the diet), then the value decreases.

I also calculated dietary diversity (H') for each month and tested differences using a G-test for goodness-of-fit with Williams' correction to assess how sakis adjusted their dietary diversity with changing ecological conditions. I used Spearman rank correlations to detail the relationship between dietary diversity and monthly food abundance (RAI).

Food Patch Definition

As mentioned above, patch size and quality are presumed to be two of the most important variables influencing primate socioecology. Therefore, a thorough quantification of what constitutes a patch is critical to testing the relationship between primate foraging and ranging behavior and resource quality and distribution. Here I present a new method for defining food patches. I used GIS to synthesize the forestry measurements explained above and produce a definition of food patch that goes beyond that of a single tree crown, which I deem too simplistic as many primate groups are rarely constrained to a single tree during feeding. This is especially true for a primate like the bearded saki, whose groups are often spread out with individual animals feeding on several different trees simultaneously.

To define patches, I superimposed a grid over the study area using two grid sizes, 100X100 m and 50X50 m. Each grid in which the study group fed was then assigned values based on the number of feeding trees it contained and on the physical characteristics of those trees related to their quality as a bearded saki resource. A food patch was, therefore, defined as a quadrat (either 100 m^2 or 50 m^2) that contained at least one feeding tree. The quality of a patch was determined by a combination of the number of feeding trees it contained, the size of those trees (measured using either dbh or crown volume), and the amount of food these trees contained (measured by phenology score):

$$\text{PQI} = \Sigma(\text{crown volume X phenology score) of all trees within the patch} \tag{5.5}$$

$$\text{PQIdbh} = \Sigma(\text{DBH X phenology score) of all trees within the patch} \tag{5.6}$$

Figures 5.1 and 5.2 show schematic representations of how patch definitions were determined using GIS. Different patch quality indices were assigned to patches depending on whether patch size was defined by dbh (PQIdbh) or crown volume (PQI). PQI values indicate the total volume of branches within the patch containing fruit or flowers. As each of these indices was used for both spatial scales, four patch quality indices were used in this study: PQIdbh and PQI for 50 m quadrats and PQIdbh and PQI for 100 m quadrats.

This measure is not mutually exclusive of previously used measures of patch size and quality, as it incorporates both dbh and crown volume and allows for a more precise assessment of “areas of high food density circumscribed by areas of low food density” (Leighton and Leighton 1982: 212). See Chapter 6 for a more thorough discussion of this method compared to other definitions of a food patch.

Results

Annual Diet

Figure 5.3 shows the overall annual diet of the study group. As predicted, bearded sakis were highly granivorous, with seeds making up 74.47% of annual feeding time. Mature fruit was the second most commonly consumed food item, making up 12.44% of feeding time. All fruit, including immature, mature, and seeds, made up almost 90% of the diet. Sakis also consumed insects and flowers, composing 10.02% and 2.23% of feeding time, respectively. The “other” category consisted of only 16 feeding records. Ten of these were the pith of young shoots of the crabwood tree (*Carapa guinanesis*), feeding on which took place two days in October. The other six records consisted of monkeys drinking from pools of water in epiphytic plants and tree recesses. On these occasions, individual sakis reached into the pools of water with their hands and brought water to their mouths repeatedly for several minutes.[*] Sakis were not observed eating leaves at any point during the study period.

Bearded sakis exhibited a tremendously diverse diet, exploiting over 215 plant species over the course of 12 months of behavioral observation (Appendix V). These species included over 100 different genera belonging to at least 39 different families. Table 5.1 shows the 100 most important species in terms of overall feeding time and Table 5.2 shows all 39 plant families by feeding time. Despite its tremendous diversity, the diet of the study group was dominated by a few species and genera. Seven species accounted for over 50% of the annual diet and over 72% of feeding records came from the top 15 species. The top five plant families (Sapotaceae, Fabaceae, Moraceae, Lecythidaceae, and Apocynaceae) accounted for over 60% of the bearded saki diet. Overall dietary diversity (H') was -3.67 and evenness (E) was 0.68. Therefore, while bearded saki dietary diversity was quite high, their diet was highly skewed to a few species.

Of the more than 215 species eaten, only 35 were utilized by the sakis for food items besides seeds and an additional 15 produced unidentifiable food items that were also consumed by the sakis. 19 plant species were targeted only for fruit (either mature or immature). The sakis exploited two species for flowers only and exploited an additional six species for flowers and

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[*] Interestingly, this method of drinking appears to be a genus specific behavior. The name *Chiropotes* comes from the Latin *chiro* meaning “by means of the hand” and potes meaning “drinker.” The name was assigned to the genus by early observers who observed this behavior and explained the behavior as a way for the monkeys to drink while keeping their beards dry (Hershkovitz 1985).

seeds. While the study group only fed on multiple food items from 14 species, several of these were among the most important plant species in their diet. Their ability to exploit plant parts in a number of states of maturity allowed the sakis to feed from some individuals of the species for over three months. For example, the sakis targeted immature seeds of *Manilkara bidentata*, the most important food species in the diet, for over two months before ripe fruit was seen on the tree. By the time most of the fruit had ripened, and other primates began to exploit the resource, much of the fruit was gone (as much as 75% in some cases, based on phenological scores collected when sakis revisited the trees). This pattern of intense exploitation of resources as they became seasonally available is represented by Figure 5.4.

Consistent with their specialized dental morphology, bearded sakis frequently ate from seeds protected by tough pods and large, indehiscent fruits protected by thick husks (i.e., genera of the Lecythidaceae and various Fabaceae families). Figures 5.5-5.7 show fruit types characteristic of trees throughout the bearded saki home range. Because of their mechanical protection and lack of edible mesocarp, dry fruits are rarely eaten by most species of primates (Norconk and Veres 2011). Yet seeds from dry fruits were among the most important food items for the study group. As shown in Appendix V, dry fruits and their seeds represented over 50% of the saki diet.

The bearded sakis in this study used their canines to split pods in half and to puncture the husks, exposing the contained seeds (Figure 5.8). Sakis also used their procumbent incisors to remove the exocarp and operculum from dehiscent fruits (esp. *Eschweilera* fruits) and to plane the pericarp from very large fruits (i.e., *Pouteria speciousa* – see Figure 5.9 and Figure 5.10). While sakis did incorporate fruit with fleshy mesocarp into their diet (esp. *Manilkara bidentata*, *Goupia glabra*, and *Geissospermum sericeum*), they usually ate seeds from immature fruits from these species that had not yet developed an edible mesocarp.

Bearded sakis were selective in their choice of plant species, with selectivity measures (w_i) indicating that they fed from both the top 13 species and 14 of the top 20 species more frequently than would be expected based on species abundance in the environment (Table 5.3, Figure 5.11). Strauss selectivity values (L) were significantly different from 0 for nine of the 14 species that were preferred. Therefore, sakis selected nine of their 20 most important feeding species significantly more often than they would be expected if they fed from all species in their home range according to their relative abundance. Further, several of the top food species were locally dominant trees for different micro-forest types (i.e., *Swartzia leiocalycina, Geissospermum sericeum*). Of the 111 tree species represented in transects, only 15 were not observed being fed upon by the study group. In addition, the ten most abundant species at the study site (according to total basal area) made up 29% of the saki annual diet. Thus, bearded sakis showed a remarkable ability to exploit virtually any tree in the forest as a food resource and were able to heavily exploit many of the most common species.

Monthly Variation in Diet

Figure 5.12 shows the percent consumption of food item by month. For all months, seeds made up a majority of feeding time, ranging from 97% of the diet in May to 41% in November. However, bearded sakis showed a great deal of variation in feeding throughout the year, with the proportion of seeds, mature fruit, insects, and flowers all showing significant intermonthly variation (G-test with Williams' correction: Seeds $G = 80.44$, $p < 0.001$; Fruit $G = 616.60$, $p <$

0.001; Insects G = 172.86, $p < 0.001$; Flowers G = 582.59, $p < 0.001$). Mature fruit consumption was highest in November and December and lowest in May. While insects and flowers made up only about 10% of the annual diet combined, there was a great deal of monthly variation in their contribution to the saki diet. Insect consumption peaked in September, accounting for 36% of feeding time. Flowers made up over 5% of the saki diet in October and November. Mature fruit consumption, ($\rho = -0.78$, $p = 0.008$), insect consumption ($\rho = -0.84$, $p = 0.002$), and flower consumption ($\rho = -0.89$, $p = 0.001$) were all significantly negatively correlated with overall seed consumption. These data indicate that, while sakis consume a high percentage of seeds year round, they supplement their diet to a large extent with fruit, insects, and flowers seasonally.

When monthly variation in food item consumption is compared to variation in food abundance, a clear feeding pattern emerges. In Figure 5.13, I show saki feeding time compared to transect phenology data for each month. Overall fruit consumption (including seeds) was significantly correlated with overall fruit abundance ($\rho = 0.64$, $p = 0.048$) but mature fruit consumption was not significantly correlated with mature fruit abundance ($\rho = -0.18$, $p = 0.627$) (Figure 5.14). The relationship between flower consumption and overall fruit abundance was not significant ($\rho = 0.75$, $p = 0.013$), although relationship between flower consumption and flower abundance was not ($\rho = 0.49$, $p = 0.156$). Nevertheless, the three months when flower feeding was highest (Sept – Nov) were three of the four months with maximum flower abundance. Insect consumption was negatively correlated with overall fruit abundance, and this result was highly significant ($\rho = -0.76$, $p = 0.011$). Therefore, while sakis consumed a high percentage of seeds in all months, they incorporated a large percentage of insects and flowers in their diet as seeds and other fruit became scarce. When fruit was most scarce during the short dry season (early September to early December), almost 40% of the saki diet consisted of non-seed food items.

The relationship between mature fruit consumption and mature fruit abundance was heavily influenced by sakis feeding on *Goupia galba* during the short dry season. This species was the most important mature fruit source for the study group by far (accounting for 45% of mature fruit feeding time) and was one of the few species targeted solely for mature fruit. It was one of the few species fruiting during the short dry season and was relatively rare and patchily distributed throughout the saki home range (relative abundance = 0.27%). It is possible that this species represents an important keystone resource for bearded sakis and other frugivores during the period of most food stress (see Discussion).

Throughout most of the year, bearded sakis searched for insects opportunistically during the course of other feeding. For example, while searching through an *Eperua falcata* tree for pods with suitable seeds, they would sift through dead leaves or pods for larvae or beetles. Slow moving and cryptic insects like katydids were eaten when encountered. During the short dry season months, however, bearded sakis employed two insect feeding strategies that were not observed during the other months. One strategy consisted of traveling in a seemingly goal-directed manner to two large *Couratari guianensis* trees (some of the largest trees in the forest) that harbored massive amounts of caterpillars that were breeding on dead leaves (this species is deciduous and loses its leaves in August and September; see Figure 5.15). The sakis would then feed from these trees for over an hour. Because this pattern of leaf loss is a consistent yearly phenological pattern for this species, it is possible these caterpillars represent a predictable, highly nutritious annual resource for the study group.

The other insect foraging strategy consisted of traveling through low-canopy forest with a high density of *Attalea* palms and searching through leaves, bark, and dead palm fronds. This foraging strategy was very similar to the extractive foraging of *Cebus* and *Saimiri* groups.

During these forays, the saki group would feed from only a few plant species, a pattern very different from their normal foraging behavior. Therefore, it appears bearded sakis were specifically targeting insects during these dry season months. Unfortunately, I was unable to assess the extent to which insect consumption was related to insect abundance. Interestingly, the short dry season months were also the months in which the study group spent the most amount of time in proximity with polyspecific groups of *Cebus apella* and *Saimiri sciureus*. It is possible that bearded saki insect foraging was facilitated by the extractive foraging of these primates and that sakis engaged in insect foraging upon encountering the polyspecific groups. However, it appeared unlikely that bearded sakis sought out these mixed-species groups (see Chapter 6).

Although the study group showed significant monthly differences in the consumption of different food items, their dietary diversity did not vary significantly across months (H' G = 12.2, p = 0.20; Eveness G = 10.40, p = 0.32). Dietary diversity was consistently high and the study group ate from more than 35 species every month except September (Table 5.4, Figure 5.16). On several occasions, they ate from 25 species or more in a single day. Monthly dietary diversity (H') was not significantly correlated with mature fruit availability ($\rho = 0.38$, $p = 0.28$), overall fruit availability ($\rho = 0.47$, $p = 0.17$), or flower availability ($\rho = -0.13$, $p = 0.73$). Similarly, evenness (E) was not related to the relative abundance of any of these resources (Mature fruit RAI $\rho = -0.01$, $p = 0.99$; Total Fruit RAI $\rho = -0.13$, $p = 0.713$; Flower RAI $\rho = -0.2$, $p = 0.95$). Therefore, despite shifting their dietary preferences for different food items in response to shifts in food abundance, bearded sakis did not expand or contract their dietary breadth in terms of plant species.

The results presented above do not support Hypothesis 2, that bearded sakis will increase dietary diversity when resources become scarce and will rely more heavily on seeds (i.e., the resources they are highly specialized to exploit) during these periods. Bearded sakis' dietary diversity in terms of number of plant species eaten was not significantly correlated with resource abundance. In addition, the study group decreased seed feeding during periods of maximum resource scarcity (seed feeding was significantly correlated with total fruit abundance). Instead, bearded sakis expanded their dietary breadth by incorporating other food items besides seeds during months when resources were most scarce. These included flowers, mature fruit, and insects.

Characteristics of Feeding Trees

The study group fed from more than 2400 individual trees during the course of the study (Figure 5.17). Taken together, these trees showed a clumped spatial distribution (Coefficient of Dispersion = 1.79). In addition, 15 of the top 20 most important species in the saki diet each showed a clumped spatial distribution (Figure 5.18, Table 5.5). These data indicate that sakis exploited patchily distributed feeding trees.

Using the sample of 1059 measured feeding trees from 17 full-day follows, the mean dbh of bearded saki feeding trees was 48.34 cm, with a mean height of 31.32 m and a mean crown volume of 461.36 m^3 (Table 5.6). Unfortunately, the small sample size precluded testing for monthly differences in feeding tree size. Bearded sakis selected feeding trees that were significantly larger than transect trees both in height and dbh (Mann-Whitney U test: Height U = 74692.00, $p < 0.001$; dbh U = 84900.50, $p < 0.001$; Figure 5.19). Feeding trees were much less variable than transect trees. As expected, dbh was a strong predictor of crown volume ($R^2 = 0.53$, $p < 0.001$), although several species were consistently different from the trendline (Figure 5.20).

While sakis did not change their dietary breadth significantly across months, they did show significant monthly differences in the number of individual feeding trees they utilized (G-test for goodness of fit G = 38.26, $p < 0.001$). Table 5.8 shows the average number of feeding trees visited per day during each month of the study period. Sakis fed from fewer trees during September, October, and November. Number of feeding trees was significantly correlated with overall fruit availability ($\rho = 0.64$, $p = 0.048$), suggesting bearded sakis had fewer trees to feed from during this period of fruit scarcity.

Characteristics of Feeding Patches

Table 5.7 shows the characteristics of bearded saki food patches for both 100 m^2 and 50 m^2 grid sizes. The mean PQIdbh for 100 m^2 food patches was 191.80 and mean PQI was 440.92 m^3. For 50 m^2 food patches the mean PQIdbh was 125.48 and mean PQI was 294.30 m^3. Patch quality values were highly correlated when two spatial scales were compared (PQIdbh $r = 0.80$, $p = .010$; PQI $r = 0.81$, $p = 0.008$). Because food patch data was only collected for 17 full-day follows, statistical power was limited. Nevertheless, there was considerable monthly variation in all measures of patch quality (mean PQI, mean PQIdbh) and both mean monthly patch quality (50 m quadrats PQIdbh $\rho = 0.67$, $p = 0.050$; 100 m quadrats PQIdbh $\rho = 0.68$, $p = 0.048$; PQI $\rho = 0.71$, $p = 0.031$) and the number of patches visited per day (50 m quadrats $\rho = 0.80$, $p = 0.10$; 100 m quadrats $\rho = 0.80$, $p = 0.01$) were correlated with monthly fruit abundance (Table 5.8, Figure 5.21). Only one measure of patch quality was not significantly correlated with total monthly fruit abundance (50 m quadrats PQI $\rho = 0.51$, $p = 0.17$). These results indicate that bearded sakis visited fewer food patches during the short dry season on both spatial scales. In addition, the overall quality of these patches (as measured by mean PQI) was much lower during the months of September and November. Thus, sakis visited fewer and lower quality food patches during these months. This is consistent with the short dry season being the period of maximum food scarcity for the study group (see Chapter 6 for description of the relationship between patch quality, patch occupancy, and ranging behavior).

Discussion

Overview of Chiropotes sagulatus feeding ecology

The data presented in this chapter provide a clear picture of the bearded saki foraging strategy. Consistent with their classification as sclerocarpic foragers by previous researchers and their specialized dental morphology, bearded sakis consumed an exceptionally high proportion of seeds during this study. Seeds made up a majority of feeding time in all months, and sakis showed an ability to exploit a tremendous variety of mechanically protected fruits. However, sakis also showed a great deal of variation in their diet seasonally and were able to incorporate high percentages of mature fruit, insects, and flowers in some months. The saki diet was also remarkable in the sheer number of exploited species, both throughout the course of the study and on individual days. This raises the question of whether seed eating provides the sakis relative immunity from the detrimental effects of seasonal food shortages, as suggested by previous research of the genus. Specifically, do seeds function as fallback foods that allow sakis to decrease dietary breadth by focusing on certain less preferred but more widely available species during periods of food scarcity?

My results suggest that the answer to this question is not a simple “yes” or “no.” While sakis did consume a high percentage of seeds in all months, it was during the short dry season (the period of greatest food scarcity by far) that seed eating fell to its lowest levels. Instead, sakis fed on insects and mature fruit in high percentages and on flowers to a lesser extent, resources that are presumably even more nutritious than seeds. As all fruit and seeds were very scarce during this period, sakis were forced to concentrate feeding on other resources that became seasonally abundant. It appears that the ability of bearded sakis to exploit a variety of resources, rather than having to rely on their unique seed eating specializations *per se*, serves as a buffer from the most intense food shortages. Instead of being dependent on a less preferred seed species as a primary fallback food, bearded sakis seem to use the mature fruit of *Goupia galba* as a high quality keystone resource. Sakis decreased their dietary diversity in terms of number of plant species during the short dry season but counteracted this by expanding their dietary breadth in terms of plant parts.

Keystone resources and their importance for rainforest communities have received a great deal of attention in the ecological literature (Howe 1977, Gilbert 1980, Terborgh 1986, Whitmore 1990, White 1994, Power and Mills 1995, Peres 2000). A keystone resource is one that provides reliable, high quality food during periods of maximum resource scarcity. Ecologists disagree on the specific definition of a keystone resource, especially on how many consumers such a resource must sustain during the lean season to be characterized as “keystone.” According to Peres (2000: 26), keystone plant species are, “those producing reliable, low-redundancy resources that are consumed by a large proportion of the bird and mammal assemblage with which they coexist.” Keystone resources are thus distinguished from fallback foods in that they serve many individuals in the ecological community and they are high quality (Lambert 1997, Peres 2000).

Many researchers have focused on figs (genus *Ficus*) as keystone resources in tropical forests throughout the world because of their asynchronous fruiting (availability throughout the year) and high quality fruits that are exploited by many frugivorous species (Terborgh 1986, Gautier-Hion 1989, Peres 1991, 2000). However, as shown in Chapter 3, there were no *Ficus* species found at this site and the forests of the Guiana Shield are characterized by a low abundance of *Ficus* species (ter Steege et al. 2000). While I was unable to quantitatively assess the importance of *G. galbra* to other frugivores at the study site, anecdotal evidence suggested that it was a high valued resource for many species. I observed at least 13 different taxa feeding from *G. galbra* trees during the short dry season, including six bird species (three *Ara* and one species each of the genera *Amazon*, *Crax*, *Psophia*), three primate species (*Ateles, Cebus apella, Chiropotes*), two peccaries (*Tayassu* and *Pecari*) and two rodents (*Dasyprocta* and *Agouti*). In addition, *G. galbra* appeared to meet one of the most important criteria for keystone resources as its fruiting patterns are "highly synchronous and pulsed peaks coincid[e] entirely with the lean season (Peres 2000: 310)." Other bearded saki researchers have found *G. galbra* to be an important saki resource during periods of the year when the abundance of most other fruits was low (Ayers 1981, Pinto 2008).

For most primates living in tropical rainforests, the long dry season is when food resources are most scarce. This is clearly not the case for bearded sakis in this forest. As shown in Chapter 3, the long dry season was actually the period of greatest food abundance for the sakis at this study site. However, most of these are dry fruits or pods from the Lecythidaceae and various Leguminosae families. They are usually heavily protected mechanically, with little edible mesocarp and, thus, not suitable for consumption by most primate species. With their specialized dentition, bearded sakis (along with *Pithecia*) are perfectly and uniquely adapted to exploiting these abundant resources. In addition, sakis are able to exploit these resources for very long periods of time (i.e., three months) due to the long maturation times of the fruits. Therefore, in this forest, the specialized craniodental features of bearded sakis allow them to take advantage of the period of greatest resource abundance. During periods of greatest resource scarcity, sakis actually become generalists *par excellence*.

This is not to say, of course, that these craniodental adaptations of bearded sakis are unimportant during the short dry season. In fact, several mechanically protected seeds were very important in the bearded saki diet during this time. Among these were Bignoniaceae and Apocynaceae lianas that fruited year round. Other researchers of bearded sakis have found these to be important families in the saki diet during periods of resource scarcity and Norconk and Veres (2011) found they were among the hardest fruits sakis consumed (Norconk 1996, Peetz 2001, Boyle 2008). Also, the ability of bearded sakis to exploit virtually all of the trees in the forest as food resources certainly buffers them against any type of resource scarcity. Due to the asynchronous fruiting of many tropical forest trees, there will always be some species fruiting. The bearded saki craniodental complex makes it likely that the animals will be able to exploit these fruiting species, regardless of the mechanical protection regime employed by the plant. Interestingly, many of the seeds consumed by the study group (including their 2nd ranked species, *Swartzia leiocalycina*) are Guyana endemics. This further supports the tremendous dietary flexibility of *Chiropotes sagulatus* in terms of plant species they are able to exploit.

Intraspecific Comparisons

The data presented above are consistent with other studies of bearded sakis, with some notable exceptions. Virtually all previous studies of *Chiropotes* have found that seeds make up a majority of feeding time (Ayres and Nessimian 1982, Mittermeier et al. 1983, van Roosmalen et al. 1988, Frazao 1991, Norconk and Kinzey 1993, Norconk 1996, Peetz 2001, Veiga and Ferrari 2006, Norconk 2007, Boyle 2008, Gregory and Norconk 2010). Along with *Cacajao*, bearded sakis consume the highest annual and monthly percentage of seeds of any primate (Ayers 1981, Norconk 2007). Three of the most important plant families to sakis in this study (Sapotaceae, Lecythidaceae, and Moraceae) were among the most important plant families in almost all other studies of *Chiropotes*, despite the range of both habitat types and degree of disturbance across studies. In addition, the results of this study are consistent with those of previous researchers, who have shown that bearded sakis supplement their diet largely with ripe fruit and insects and, to a lesser extent, flowers. In most studies, bearded sakis have very rarely been observed eating leaves, although Ayres (1981) reported that leaves made up 7% of the diet of *Chiropotes albinasus* in Brazil.

However, the annual percentage of seeds consumed by bearded sakis in this study, as well as the percentage of seed consumption in certain months, was higher than almost any previous study of the species. One of the primary reasons for this discrepancy is likely the composition of the forest at this study site. As shown above and in Chapter 3, plant species bearing mature drupes with fleshy, edible mesocarp were relatively rare at this study site. Therefore, the availability of edible mature fruit was likely low, even during periods of high mature fruit availability. Sakis were probably limited in the amount of fruit they could consume. Instead, the forest at the study site (and elsewhere throughout Guyana) was particularly rich in plant species bearing fruit with mechanically protected but relatively soft seeds (ter Steege et al. 2006, Norconk and Veres 2011).

Another possible explanation for the increased granivory of this bearded saki group relative to others that have been followed may be the undisturbed and continuous forest at this study site. As shown in Chapter 1, the majority of previous studies of the genus *Chiropotes*, especially long-term studies, have been conducted on island habitats or in forest fragments (e.g., Bobadilla and Ferrari 2000, Peetz 2001, Setz et al. 2008, Boyle 2008, Boyle et al. 2009). While it is unclear why bearded sakis in fragmented forests would be more frugivorous, a recent long-term study of *Chiropotes sagulatus* in continuous forest in Suriname that is comparable to my own research showed equally high levels of seed consumption (Gregory 2011). In fact, Gregory (2011) reported that bearded sakis were even more granivorous, with seed eating ranging from a peak of 96% in the short dry season to 77% in the long dry season. She also found that they increased dietary breadth in terms of food type during periods of resource scarcity, such as during the long dry season, and that their most important plant families were Sapotaceae and Lecythidaceae. It is possible that the fragmented habitats of previous studies harbor higher percentages of fleshy fruited trees than the typical bearded saki habitat. Consistent with this hypothesis, several of these sites were much higher in species of the Moraceae and Burseraceae (Norconk 1996, Peetz 2001, Veiga and Ferrari 2006). These families are characterized by fleshy drupes and subglobose, edible fruits. Many colonizing species likely to be found in more open or fragmented habitats have similar fruits. However, this hypothesis requires further testing.

The most notable difference between the results of this study and previous research on bearded sakis is the high percentage of insect consumption in this study group. All previous studies have reported some insect consumption, and the annual percentage of insect feeding in this study was only slightly higher. However, only Veiga and Ferrari 2006 found similarly high levels of insectivory to that of the study group in September and October (Ayres and Nessimian 1982, Mittermeier et al. 1983, van Roosmalen et al. 1988, Frazao 1991, Norconk 1996, Peetz 2001, Boyle 2008, Gregory and Norconk 2010). As all studies of bearded sakis have also used scan sampling, this discrepancy is unlikely to be a result of methodological differences. One possible explanation is that the mass concentrations of edible caterpillars observed in this study were a rare event that caused insect predation to be particularly high in the year of this study. Although I was unable to test this particular hypothesis, I did note that the study group also consumed a variety of insects in addition to the caterpillars. Thus, even if caterpillars are excluded from the analysis, bearded sakis were still highly insectivorous during September and October (18% and 10% of feeding time, respectively). Due to the lack of data on the genus *Chiropotes*, especially in continuous forest, and the degree of behavioral flexibility of the genus indicated by the few studies there have been, the most parsimonious explanation may be that the ability to consume a large percentage of insects seasonally is a characteristic behavior of the genus. This is supported by the specialized insect foraging strategies of the sakis in this study.

Comparison with other primates

The ability to exploit seeds as a resource is an adaptation not limited to the pitheciines. Many species of catarrhine, and at least one non-pitheciine platyrrhine are known to incorporate a large percentage of seeds in their diets (Kinzey 1974, Shellis et al. 1998, Fashing 2007, Kirkpatrick 2007, Norconk and Veres 2011). Norconk et al. (2006) have argued that primates show four distinct methods for seed eating based on behavioral and morphological differences.

One method is extractive foraging, in which manual dexterity (and tools in the case of *Cebus* and *Pan*) are used to extract mechanically protected seeds. Primates employing this strategy generally lack dental adaptations specific to seed eating and, instead, rely on their behavioral adaptations as extractive foragers to access seeds. Examples of extractive seed eaters include *Cebus apella*, *Daubentonia*, and several species of baboon (Cartmill 1974, Kinzey 1974, Daegling 1992, Dumont 1995, Kitko et al. 1996, Shellis et al. 1998, Fragaszy et al. 2004, Sterling and McCreless 2006, Visalberghi et al. 2009, Norconk and Veres 2011).

Another strategy of seed predation, used by *Cercocebus* and *Mandrillus*, is durophagy, the use of powerful jaws and specialized posterior teeth to crush hard seeds from the forest floor (Norconk et al. 2006). This specialization allows these dietary generalists to eat a variety of food items, including large percentages of seeds in some cases (Chalmers 1968, Fleagle and McGraw 1999, 2002, Poulsen et al. 2001). Some species of baboons are even able to masticate seeds much harder (two or three orders of magnitude in some cases) than pitheciines (Norconk and Veres 2011). A third strategy is used by several species of folivorous primates, including *Propithecus* and many species of African and Asian colobines (Norconk and Veres 2011). The specialized bilophodont molars and well-developed shearing crests of these primates are primarily adaptations for folivory but allow them to be effective seed predators as well (Maier 1977, Kay and Hylander 1978, Lucas and Teaford 1994, Cuozzo and Yamashita 2006, Kirkpatrick 2007). For example, some species of *Procolobus* spend over 50% of their annual feeding time consuming seeds (Fashing 2007). However, these primates generally concentrate on only a few plant species for seed consumption and appear to lack specialized seed-eating adaptations *per se*. Instead, dietary specializations in these genera may be exaptations that allowed them to expand into seed eating niches (Norconk and Veres 2011 but see Koyabu and Endo 2010).

Norconk and Veres (2011) argue that almost all of the primate seed-predators that employ these three strategies rely on seeds as a secondary resource or a fallback food. While their various seed-eating adaptations provide them with valuable resources during periods of food scarcity, they generally prefer other food sources when those are available (i.e., mature fruit, young leaves, insects). In contrast, recent research on the pitheciines shows that they generally prefer seeds and consume them preferentially when available (Bowler and Bodmer 2011, Norconk and Veres 2011). This has led Norconk et al. (2006) to suggest that they are the only primates whose primary feeding adaptation is seed eating. Yet pitheciines show remarkable variability in the percentages of non-seed items that they incorporate in their diet. Some populations of *Pithecia*, especially larger bodied western Amazonian species, consume high percentages of leaves (up to 18% in some months; Peres 1993, Setz 1993, Homburg 1997, Norconk 1996). *Pithecia pithecia*, *Chiropotes utahickae*, and *Chiropotes satanas* rely on flowers for up to 20% of their diet (Veiga and Ferrari 2006, Santos 2002). *Cacajao calvus* and *Chiropotes albinasus* spend more than half their feeding time eating fleshy mature fruit (Ayers 1989, Aquino 1998). While the pitheciines are still among the least studied Neotropical primates, these recent studies suggest a tremendous flexibility in their foraging behavior.

The results of this study support this view and provide important insight into the feeding ecology of *Chiropotes sagulatus*. As suggested by Norconk and Veres (2011), they are clearly specialized sclerocarpic seed-eaters, able to exploit a wide variety of mechanically protected seeds and rely on them for a very high percentage of their diet. But bearded sakis are also generalists, showing a great deal of behavioral flexibility that is typical of most members of the primate order. *Chiropotes sagulatus* is able to exploit a tremendous diversity of food items and an astounding variety of food plant species. This ability allows bearded sakis to take advantage of plant species and food items as them become abundant. The diet of many primates, especially frugivores, is highly correlated with the resource abundance. When fruit becomes more widely available, they exploit it more intensively (van Roosmalen 1985, Ayers 1986, Chapman 1990, Stevenson et al. 1994, Di Fiore 1997). But the ability of bearded sakis to eat food items in a number of states of maturity (i.e., flowers, immature seeds, mature fruit) gives them a long temporal window for feeding not afforded to most frugivores. Because of their huge dietary diversity in plant species, bearded sakis are also less limited than many other frugivorous primates in the number of individual feeding trees available to them. Thus, the ability to effectively forage for insects, exploit flowers and mature fruit, and utilize their unique seed-eating adaptations allow bearded sakis to subsist in a lowland tropical rainforest environment that is characterized by resources that are patchily distributed in time and space.

Table 5.1. The top 100 species consumed by bearded sakis during the course of the study period, including the type of fruit and the food items eaten from them.

Common Name	Scientific Name	Family	Percent of Diet	Fruit Type	Parts Eaten
Ballata	*Manilkara bidentata*	Sapotaceae	11.55%	Drupe	Sd, MF, IF
Wamara	*Swartzia leiocalycina*	Fabaceae: Papilionaceae	11.48%	Pod, dehiscent	Sd
Sheu	*??*	??	7.49%	Capsule	Sd
A	*Prieurella* spp.	Sapotaceae	7.10%	Berry	Sd, MF, IF
Sincona	*Geissospermum sericeum*	Apocynaceae	5.60%	Drupe	Sd, MF, IF
Kokritiballi	*Pouteria cuspidata*	Sapotaceae	4.56%	Berry	Sd
Kabukalli	*Goupia glabra*	Goupiaceae	3.51%	Berry	MF
Marishiballi	*Licania densiflora*	Chrysobalanaceae	3.17%	Drupe	Sd
Black Kakerelli	*Eschweilera sagotiana*	Lecythidaceae	2.79%	Pyxidium	Sd
Dukaliballi	*Brosimum parinarioides*	Moraceae	2.74%	Pseudo	Sd
Maporokon	*Inga alba*	Fabaceae: Mimosaceae	2.69%	Pod, indehiscent	MF
Buruma	*Pourouma guianensis*	Moraceae	2.51%	Drupe	Sd, MF
Tibikushi	*Brosimum guianense*	Moraceae	2.25%	Pseudo	Sd, MF
Wina Kakerelli	*Eschweilera corrugata*	Lecythidaceae	1.79%	Pyxidium	Sd, Fl
Mora	*Mora excelsa*	Fabaceae: Caesalpiniaceae	1.67%	Pod, dehiscent	Sd
Mahicaballi	*Phyllanthus* spp.	Euphorbiaceae	1.30%	Capsule	Sd
Hiawaballi	*Tetragastris altissima*	Burseraceae	1.24%	Drupe	Sd
Smooth Leaf Kakerelli	*Eschweilera decolorans*	Lecythidaceae	1.15%	Pyxidium	Sd, Fl
Wadara	*Couratari guianensis*	Lecythidaceae	1.11%	Pyxidium	Sd
Kauta	*Licania alba*	Chrysobalanaceae	1.02%	Drupe	Sd
Suya	*Pouteria speciosa*	Sapotaceae	0.96%	Berry	MF, IF
Baboon Inga	*Inga cinnamonea*	Fabaceae: Mimosaceae	0.79%	Pod, indehiscent	Sd
Arrowpoint Tree	*??*	??	0.75%	Aggregate	Sd
Kokrite	*Attalea regia*	Palmae	0.72%	Nut	MF, IF
	Brosimum rubescens	Moraceae	0.67%	Pseudo	Sd, MF
Kaditiri	*Sclerolobium guianense*	Fabaceae: Caesalpiniaceae	0.64%	Pod, indehiscent	Fl, Sd
Asepoko	*Pouteria guianensis*	Sapotaceae	0.62%	Berry	Sd, Fl
Konoko	*Licania majuscula*	Chrysobalanaceae	0.54%	Drupe	Sd
	??	??	0.50%	Capsule, indehiscent	Sd
	Moutabea guianensis	Polygalaceae	0.49%	Drupe	Sd
	Sloanea acutiflora	Elaeocarpaceae	0.48%		Sd
Dukali	*Parahancornia fasciculata*	Apocynaceae	0.46%	Berry	Sd
Wallaba	*Eperua falcata*	Fabaceae: Caesalpiniaceae	0.44%	Pod, indehiscent	Sd
Kakerelli	*Eschweilera chartacea*	Lecythidaceae	0.43%	Pyxidium	Sd, Fl
	??	??	0.41%	Berry	Sd, MF
Rubber	*Hevea guianensis*	Euphorbiaceae	0.41%	Capsule	Sd
	Eschweilera simiorum	Lecythidaceae	0.38%	Pyxidium	Sd
	Helicostylia tomentosa	Moraceae	0.35%	Pseudo	Sd, MF
		Burseraceae	0.35%	Drupe	Sd
Kuyama	*Xylopa nitida*	Annonaceae	0.33%	Apocarp	Sd
Liquorice	*Pradosia schomburgkiana*	Sapotaceae	0.32%	Berry	Sd
	Eremoluma sagotiana	Sapotaceae	0.31%	Berry	Sd
Inga	*Inga bourgoni*	Fabaceae: Mimosaceae	0.30%	Pod, indehiscent	Sd
Haiariballi	*Alexa wachenheimii*	Fabaceae: Papilionaceae	0.28%	Pod, dehiscent	Sd

	Adenocalymna inundatum	Bignoniaceae	0.28%	Capsule, indehiscent	Sd
Sand Baromalli	*Catostemma fragrans*	Bombacaceae	0.26%	Capsule	MF, IF
Asepokoballi	*Pouteria caimito*	Sapotaceae	0.24%	Berry	Sd
	Gustavia augusta	Lecythidaceae	0.24%	Capsule, indehiscent	Sd
	Chrysophyllum auratum	Sapotaceae	0.23%	Berry	Sd
	Nemaluma engleri	Sapotaceae	0.23%	Berry	Sd
	??	??	0.21%	Drupe	Sd
	Arrabidaea nigrescens	Bignoniaceae	0.20%	Capsule, indehiscent	Sd
Asashi	*Rheedia* spp. 1	Guttiferae	0.20%	Berry	Sd
Smooth Skin Arara	*Guatteria spp.*	Annonaceae	0.20%		Sd
	Pradosia ptychandra	Sapotaceae	0.19%	Drupe	Sd
Crabwood	*Carapa guianensis*	Melastomataceae	0.19%	Capsule	Sd, Pith
Marishiballi	*Licania* spp.1	Chrysobalanaceae	0.18%	Drupe	Sd
	??	Lecythidaceae	0.16%	Pyxidium	Sd
	Iryanthera sagotiana	Myristicaceae	0.16%	Capsule	Sd
Swamp Corkwood	*Pterocarpus officinalis*	Fabaceae: Papilionaceae	0.15%	Pod, indehiscent	Sd
Congo Pump	*Cecropia* spp.	Moraceae	0.14%	Fruiting spike	IF, MF
	Macrolobium acaciifolium	Fabaceae: Caesalpiniaceae	0.14%	Pod, dehiscent	Sd
Monkey Pot	*Lecythis davisii*	Lecythidaceae	0.13%	Pyxidium, indehiscent	Sd
	Pachyptera kerere	Bignoniaceae	0.12%	Capsule	Sd
	Peritassa compta	Celastraceae	0.12%		Sd
	Schradera surinamensis	Rubiaceae	0.11%		MF
		Euphorbiaceae	0.11%		Sd
	Brosimum lactescens	Moraceae	0.10%	Pseudo	Sd
Inga	*Inga rubiginosa*	Fabaceae: Mimosaceae	0.10%	Pod, indehiscent	Sd
	Neoxythece dura	Sapotaceae	0.10%	Berry	Sd
Maho	*Sterculia rugosa*	Sterculiaceae	0.10%	Capsule	Sd
Huarusa	*Abarema jupunba*	Fabaceae: Mimosaceae	0.10%	Pod, indehiscent	Sd
Burada	*Parinari campestris*	Chrysobalanaceae	0.10%	Drupe	Sd, MF, IF
	Achrouteria pomifera	Sapotaceae	0.10%	Berry	Sd
	Monstera adansonii	Araceae	0.10%	Aggregate	IF, MF
	Odontadenia nitida	Apocynaceae	0.10%	Follicle	Sd
	Odontadenia macrantha	Apocynaceae	0.10%	Follicle	Sd
Manni	*Symphonia globulifera*	Guttiferae	0.10%	Berry	Sd
Duru	*Apeiba echinata*	Tiliaceae	0.09%	Capsule	Sd
Red Kauta	*Licania* spp.2	Chrysobalanaceae	0.09%	Drupe	Sd
	Memora flaviflora	Bignoniaceae	0.09%	Capsule	Sd
Red Ruri	*Chaetocarpus schomburgkianus*	Euphorbiaceae	0.09%		Sd
Nabbi	*Heteropsis jenmani*	Araceae	0.09%	Aggregate	MF, IF
Inga	*Inga pezizifera*	Moraceae	0.09%	Pod, indehiscent	MF
Kurihikuyuku	*Anaxagorea dolichocarpa*	Annonaceae	0.09%		Sd
	??	??	0.09%	Capsule	Sd
Shibidan	*Aspidosperma vargasii*	Apocynaceae	0.08%	Follicle	Sd
	Calycolpus spp.	Myrtaceae	0.08%	Berry	Sd
	Memora schomburgkii	Bignoniaceae	0.08%	Capsule	Sd
	Hyeronima laxiflora	Euphorbiaceae	0.08%	Drupe	Sd
	Pradosia spp. 1	Sapotaceae	0.07%	Berry	Sd, IF

	??	??	0.07%		Sd, FL
	Tetracera spp.	Dillenioaceae	0.07%	Follicle	Sd
	Couma spp.	Apocynaceae	0.07%	Berry	Sd
Hiponi	*Parkia pendula*	Fabaceae: Mimosaceae	0.07%	Pod, dehiscent	Sd
	Vochysia guianensis	Vochysiaceae	0.07%		Sd
	Pradosia spp.2	Sapotaceae	0.06%	Berry	Sd
Maniriballi	*Pithecellobium corymbosum*	Fabaceae: Mimosaceae	0.06%	Pod, indehiscent	Sd
Single Leaf Maho	*Sterculia pruriens*	Sterculiaceae	0.06%	Capsule	Sd
	Protium hostmannii	Burseraceae	0.06%	Drupe	Sd

Table 5.2. Plant families eaten by the study group ranked by percent of feeding time.

Family	Percent of Diet
Sapotaceae	27.52%
Fabaceae: Papilionaceae	12.50%
Fabaceae: Mimosaceae	4.41%
Fabaceae: Caesalpiniaceae	3.02%
Moraceae	9.10%
Lecythidaceae	8.53%
Apocynaceae	6.62%
Chrysobalanaceae	5.28%
Goupiaceae	3.60%
Euphorbiaceae	2.29%
Burseraceae	1.38%
Palmae	0.83%
Bignoniaceae	0.82%
Annonaceae	0.69%
Polygalaceae	0.54%
Elaeocarpaceae	0.49%
Guttiferae	0.31%
Bombacaceae	0.27%
Myristicaceae	0.24%
Melastomataceae	0.19%
Araceae	0.19%
Loganiaceae	0.18%
Sterculiaceae	0.17%
Celastraceae	0.15%
Rubiaceae	0.14%
Tiliaceae	0.09%
Simaroubaceae	0.09%
Myrtaceae	0.08%
Lauraceae	0.07%
Vochysiaceae	0.07%
Icacinaceae	0.06%
Sapindaceae	0.06%
Dioscoreaceae	0.04%
Humiriaceae	0.04%
Myrsinaceae	0.03%
Malpighiaceae	0.03%
Gentaceae	0.02%
Combretaceae	0.02%
Nyctaginaceae	0.01%
Unknown	9.84%

Table 5.3. Selectivity indices for the top 20 bearded saki food species.

Species	**% feeding time**	**RAI**	**Selection Ratio**	**Strauss' (L)**	**G**	**Sign.**
Manilkara bidentata	11.55%	0.99%	11.67	**0.106**	**60.97**	**$p < 0.001$**
Swartzia leiocalycina	11.48%	6.54%	1.76	**0.049**	**8.80**	**$p = 0.003$**
Sheu	7.49%	2.45%	3.06	**0.050**	**17.02**	**$p < 0.001$**
Prieurella spp.	7.10%	1.57%	4.52	**0.055**	**23.75**	**$p < 0.001$**
Geissospermum sericeum	5.59%	1.70%	3.29	**0.039**	**14.01**	**$p < 0.001$**
Pouteria cuspidata	4.78%	0.54%	8.85	**0.042**	**23.70**	**$p < 0.001$**
Goupia glabra	3.51%	0.27%	13.00	**0.032**	**19.97**	**$p < 0.001$**
Licania densiflora	3.17%	1.05%	3.02	**0.021**	**7.30**	**$p = 0.007$**
Eschweilera sagotiana	2.83%	2.52%	1.12	0.003	0.13	$p = 0.721$
Brosimum parinarioides	2.74%	1.69%	1.62	0.010	1.74	$p = 0.187$
Inga alba	2.69%	2.24%	1.20	0.005	0.29	$p = 0.588$
Pourouma guianensis	2.51%	1.27%	1.98	0.012	2.82	$p = 0.093$
Brosimum guianense	2.30%	1.15%	2.00	0.012	2.66	$p = 0.103$
Eschweilera corrugata	1.80%	2.04%	0.88	-0.002	0.11	$p = 0.739$
Mora excelsa	1.66%	4.59%	0.36	**-0.029**	**11.75**	**$p < 0.001$**
Phyllanthus spp.	1.53%	3.17%	0.48	**-0.016**	**4.66**	**$p = 0.031$**
Tetragastris altissima	1.24%	3.15%	0.39	**-0.019**	**7.04**	**$p = 0.008$**
Couratari guianensis	1.15%	0.10%	11.54	**0.011**	**7.11**	**$p = 0.008$**
Licania alba	1.11%	5.11%	0.22	**-0.040**	**24.47**	**$p < 0.001$**
Eschweilera decolorans	1.02%	3.00%	0.34	**-0.020**	**8.52**	**$p = 0.004$**

Table 5.4. Measures of bearded saki monthly dietary diversity. (H’) is the Shannon-Weiner index of dietary diversity, (E) is Pielou’s index of Eveness, (#Sp) is the total number of species eaten by the study group for that month, and the other 10 columns are the top 5 species eaten for each month and their proportion of the study group diet for that month.

Month	**H'**	**E**	**# Sp**	**Species 1**	**%**	**Species 2**	**%**	**Species 3**	**%**	**Species 4**	**%**	**Species 5**	**%**
Jan	2.26	0.60	42	*M. bidentata*	46.22	*Prieurella* spp.	7.19	*E. sagotiana*	7.07	*P. campestris*	6.95	*P. cuspidata*	5.36
Feb	2.42	0.58	64	*M. bidentata*	38.54	*Prieurella* spp.	17.79	*E. sagotiana*	9.88	*P. cuspidata*	3.78	*I. alba*	3.23
Mar	3.03	0.73	64	*Sheu*	16.98	*Prieurella* spp.	13.61	*I. alba*	11.89	*M. excelsa*	7.38	*E. corrugata*	6.63
Apr	2.58	0.64	55	*Sheu*	28.31	*G. sericeum*	19.66	*S.leiocalycina*	12.80	*Prieurella spp.*	4.55	*P. cuspidata*	4.38
May	2.68	0.67	55	*S. leiocalycina*	37.64	*G. sericeum*	10.31	*B. guianensis*	6.59	*Sheu*	5.03	*P. cuspidata*	3.36
Jun	2.53	0.64	51	*S. leiocalycina*	42.55	*G. sericeum*	7.89	*Sheu*	6.61	*B. guianensis*	4.87	*B. parinarioides*	4.19
Sep	2.41	0.71	29	*B. parinarioides*	26.63	*P. cuspidata*	18.30	*Phyllanthus* spp.	16.65	*?*	8.41	*C.fragrans*	4.62
Oct	2.92	0.75	49	*L. densiflora*	13.95	*B. parinarioides*	13.78	*P. cuspidata*	13.62	*Phyllanthus spp.*	11.41	*G. glabra*	7.57
Nov	2.54	0.68	41	*G. glabra*	38.10	*B. parinarioides*	9.72	*P. cuspidata*	6.52	*P. speciosa*	6.41	*L. densiflora*	5.36
Dec	2.76	0.74	42	*L. densiflora*	26.15	*G. glabra*	18.47	*P. speciosa*	7.22	*P. campestris*	4.30	*X. nitida*	3.82
G	12.2	10.40	**26.83**	-	-	-	-	-	-	-	-	-	-
p	0.20	0.32	**0.001**	-	-	-	-	-	-	-	-	-	-

Table 5.5. Coefficient of dispersion for the top 10 most important bearded saki food species.

Tree Species	Common Name	# feeding trees	Coefficient of Dispersion (40X40m quadrats)
Manilkara bidentata	Ballata	148	1.41
Swartzia leiocalycina	Wamara	179	1.42
	Sheu	181	1.43
Prieurella spp.	NA	143	1.23
Geissospermum sericeum	Manyokiniballi	177	1.70
Pouteria cuspidata	Kokritiballi	73	1.09
Goupia glabra	Kabukalli	47	1.16
Licania densiflora	Marishiballi	55	1.11
Eschweilera sagotiana	Black Kakerelli	90	1.31
Brosimum parinarioides	Dukaliballi	10	1.00
Total for all feeding trees		**2342**	**1.79**

Coefficient of dispersion > 1 indicates a clumped distribution. Coefficient of dispersion < 1 indicates a scattered or uniform distribution. Coefficient of dispersion = 1 indicates randomness.

Table 5.6. Physical characteristics of measured bearded saki feeding trees versus transect trees.

Statistic	**Dbh**	**Crown Volume**	**Height**
Feeding Trees (n = 1059)			
Mean	47.52	457.67	31.49
Std	20.00	317.41	5.51
Max	159.00	2985.20	49.00
Min	2.18	7.635	10.00
Transect Trees (n = 443)			
Mean	23.71	NA	16.00
Std	17.55	NA	8.40
Max	181.00	NA	4.00
Min	10.00	NA	46.00
Mann-Whitney results for differences in means			
U	74692.00	NA	84900.50
p	< 0.001	NA	< 0.001

Table 5.7. Characteristics of Bearded Saki Feeding Patches. Means for dbh and crown volume are means of totals of these measures for each feeding tree within the patch.

Patch Size	n	Dbh	CrwnVol	PQIdbh	PQI
50X50 (mean)	801	61.01	611.83	125.48	294.30
95%CI Lower		58.40	565.56	118.54	282.77
95%CI Upper		63.57	664.17	132.50	329.49
50X50 (Std)	801	38.97	732.11	100.39	342.17
100X100 (mean)	530	92.92	936.15	191.80	440.92
95%CI Lower		87.35	855.59	174.80	416.74
95%CI Upper		99.17	1021.29	204.46	492.79
100X100 (Std)	530	72.95	1021.08	164.74	435.26

Table 5.8. Characteristics of bearded saki food patches by Month.

Month (# of days)	Mean # feeding trees/day	Mean # patches/ day	Mean PQIdbh ($100m^2$)	Mean PQI ($100m^2$)	Mean PQIdbh ($50m^2$)	Mean PQI($50m^2$)
January	48.25	41.3	193.49	465.57	134.00	324.82
February	64.83	54.0	262.92	559.29	166.86	355.56
March	81.20	64.3	212.50	527.09	132.43	342.22
April	75.50	NA	NA	NA	NA	NA
May	77.00	57.7	260.44	598.35	142.06	326.37
June	82.67	53.0	229.22	521.66	126.07	286.91
September	37.00	29.3	87.61	211.84	69.82	169.70
October	35.00	31.7	112.99	330.19	88.77	340.86
November	45.60	37.3	153.84	429.03	95.07	265.13
December	63.33	40.3	122.04	325.26	88.99	237.17
G-value	**38.25**	**26.51**				
p-value	**< 0.001**	**< 0.001**				
Annual Mean	61.71	45.43	125.48	440.92	191.80	294.30

Figure 5.1. Schematic representation of the way food patches were defined in GIS for this study.

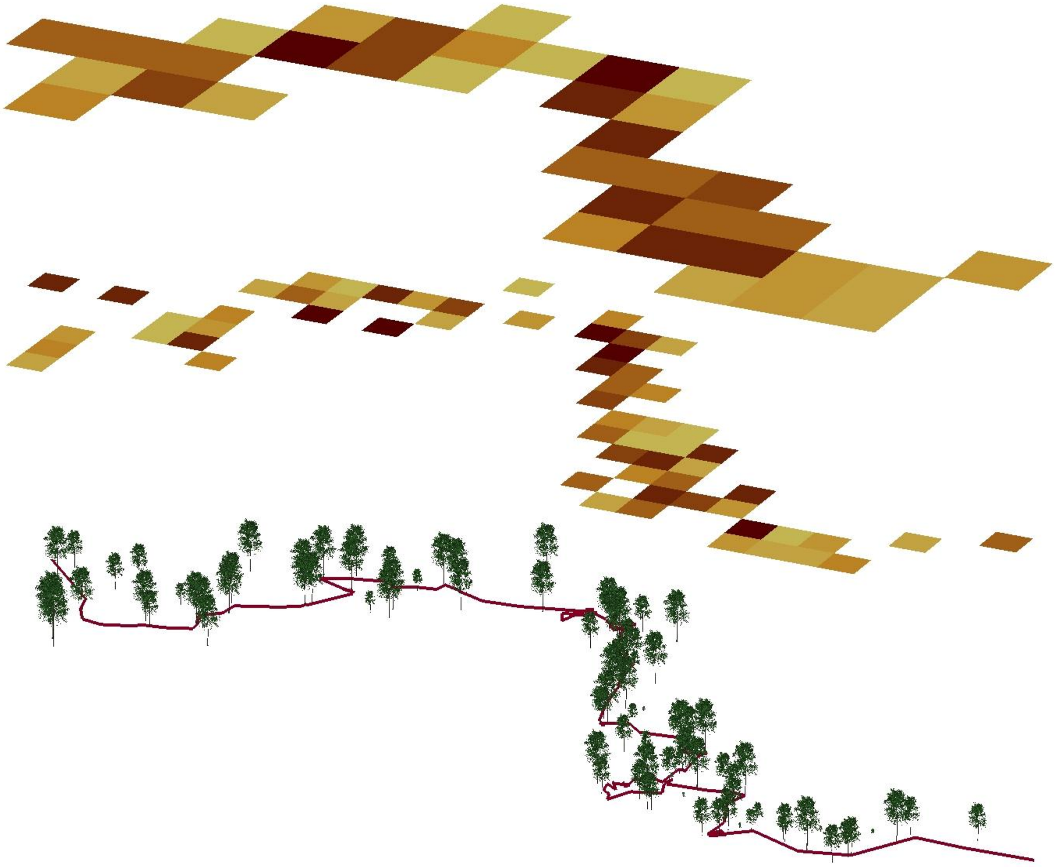
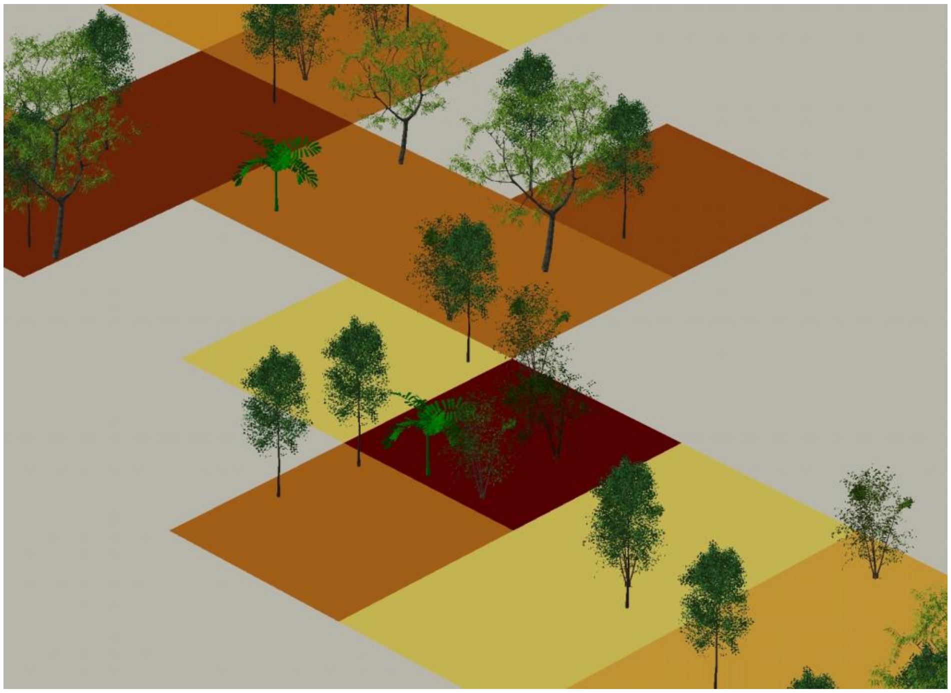


Figure 5.2. Three-dimensional representation of patch definitions for 50m (A) and 100m (B) spatial scales. Tree sizes are based on relative dbh sizes. Darker patches have higher patch quality scores (FAIDbh). Notice the central patch receives a high patch quality score because it contains several feeding trees, despite the relatively small sizes of these trees.

(A)



(B)

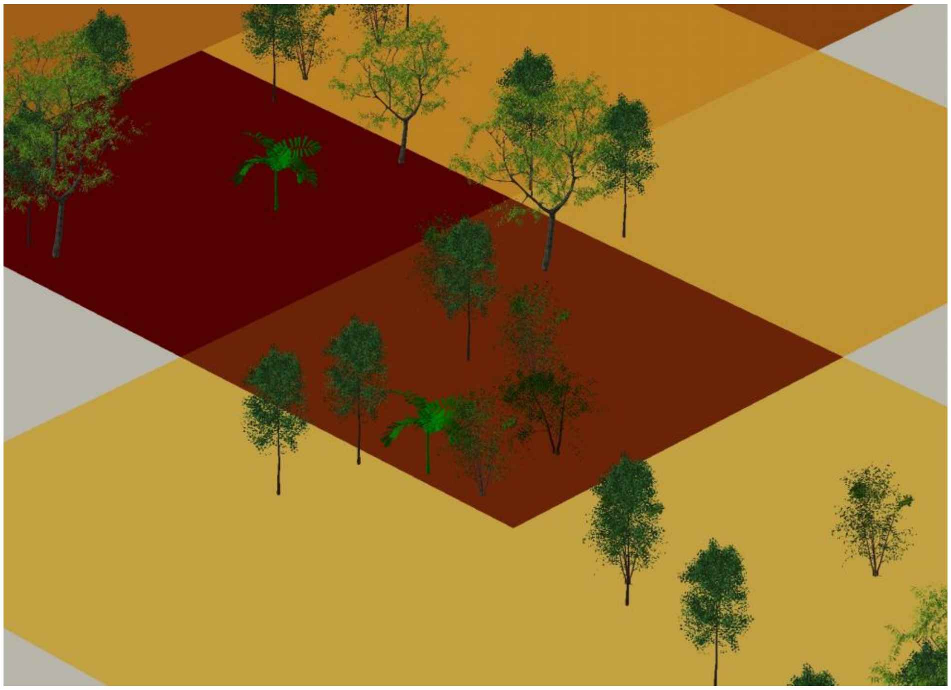


Figure 5.3. Annual diet by plant part for bearded sakis.

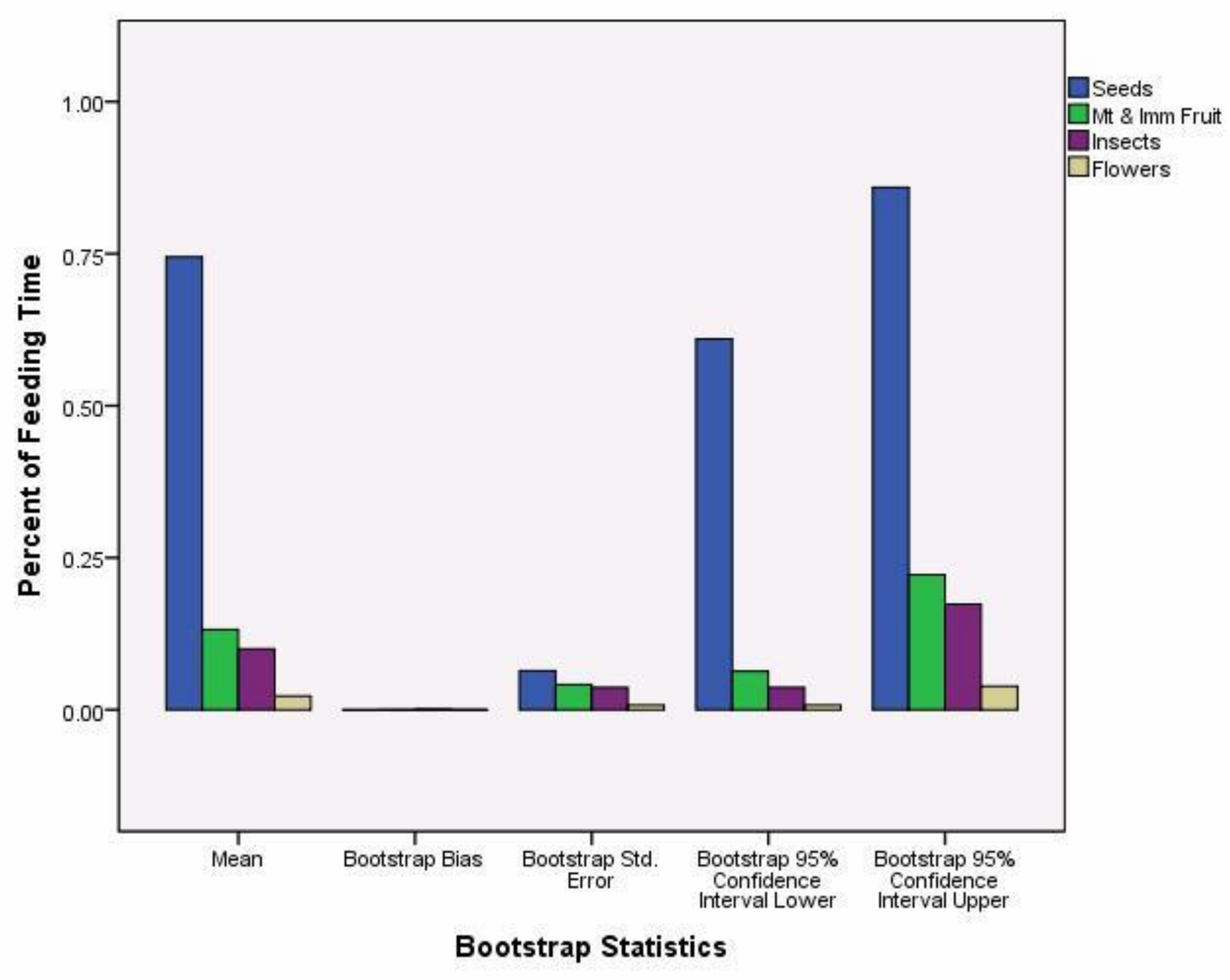


Figure 5.4. Change in time bearded sakis spent feeding on their top 10 plant species throughout the year. The ability of bearded sakis to exploit the same species for three months or more because of their ability to consume fruit/seeds in different states of maturity can clearly be seen.

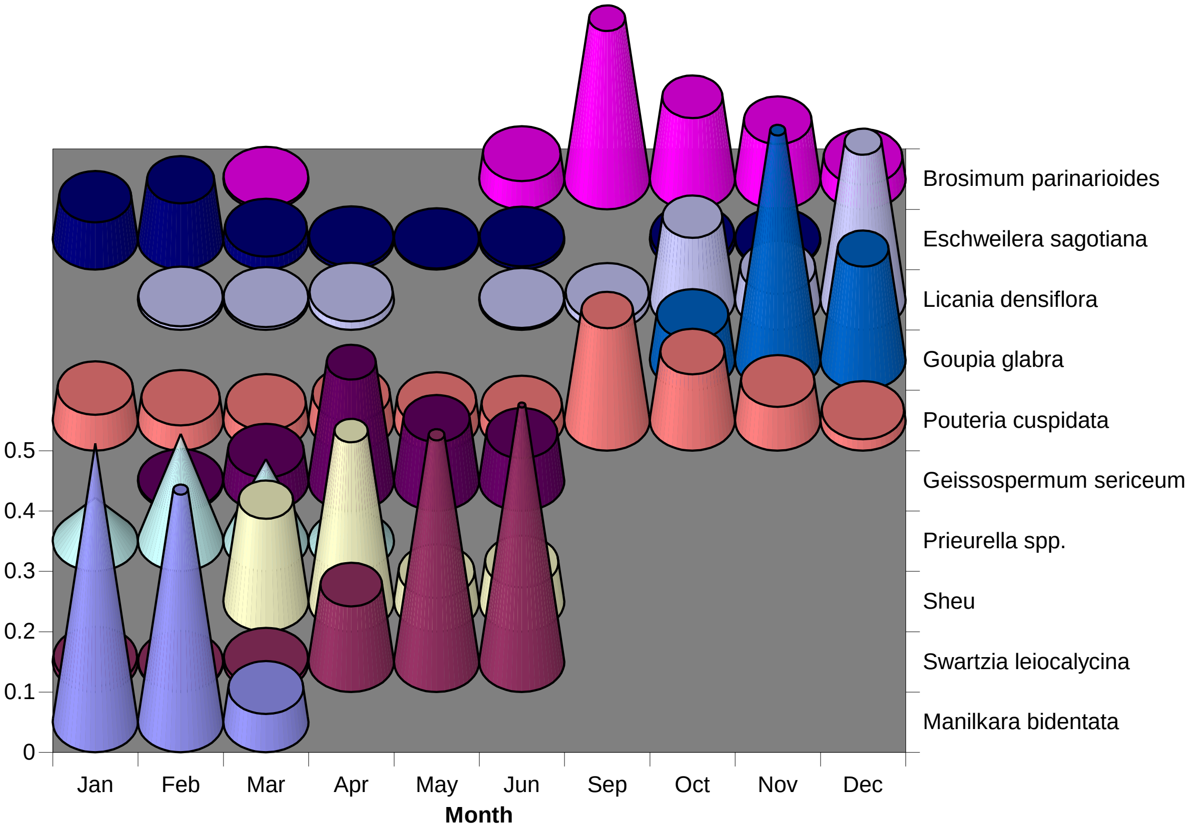


Figure 5.5. Diagram of 7 types of dry fruits and pictures of actual examples of each type eaten by the study group (Modified from Lawrence 1963). A) Samara (Acer) (*Chaunochiton kappleri*); B) Samara (Ptelea) (*Plerocarpus officinalis*); C) Follicle (*Odontadenia nitida*); D) Legume (*Eperua falcata*); E) Lomuntum (*Mimosa micracantha*); F) Capsule (*Gustavia augusta*); G) Pyxidium (*Coutari stellata*)

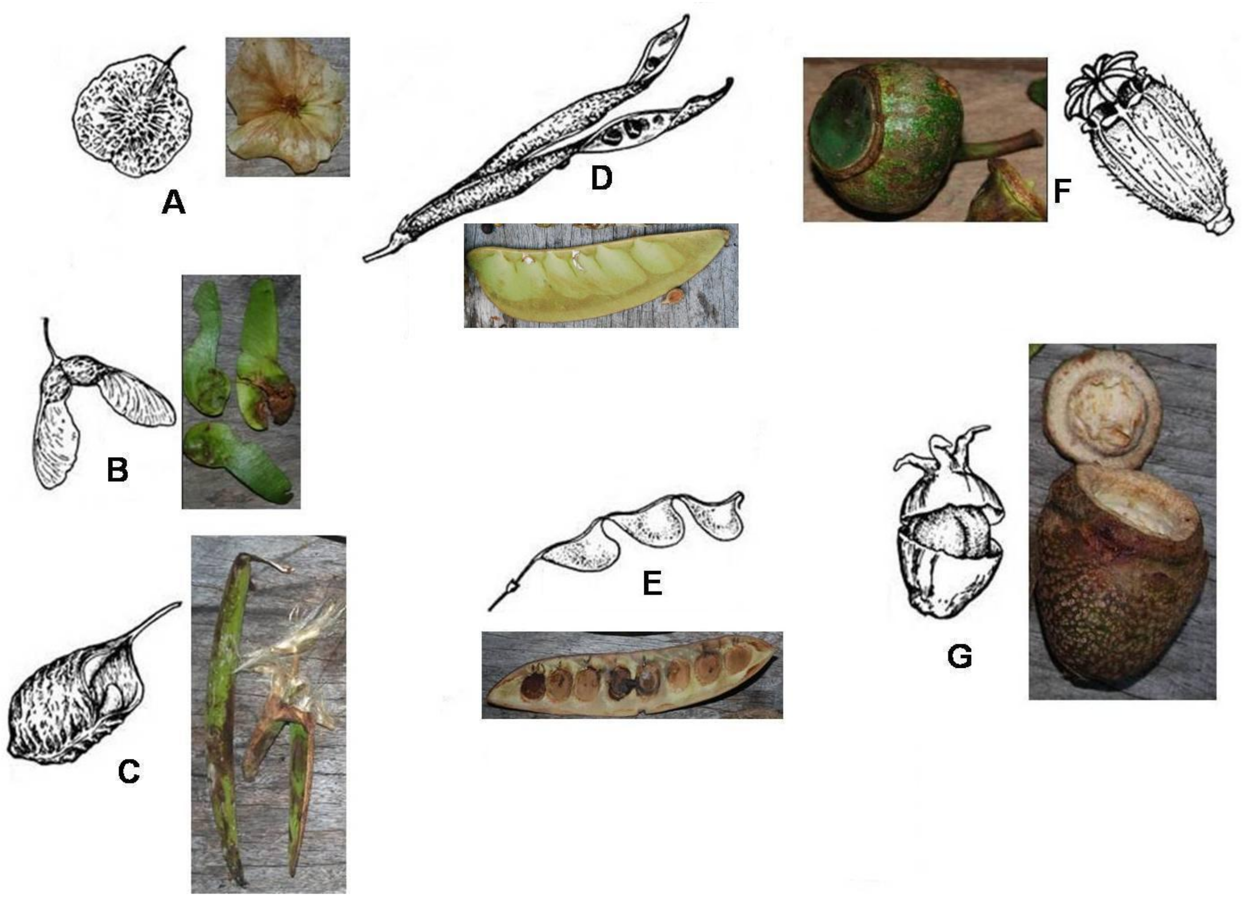


Figure 5.6. Diagram of Fleshy Fruit Types and examples eaten by the study group (Modified from Lawrence 1963). (A) Drupe (*Manilkara bidentata*); (B) Berry (*Goupia galbra*); (C) Aggregate Fruit (*Heteropsis jenmani*)

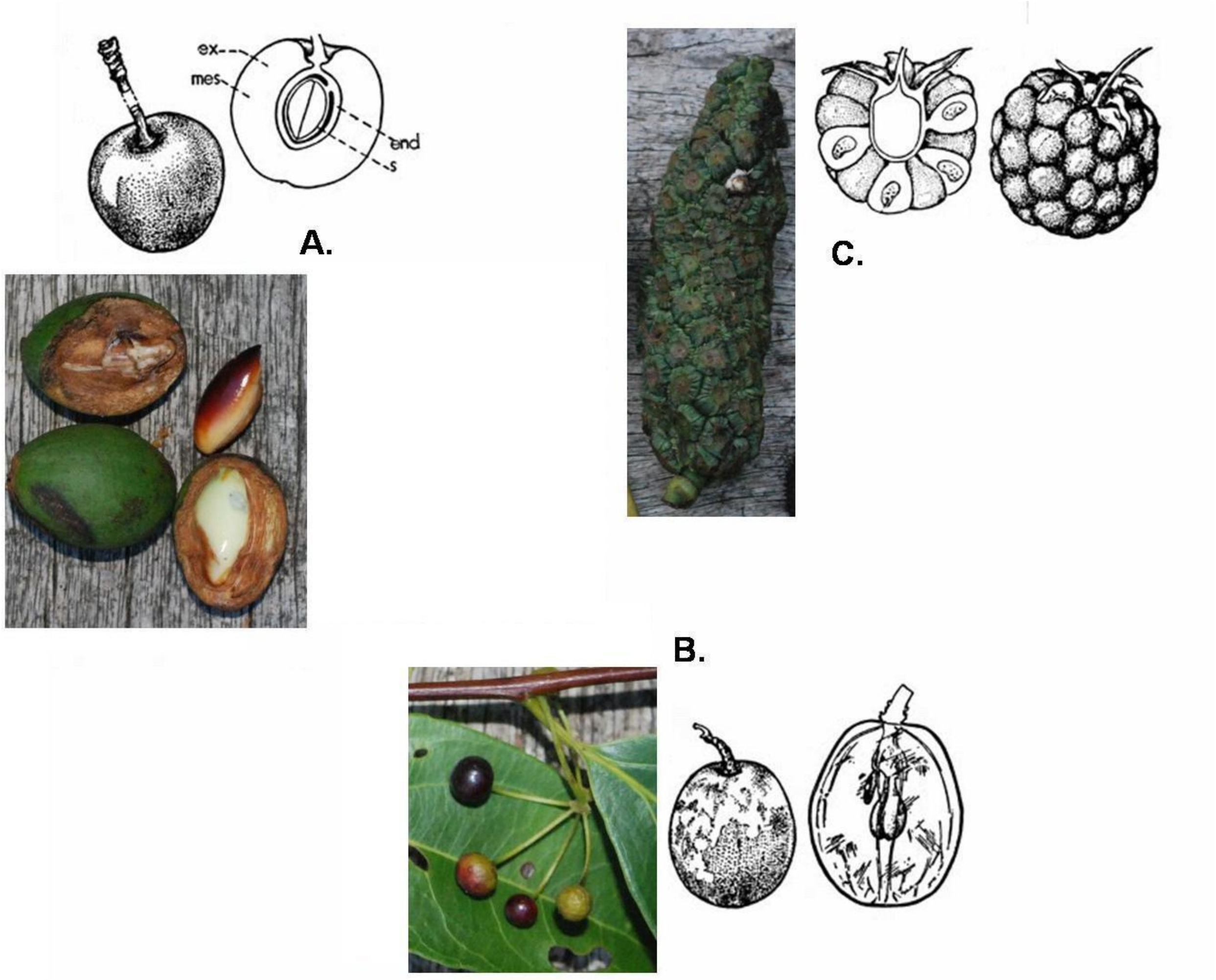
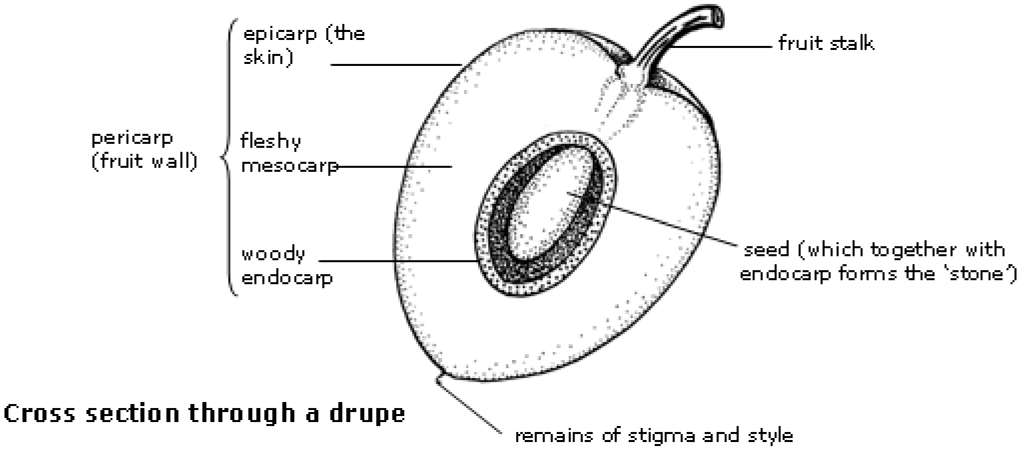


Figure 5.7. (A) Cross-section of a typical fleshy fruit showing fruit parts referred to in the text.(B) Cross section of a typical seed. (Modified from the Plant Science Image Database)

(A)



(B)

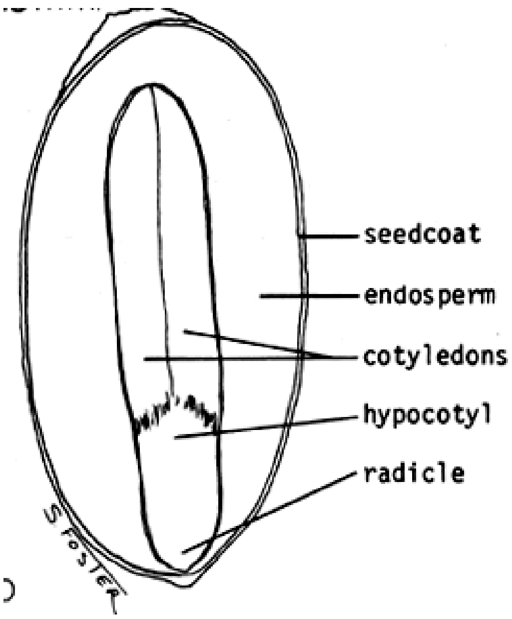
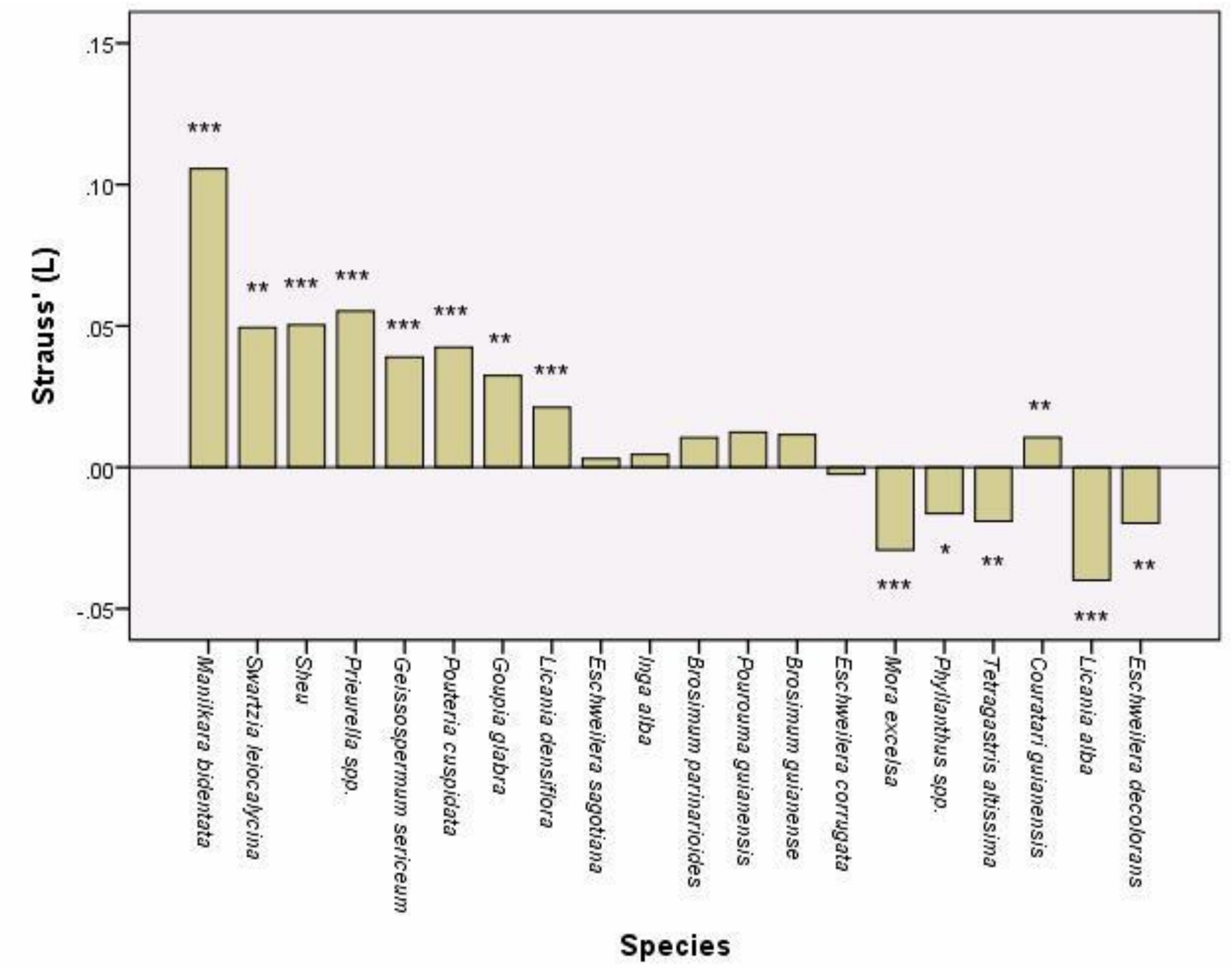


Figure 5.8. An *Eschweilera corrugata* (Lecythidaceae) fruit that has been split open by a bearded saki, revealing the soft seed. The seed was then removed by the individual and masticated.

Figure 5.9. *Pouteria speciosa* (Sapotaceae) fruit with the exocarp removed by a bearded saki. The sakis used their specialized procumbent incisors to scrape off the firm, adherent mesocarp. Sakis were not observed eating the seed of this species.

Figure 5.10. Fruit and seeds consumed over the course of a representative full-day follow in October. The fruits show the typical signs of bearded saki feeding, including crushed exocarps, husks ripped by saki canines, and pericarps scraped off with saki incisors.

Figure 5.11. Strauss selectivity indices for the top 20 bearded saki food species.



* indicates value of L is significantly different from 0 at the $p < 0.05$ level.

** indicates significance at the $p < 0.01$ level.

*** indicates significance at the $p < 0.001$ level.

Figure 5.12. Bearded saki feeding time by month.

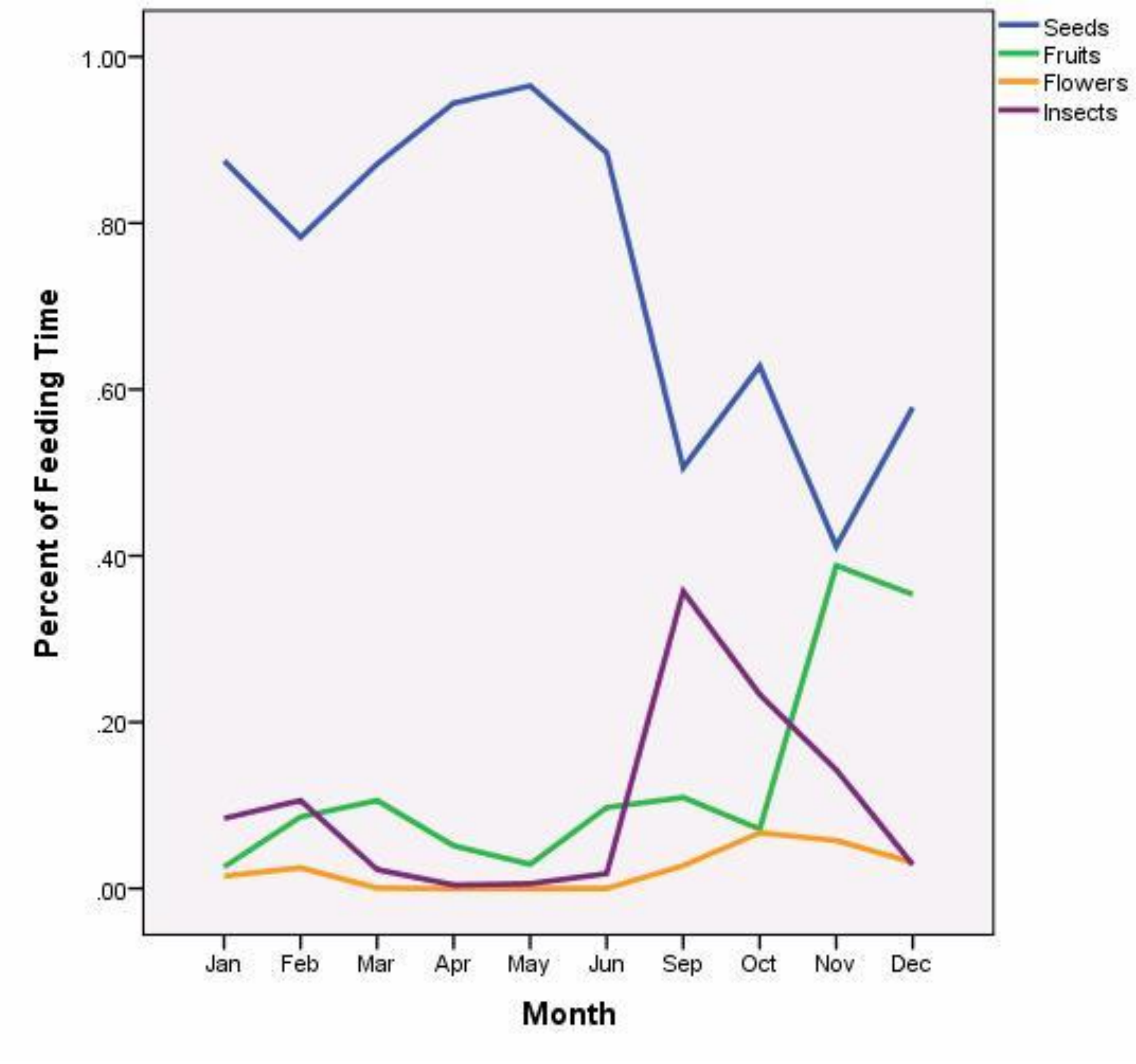


Figure 5.13. Monthly diet compared to monthly food abundance

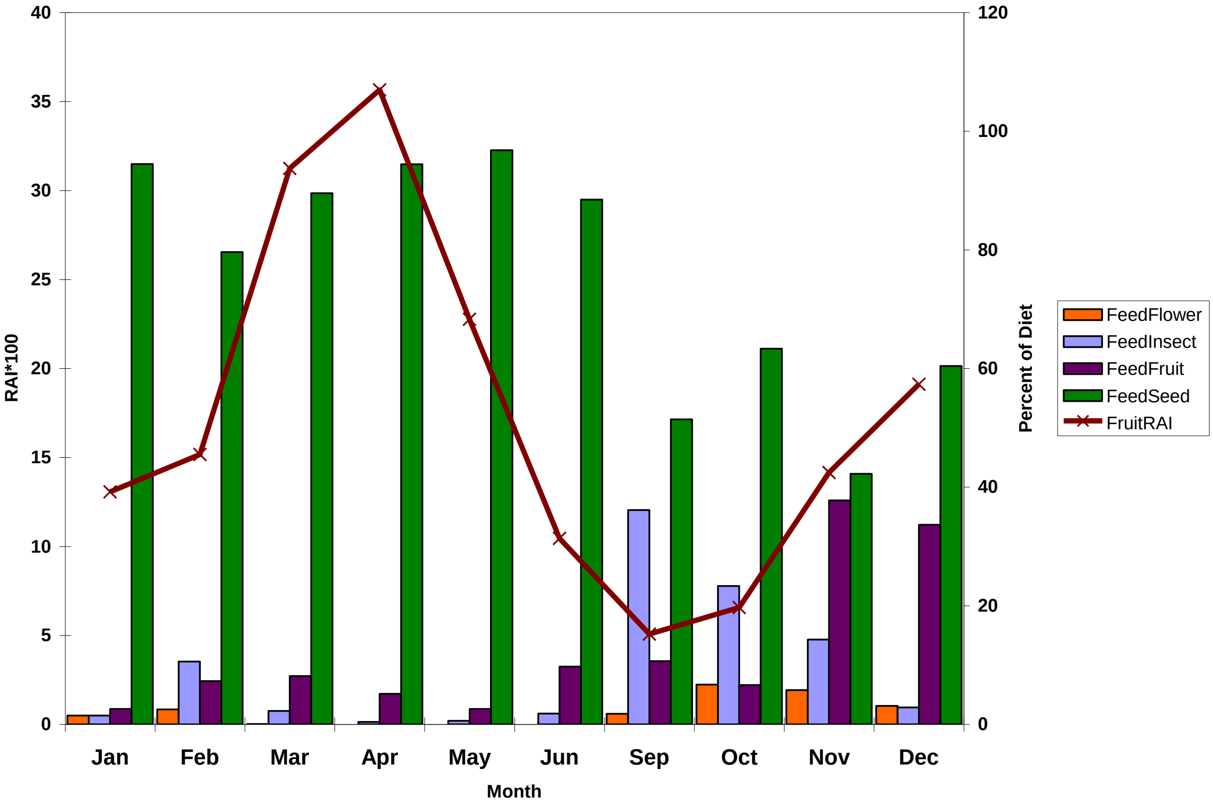
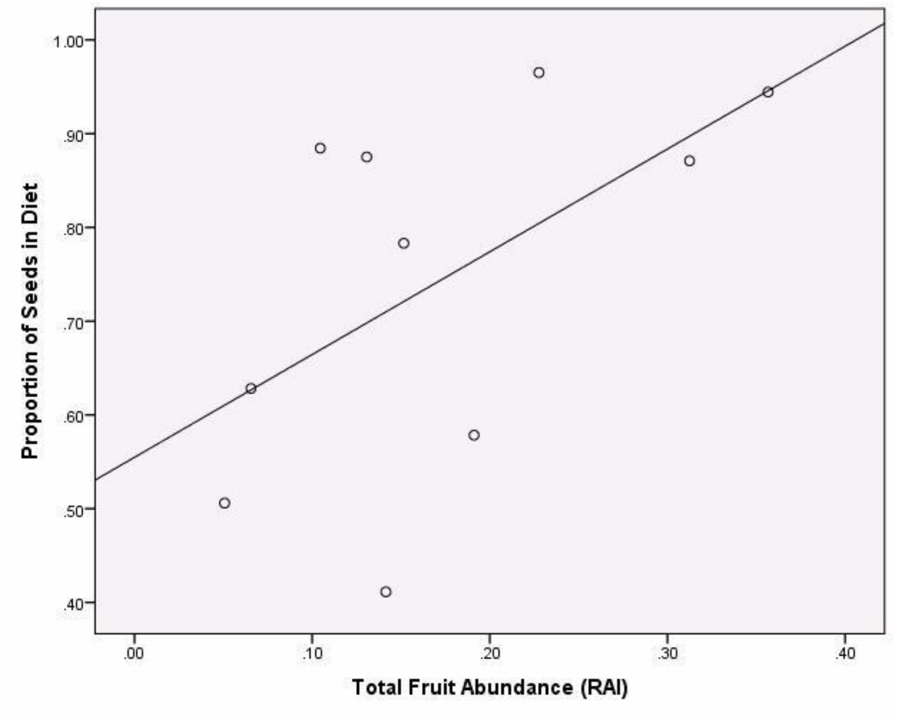


Figure 5.14. Monthly regressions between feeding time for two plant parts and measures of total fruit abundance (RAI). (A) Seed feeding by total fruit RAI; (B) Insect feeding by total fruit RAI.

(A)



(B)

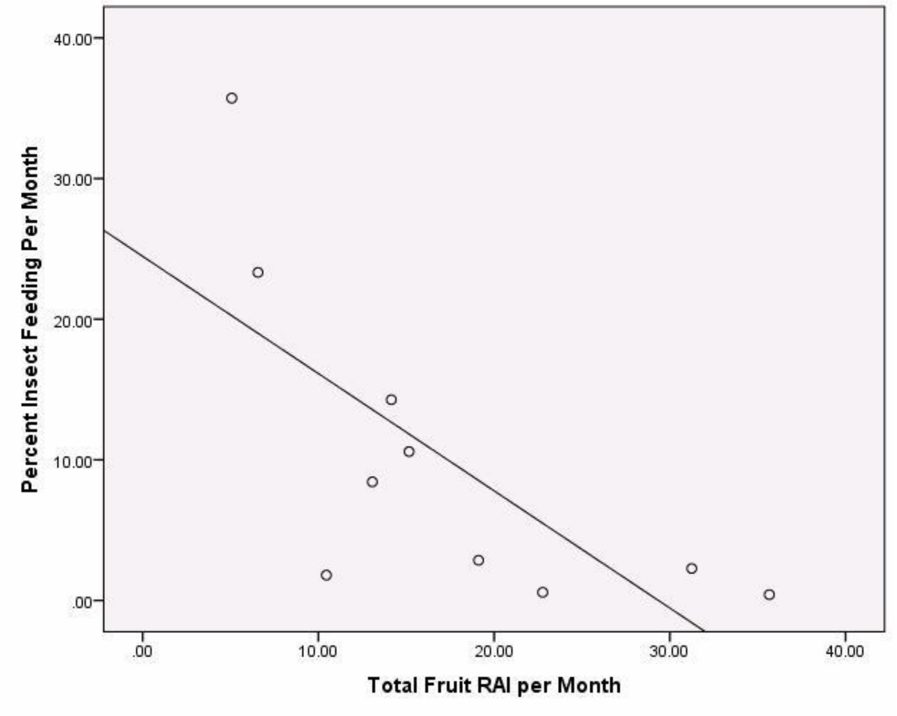


Figure 5.15. Caterpillars consumed in September and October by bearded sakis. These caterpillars were found in extremely high concentrations on certain large *Couratari guianensis* trees during these months. The caterpillar in the middle of the photograph has been masticated by a bearded saki.

Figure 5.16. Dietary diversity by month as measured by the Shannon-Wiener index of diversity (H') and Pielou's index of Evenness (E).

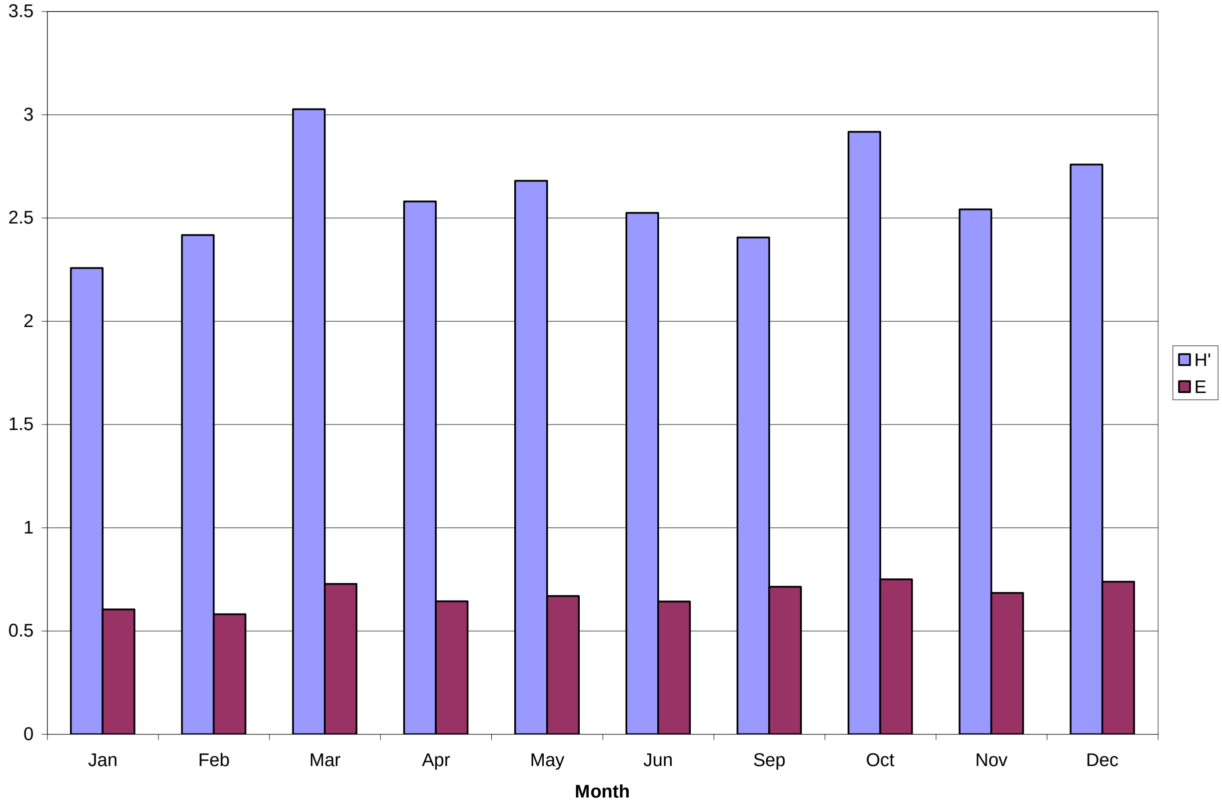


Figure 5.17. Map of all feeding trees used during the course of the study surrounded by the study group's home range (minimum convex polygon).

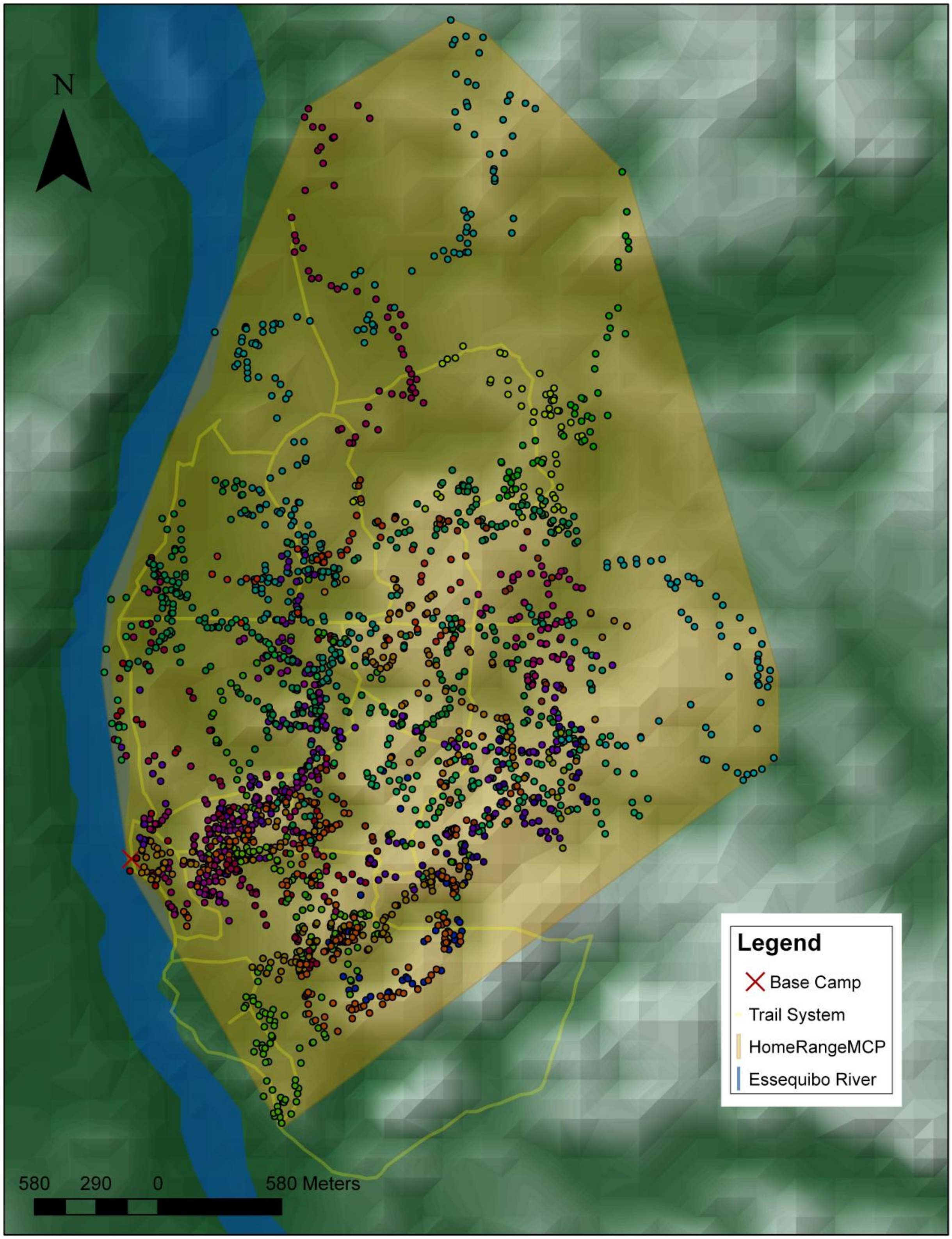


Figure 5.18. Map of all individual feeding trees of the top 10 plant species in the bearded saki diet.

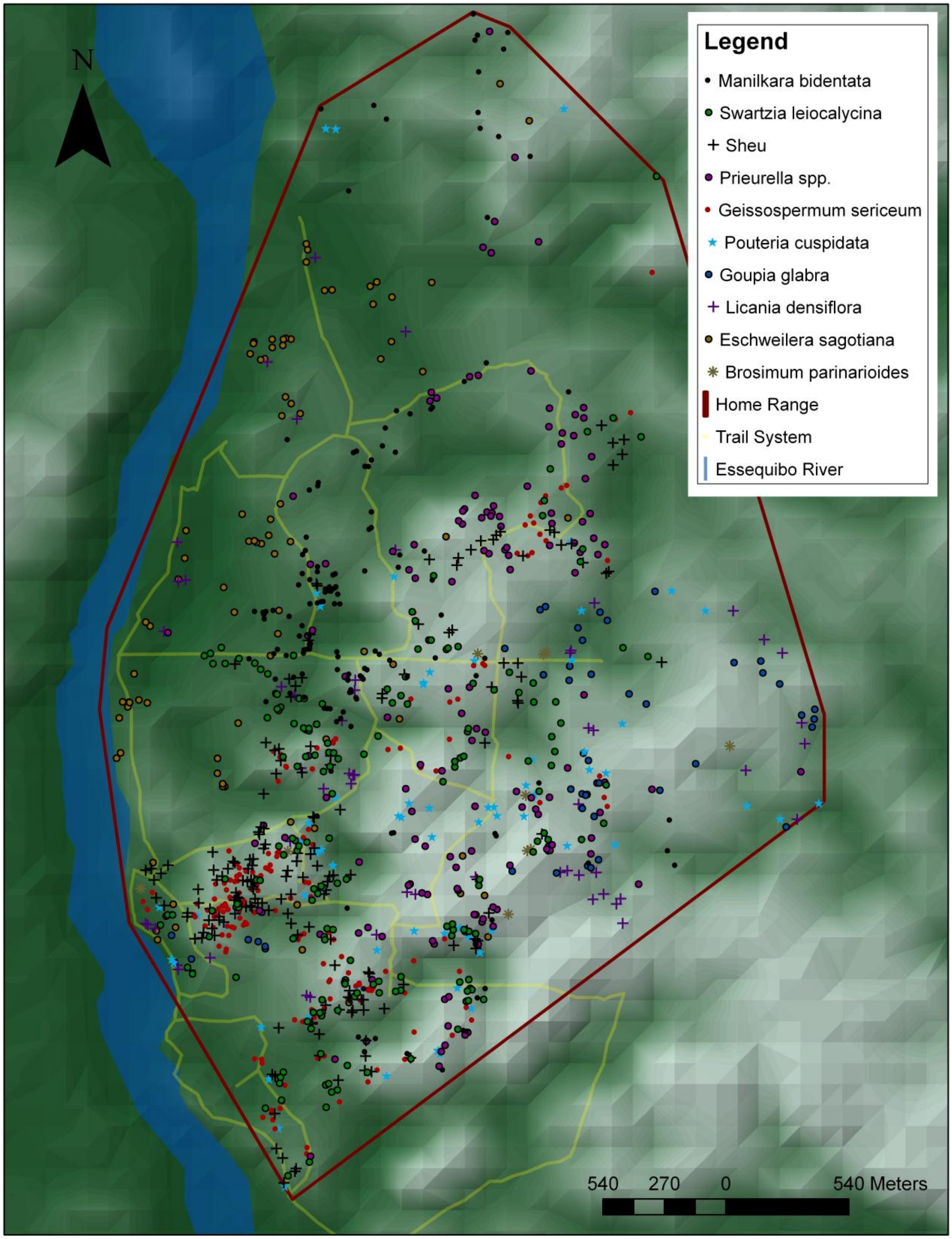
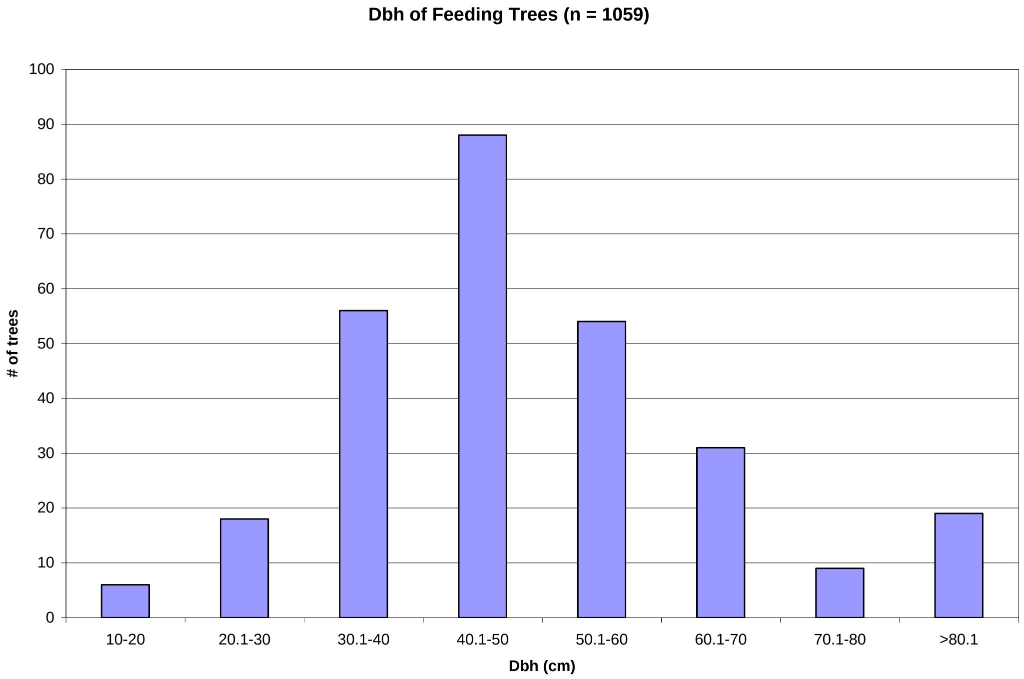


Figure 5.19. Frequency distributions of diameter at breast height (DBH) of (A) bearded saki feeding trees; and (B) transect trees showing the much larger sizes of feeding trees.

(A)



(B)

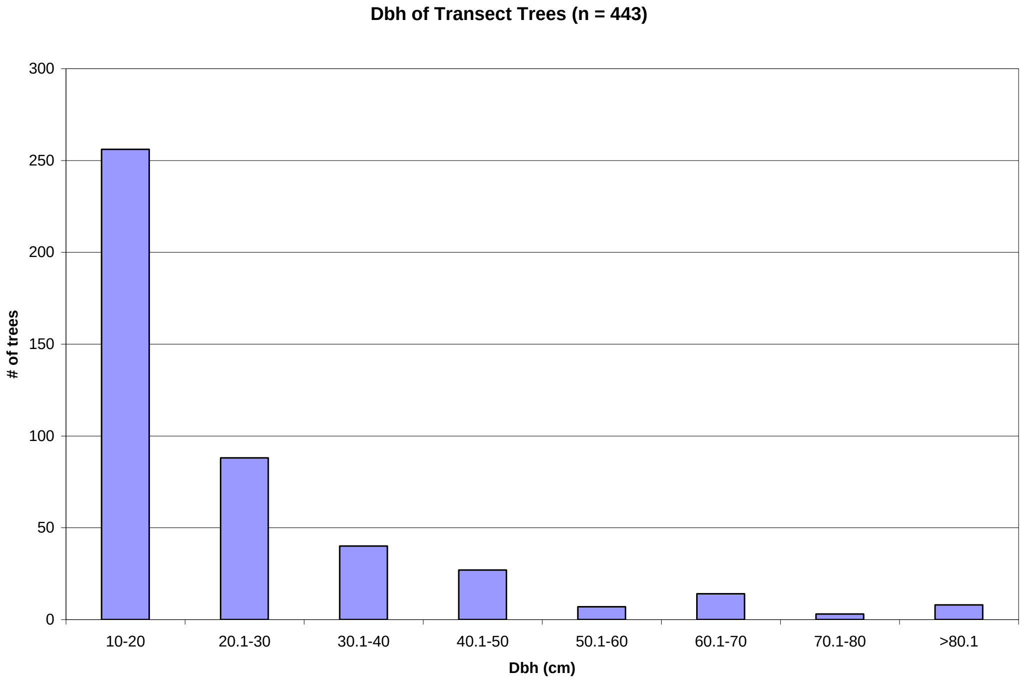
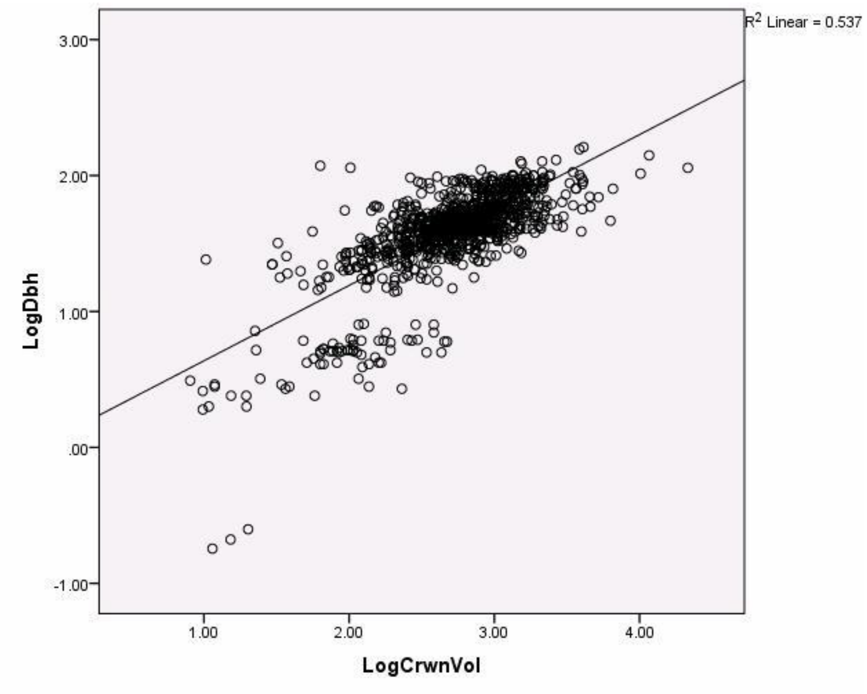


Figure 5.20. Diameter at breast height (dbh) by crown volume for (A) all measured feeding trees and (B) for the top 10 food species.

(A)



(B)

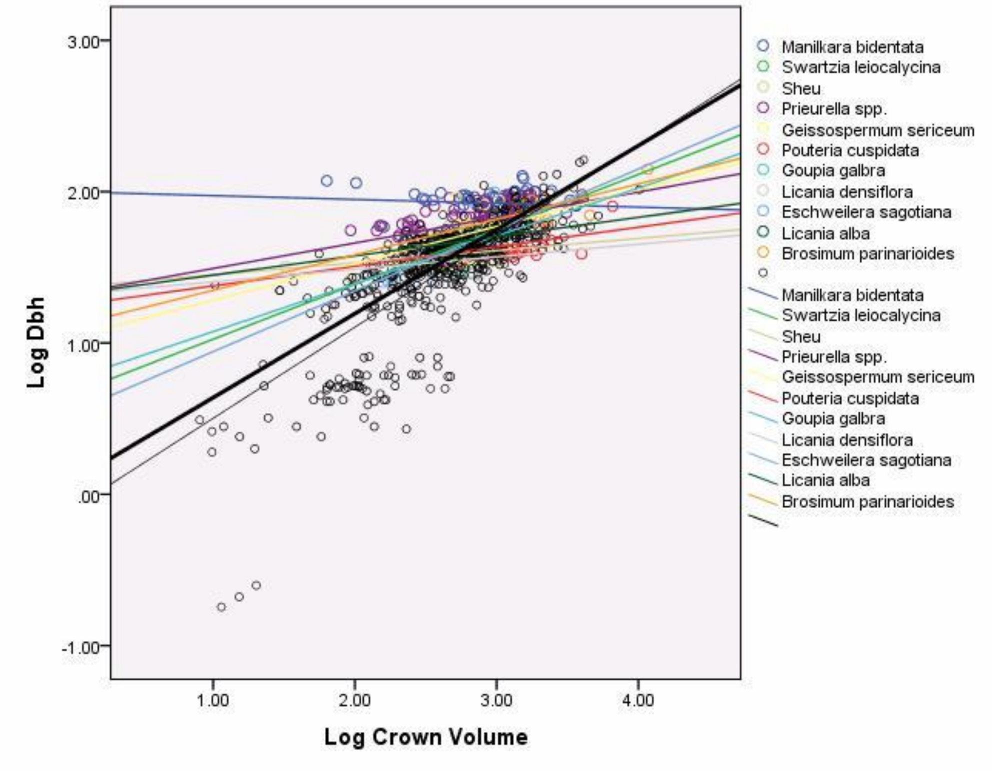
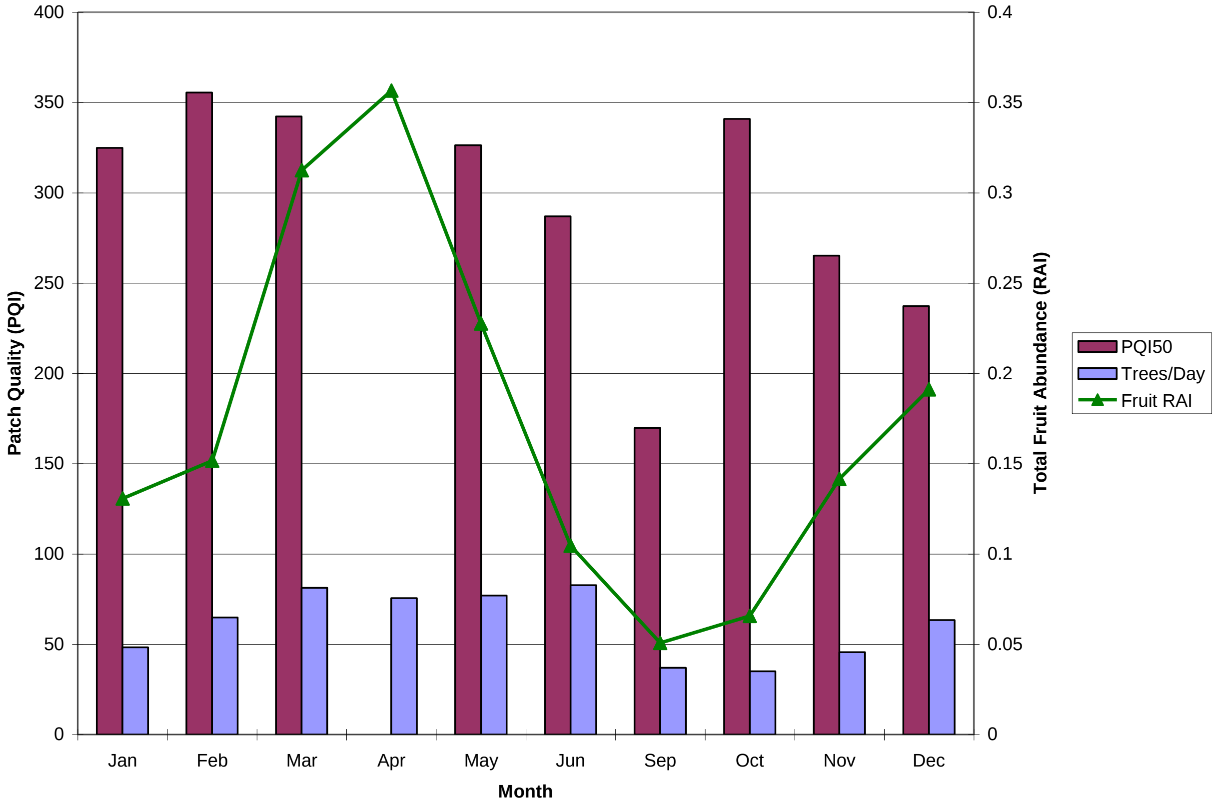


Figure 5.21. Number of feeding trees per day and mean food patch PQI (for 50m quadrats) by month compared to overall fruit availability.



CHAPTER 6 – RANGING BEHAVIOR, PATCH USE, AND GROUP COHESIVENESS

Introduction

Much of the research in primate ecology focuses on how primates move about their environment during the course of the year. Primatologists have long investigated the relationship between these ranging patterns and ecological variables (e.g., Milton and May 1976, Clutton-Brock and Harvey 1977, Leighton and Leighton 1982, Terborgh 1983, Symington 1988, White and Wrangham 1988, Chapman 1988, 1990, Strier 1989, van Schaik 1989, Janson 1992, Pinto et al. 1993, Phillips 1995, Sterk et al. 1997, Kirkpatrick et al. 1998, Koenig et al. 1998, Stevenson et al. 1998, Pruetz 1999, Chapman and Chapman 2000, Dias and Strier 2003). Central to most of this research has been a focus on feeding competition (both within and between groups) as the primary force dictating primate ranging behavior. While these studies have shown tremendous variability in ranging patterns across both primate species and study sites, primatologists have suggested several consistent patterns concerning the relationship between ranging behavior and ecological conditions. The first of these, as suggested by the Ecological Constraints Model (ECM), is that primate group size is positively correlated with both daily path length and home range size (Chapman and Chapman 2000). Using explanations derived from optimal foraging theory, researchers have hypothesized that the benefits of increased group size decrease at a slower rate than the costs of intragroup feeding competition for a finite set of resources (van Schaik 1983, Terborgh and Janson 1986, Janson 1988, Isbell 1991, Wrangham et al. 1993, Janson and Goldsmith 1995). As individuals living in large groups should suffer from increased intragroup feeding competition, they must travel further each day and use larger supply areas to meet the increased nutritional requirements associated with more individuals in the group. The second pattern is that home range size and daily path length are negatively correlated with habitat quality (Schoener 1971, Clutton-Brock and Harvey 1977). Individuals in primate groups that occupy less productive habitats are expected to have less food and, thus, range over larger areas to obtain the same amount of nutrients as groups living in more productive habitats.

However, other researchers have challenged the notion that these patterns hold across primates and that pervasive feeding competition is the primary driver of ranging behavior (Chivers 1991, Sussman et al. 2005, Sussman and Garber 2011). For example, Sussman et al. (2005) have suggested that primates use a variety of behavioral strategies to mitigate feeding competition and that competition may not be nearly as important in shaping primate sociality as has traditionally been assumed. These researchers have pointed to the tremendous behavioral flexibility of primates that buffers them against the effects of feeding competition. For example, primates appear to show a great deal of variability in the ways that they adjust ranging behavior during periods of food scarcity. While some primates appear to visit more food patches and increase foraging effort when resources are scarce, many other primates employ a strategy of energy minimization during periods of maximum food scarcity (Raemakers 1980, Milton 1981, Strier 1986, Nunes 1995). In addition, many species of primates form subgroups or increase group spread in response to resource scarcity. Subgrouping has been reported for a variety of primate species, although patterns of group formation, ranging, and group membership often differ among taxa (e.g., Dunbar and Nathan 1972, Ayres 1981, 1986, Pereira et al. 1988, Symington 1988, Chapman 1990, Kinzey and Cunningham 1994, Norconk and Kinzey 1994, Jamieson 1998, Garber et al. 1999, Swedell 2002, Dias and Strier 2003, Veiga et al. 2006).

While the fission-fusion social systems of *Ateles* and *Pan* have inspired a great deal of research in the primate literature, other patterns of group fissioning have received less attention.

Alternative patterns of subgrouping have been reported in a wide variety of primate species (*Papio papio*: Dunbar and Nathan 1972; Papio hamdryas: Kummer 1968, Sedell 2002; *Cercocebus albigena*: Waser 1997; *Cacajao calvus*: Ayres 1981, 1986; *Cebus apella*: Terbourgh 1983; *Varecia variegata*: Pereira et al. 1988; *Alouatta palliata*: Chapman 1990, Garber et al. 1999; *Macaca fasicularis*: Jamieson 1998, Sussman et al. 2011; *Lemur fulvus coronatus* and *Lemur sanfordi*: Freed 1998). In addition, several researchers have suggested that primates in otherwise cohesive groups may adjust group spread to mitigate intragroup feeding competition when feeding in low quality food patches. For example, Peres (1996) and Di Fiore (1997) suggested that woolly monkeys minimize direct feeding competition by spreading out over several feeding trees. Similarly, Dias and Strier (2003) reported that muriquis increase group spread when food patches decrease in size. For bearded sakis specifically, Norconk and Kinzey (1994) reported that groups of *Chiropotes sagulatus* in Suriname increased group spread when they entered food patches.

However, assessing the relationship between patch quality and group spread is limited in these studies by food patch definitions that do not account for multiple feeding trees. In addition, researchers have struggled with finding adequate measures of group spread that go beyond simple visual estimation. Quantifying exactly what is meant by group fissioning and how patterns of group fissioning vary within a species depending on differences in food availability and patch size is important for better understanding this common behavioral response to feeding competition. Further, expanding the ways in which a feeding “patch” is defined is necessary for a better characterization of the relationship between patterns of group fissioning and food abundance/distribution.

In this chapter, I describe the ranging behavior, group cohesiveness, and patch use of bearded sakis in Guyana. I begin by presenting home range size and use patterns and daily path lengths and how these vary seasonally. I then analyze bearded saki patch use and investigate the relationship between bearded saki cohesiveness and food patch quality. Finally, I compare the results of this study with other studies of bearded saki ranging behavior and the ranging patterns of other species of primates. The primary research question addressed in this chapter is:

Research Question 3. How do bearded sakis adjust group cohesiveness and food patch use in response to changes in food patch quality and monthly resource abundance?:

Based on the predictions of the ECM and previous research relating primate patch use and intragroup feeding competition, I developed four specific hypotheses relating to this question:

3. Sakis will spend more time feeding in higher quality food patches.

- Higher quality patches contain more total energy and are depleted at a slower rate than lower quality patches. Therefore, sakis should be able to feed longer in high quality patches before the costs of staying in the patch become higher than the costs of traveling to the next one.

4. Sakis will increase group spread in lower quality food patches.

- The ECM predicts that intragroup feeding competition will be lower in high quality food patches and higher in low quality food patches. Therefore, sakis should mitigate the effects of this competition by spreading out or fissioning.

5. Sakis will be more cohesive during traveling than during feeding.

- As intragroup feeding competition should be higher during feeding, sakis should be more cohesive when traveling.

6. Sakis will be more cohesive when resources are higher quality and more abundant and less cohesive when resources are of lower quality and more scarce.

    - Intragroup feeding competition should be highest during the months when resources are least abundant (in this study, the short dry season). Therefore, if group fissioning is a behavioral strategy that bearded sakis use to mitigate intragroup feeding competition, they should be less cohesive during this time. Similarly, bearded sakis should be less cohesive when monthly path quality is lower.

I also address:

Research Question 4. How do bearded sakis adjust their ranging behavior in response to seasonal variation in resource abundance? I hypothesize that:

7. Sakis will travel significantly further when patch quality is low.

    - Low quality patches contain fewer nutrients than higher quality patches. Therefore, groups feeding on lower quality patches will need to visit more of them to obtain the same number of nutrients as they would if feeding on higher quality patches.

Methods

Data Collection

During each five minute scan, I recorded the location of the approximate center of the study group using a handheld GPS unit (Garmin etrex VistaHCX). Despite the tall, closed canopy forest at the study site, GPS accuracy was very high, with location estimates almost always within four meters. GPS locations surrounding the study group were also obtained during five minute scans by two field assistants. This allowed for calculations of group spread every five minutes throughout the day. These estimates of group spread were more quantitative than simple visual estimates. GPS locations were then used for home and day range calculations.

Data Analysis

Home Range

There is an extensive literature on methods for producing the most accurate estimates of animal home range sizes (Worton 1987, Seaman and Powell 1996, Powell 2000, Rodgers and Carr 2002, Boyle et al. 2009). Due to the variability in estimates these methods produce, and the controversy regarding the most accurate method, four different methods were used for this study. They included the minimum convex polygon (MCP), grid, fixed kernel, and adaptive kernel methods.

The most commonly used method in primate studies, and the most simple, is the MCP method (Boyle et al. 2009). This method consists of constructing a polygon surrounding the peripheral points of a group such that external angles are greater than 180 degrees (Mohr 1947). Percent minimum convex polygon methods create polygons from a subset of total locations that is chosen using one of several percentage selection methods (Kenward 1987, Harris et al. 1990). The advantages of the MCP method include simplicity, applicability to comparisons with other studies, and their relative accuracy (but see Boyle et al. 2009). In this study, I used both 100% and 95% MCP estimates. These are commonly used percentages and facilitate interstudy comparisons. The 95% selection method is based on the amount of area each point contributes to the MCP (White and Garrot 1990).

The grid method of home range estimation consists of superimposing a grid (100 m^2 grids are commonly used for large home ranges) over the study area and assessing the total area of grids that contain GPS location points. This method was commonly used in primate studies prior to kernel analyses and is, therefore, important for comparisons with earlier literature (Mturi 1993, Stevenson et al. 1994, Di Fiore 1997, Fleury and Gautier-Hion 1999, Korstjens 2001, Boyle et al. 2009).

The kernel method of estimating home range size is a nonparametric statistical analysis that describes the probability of finding an animal at any particular locality (Worton 1989, Seaman et al. 1999, Powell 2000, Millspaugh et al. 2006). This method has generally been considered more accurate than MCP, although several authors have challenged this notion (Powell 2000, Pimley et al. 2005, Hemson et al. 2005, Boyle et al. 2009) In the past decade, it has become a commonly used method in primate studies (Boyle et al. 2009). Home range estimates are based on probability contour lines (isopleths) that are user defined (50%, 90%, and 95% are commonly used in ecological studies). These isopleths create polygons that enclose probability estimates for the home range utilization distribution. Kernel methods include both fixed kernel and adaptive kernel analyses. Fixed kernel analysis assumes that the width of the kernel placed at each observation is the same throughout the utilization distribution while adaptive kernel analysis allows kernel width to vary. However, as controversy exists over which of these methods is more accurate and which are appropriate for specific data distributions (Warton 1989, Seaman and Powell 1996, Boyle et al. 2009), I conducted both.

Daily Path Lengths

Estimates of daily path lengths were obtained by summing the distances between sequential five minute scan locations of the approximate center of the bearded saki group during 44 full-day follows. While this method allows for highly accurate estimates of the horizontal distance traveled, it does not incorporate any measure of vertical travel throughout the day. Therefore, daily path estimates are underestimates of the actual distance traveled. However, the study site was relatively flat so these estimates are likely to be relatively accurate. Most previous studies of primate ranging behavior have used fewer locations throughout the day (i.e., locations obtained every 10 or 15 minutes) to obtain daily path lengths. Because of this, the daily path lengths reported in this study are likely to be longer.

Group Cohesiveness

For the purposes of this study, I measured cohesiveness in three ways. First, I measured the spread of the saki group every five minutes throughout the day with the aid of two field assistants. The three locations for each five minute scan were then used to produce the maximum linear distance between any two of them (indicating the approximate spread of the study group). Group spread values were then assigned to 100 m and 50 m quadrats for GIS analysis (see below). In many cases, it was not possible to account for all members of the 65+ animals of the study group and it was clear that some individuals were located quite far away, over 2 km from the others. While group spread was still a useful measure of cohesiveness for the smaller foraging party where it was measured, it became clear that alternative methods of cohesiveness were needed to account for group spread that consisted of actual subgrouping.

The second measure of group cohesiveness I used quantifies subgrouping. For this measure, I used mean daily group size. Group size was generally based on a census conducted at the beginning of each full-day follow. This measure was assumed to be constant during the day, although it is possible animals left the main group in small groups (3-10 individuals) without being seen by me or my field assistants. Because of the large number of individuals in the study group, their spread, and their rapid travel, I was often unable to take counts throughout the day. When I was able to take multiple group counts during the course of a single day, they suggested daily group sizes were very consistent. This is contrasted with group spread, which changed throughout the day and was able to be reconstructed from the GPS values.

My third method for measuring bearded saki group cohesiveness was the average number of individuals per scan. This can be considered a gross measure of cohesiveness, as scans never included all individuals in the group. Smaller scans are likely to be more accurate than larger scans because it was easier to sample most of the group members when group sizes were smaller. Therefore, the variance in number of individuals per scan is likely less than the actual variance in group sizes.

GIS analysis

GIS was used to assess whether these measures of cohesiveness were correlated with food patch quality. Because of their ability to simultaneously analyze large amounts of spatial data, GIS represent powerful tools for analyzing the relationship between group cohesiveness and ecological variables. To model these relationships, grids of 100 m^2 and 50 m^2 quadrats were superimposed over each daily path taken by the study group. Each quadrat that the sakis traveled through received a group spread value based on the linear group spread distance of the saki group as they traveled through it. Figure 6.1 shows the results of this analysis for a representative (May 4th) daily path. Group spread quadrats were then superimposed over food patch quadrats to compare group spread and food patch quality (Figure 6.2). Figure 6.3 is a schematic diagram showing how the Geographic Information System was constructed. This analysis allowed me to test how group spread was affected by both the quality and spatial distribution of food patches, rather than analyzing the number of sakis in each feeding tree individually. For other measures of group cohesiveness, daily and monthly patch quality averages (see Chapter 5 for methods of patch definition) were obtained and compared to daily and monthly variation in group size and number of individuals per scan.

To analyze group cohesiveness during travel versus during feeding, I compared group spread averages in food patches (i.e., quadrats that contained at least one feeding tree) to group spread in quadrats where feeding did not take place. I also compared the average group spread during scans where the most common activity was travel versus during scans where the most common activity was feeding. To assess the relationship between patch quality and patch occupancy, I correlated the quality of a food patch and the number of five minute scans obtained in that quadrat. This provided a measure of total time spent in each feeding quadrat (i.e., food patch).

Results

Home Range and Core Areas

In Table 6.1, I show the home range estimates obtained for the study group using four different methods. Bearded sakis ranged over an extremely large area during this study (home range sizes between 722 ha and 1021 ha). Figures 6.4 and 6.5 show the home ranges obtained from these methods. Estimates were highly consistent, indicating that a home range size of approximately 1000 ha is an accurate estimate for the study group. Another indication of the accuracy of this home range estimate can be seen in a graph of the cumulative number of quadrats entered by the study group each month (Figure 6.6). This graph shows that the number of quadrats entered approached an upper asymptote. Not surprisingly, the grid method gave the smallest home range estimate and the adaptive kernel method produced the largest.

Kernel analysis of the bearded saki ranging pattern shows that the sakis did not use all areas of their home range uniformly. The study group used a core area (based on 50% of observations) that was much smaller (250 ha) than their overall home range size. In addition, there were several areas of the home range where the study group was never observed. It is possible that some of these areas consisted of habitat types not suitable for bearded sakis. For example, portions of the far western part of the home range contained an area of scrubby, dense, and extremely low forest. The sakis were never observed in this scrub and appeared to intentionally skirt around it during the day of travel when I observed them in this western region.

To assess seasonal variability in home range use, I used kernel analyses to calculate home ranges for all locations during two-month periods (i.e., January-February, March-April, etc.). Seasonal home range sizes are shown in Figure 6.7 and Table 6.2. I was not able to assess monthly variation in home range use because I deemed the number of full-day follows for each month insufficient for accurate estimates. Nevertheless, these two-month home ranges shed some light on how sakis changed their ranging patterns seasonally. Two-month home ranges were relatively consistent in size except for the January-February home range, which was almost as large as the home range for the entire 12-month study period. One possible reason for the huge home range size during these months is the preference of the study group for the seeds of their number one resource, *Manilkara bidentata*. During these months, sakis appeared to travel to the far reaches of their home range where there were high concentrations of *Manilkara* trees. For example, the study group traveled to the far north of their home range twice during this period but not during any other time throughout the study. One of these daily paths was the longest taken by the study group. This far northern portion of the home range contained several large *Manilkara bidentata* trees that appeared to be the focus of these daily paths as the study group traveled relatively quickly until it arrived in the *Manilkara* patch, upon which it fed for a long period and traveled very little after leaving. Most *Manilkara bidentata* trees stopped fruiting at the end of February and the species only fruits once every three or four years (Polak 1992).

The study group used the smallest total home range size and core areas during the short dry season (September through December), when resource abundance was lowest. Unfortunately, statistical analysis of this relationship was not possible due to small sample sizes.

Daily Path Length

In Table 6.3, I show the average daily path length of the study group for each month and for the total study period. In Figure 6.8, I show a map of the combined daily paths for all full-day follows. Bearded sakis traveled 4 km on an average day, with a maximum of 6.5 km and a minimum of 2.8 km. There was some monthly variation in daily path length, with sakis traveling the furthest distances in February (4.7 km) and the shortest in June (3.3 km). Variation in daily path length did show significant variation across months (Kruskal-Wallis test with month used as the factor $H = 20.28$, $p = 0.016$), but daily path length was not significantly correlated with total fruit availability ($\rho = 0.22$, $p = 0.533$) or average month patch quality (PQI for 50 m quadrats $\rho = 0.43$, $p = 0.244$; PQI for 100 m quadrats $\rho = 0.22$, $p = 0.576$).

Group cohesiveness

Means for the three measures of group cohesiveness are shown in Table 6.4. The mean group spread was 144.10 m, with a maximum of 1293 m, a minimum of 8 m, and a standard deviation of 179.89 m. Group spread showed significant hourly variation (Kruskall-Wallis test with hour used as the factor $H = 84.86$, $p < 0.001$; Figure 6.9). The study group would generally begin the day relatively cohesive, then spread out as the day progressed, and maximum group spread was usually recorded around noon or 1PM. Bearded sakis would gradually coalesce as dusk approached and would usually sleep in a cohesive group. Figure 6.10 shows this pattern for a typical full-day follow.

The mean foraging group size measured for the study group was 36.13 individuals, with a maximum of 65, a minimum of 6, and a standard deviation of 13.86. Mean number of individuals per scan was 16.24, with a maximum of 45, a minimum of 5, and a standard deviation of 6.72. Results of monthly variation in group cohesiveness are reported below in the context of addressing the specific research hypotheses.

Patch Quality and Group Cohesiveness

The first hypothesis—that sakis would spend more time feeding in higher quality feeding patches—was supported by the results of this study (Figure 6.11). Patch occupancy, as measured by number of scans, was significantly positively correlated with both PQI (50 m $r = 0.20$, $p < 0.001$; 100 m $r = 0.32$, $p < 0.001$) and PQIdbh (50 m $r = 0.23$, $p < 0.001$; 100 m $r = 0.41$, $p < 0.001$). However, when controlling for number of feeding trees per patch this relationship was much weaker (PQIdbh 50 m quadrats $r = 0.15$, $p = 0.001$; 100 m quadrats $r = 0.14$, $p = 0.004$).

On average, sakis spent 20 minutes and 45 seconds (mean of 4.15 scans) in feeding quadrats. Table 6.6 shows monthly variation in saki patch use.

The second hypothesis—that sakis would be more cohesive in higher quality food patches and less cohesive in lower quality patches—was not supported (Figure 6.12). Group spread was not significantly correlated with patch quality as measured by PQI ($r = 0.09$, $p = 0.063$) or PQIdbh ($r = 0.08$, $p = 0.090$) for 100 m quadrats or with PQI ($r = 0.07$, $p = 0.067$) for 50 m quadrats. While these results approached significance at the $\alpha = 0.05$ level and group spread was significantly correlated with PQIdbh for 50 m quadrats ($r = 0.11$, $p = 0.006$), the relationship was in the opposite direction of that predicted by the ECM. Group spread was actually greater in higher quality patches. Interestingly, this relationship became more pronounced when controlling for the number of feeding trees per patch (PQIdbh partial $r = 0.14$, $p < 0.001$). Therefore, it appears bearded sakis may be increasing group spread in higher quality patches simply because these patches are larger (in terms of crown area). Because I only measured group size once per day due to the contraints of estimating the numbers of so many monkeys, I was unable to assess the relationship between group size and patch quality for each individual patch.

The third hypothesis—that bearded sakis would be more cohesive during traveling than during feeding—was not supported by the results of this study (Figure 6.13). Mean group spread in feeding quadrats was 158.65 m while mean group spread in quadrats where no feeding took place was 170.65 m. These means were not significantly different (Mann-Whitney $U = 38584$, $Z = -1.58$, $p = 0.114$). Group spread did vary significantly by activity (Mann-Whitney $T = 12.30$, $p = 0.006$; Figure 6.10). However, this variation was dictated by social behavior, not feeding. Mean group spread was not significantly different during feeding versus other activities (T =

1.71, $p = 0.086$) but group spread was significantly lower during social behavior than during all other activities ($T = -5.16$, $p < 0.001$). Group spread during social behavior was approximately half what it was during any other activity (Figure 6.14).

To address the fourth hypothesis—that bearded sakis would be more cohesive during periods when resource availability was highest—I tested all three measures of cohesiveness with monthly total fruit abundance (RAI) and mean monthly and daily patch quality (PQI). It became clear during analysis that all three cohesiveness measures were necessary to ascertain how sakis adjust their grouping patterns each month. Group spread was not significantly correlated with either monthly fruit abundance ($\rho = 0.38$, $p = 0.308$) or monthly patch quality (PQI 50 m quadrats $r = -0.15$, $p = 0.576$; PQI 100 m quadrats $r = 0.11$, $p = 0.667$). Therefore, bearded sakis did not appear to adjust group spread as a way of decreasing intragroup feeding competition seasonally.

The two other measures of group cohesiveness show that bearded saki cohesiveness was related to overall fruit abundance and strongly related with food patch quality. Mean minimum group size and number of individuals per scan were positively correlated with total fruit abundance but these results where not significant for individuals per scan (Group size $r = 0.63$, $p = 0.050$; Indv per scan $r = 0.48$, $p = 0.165$) (Figure 6.15 and Figure 6.16). However, both minimum daily group size and number of individuals per scan were highly positively correlated with patch quality (see Table 6.7). These results were significant in all cases. In fact, patch quality explained between 50% and 72% of the variation in group size depending on how patch quality was defined (Figure 6.17, Figure 6.19). This indicates that patch quality was one of the primary determinants of subgroup size. The smallest subgroup sizes were observed during October and November (the period of maximum fruit scarcity), when bearded sakis would sometimes travel in groups of fewer than 15 individuals. Mean subgroup size during these months was approximately 25 individuals (Figure 6.18). These foraging parties would travel independent of one another for several days at a time. On the few occasions when more than one subgroup was located, groups were isolated by several kilometers. In contrast, subgrouping was rare in other months, when bearded sakis would often travel as a group of over 60 individuals. Mean group sizes between January and May were around 45 individuals. Given the difficulty of locating all group members, the true average group size during these months may well have been 60 individuals. Taken together, these results support Hypothesis 4.

Finally, the fifth hypothesis—that sakis would travel significantly further when mean daily patch quality was lower—was not supported. Mean daily path length was not significantly correlated with mean daily patch quality for either spatial scale (50 m quadrats PQI $r = -0.25$, $p = 0.333$; 100 m quadrats $r = -0.20$, $p = 0.442$) (Figure 6.20). In addition, mean monthly day range was not significantly correlated with total fruit abundance ($r = 0.33$, $p = 0.53$), with group size ($r = 0.29$, $p = 0.071$), or with number of individuals per scan for each day ($r = 0.25$, $p = 0.119$).

Discussion

The Bearded Saki Ranging Pattern

Optimal foraging theory predicts that primates faced with resource scarcity should modify their ranging behavior to deal with the increased intragroup feeding competition created by more patchily distributed resources. Researchers have suggested several ways primates can compensate for reduced feeding efficiency during lean months. For example, groups can increase daily path lengths and the number of feeding trees they visit. As less food is available in each tree/patch, individuals must visit more trees/patches to obtain the same amount of food as during times of more abundance. Alternatively, primates can broaden dietary breadth to include lower quality, less preferred food resources or change their rate of feeding in each patch. The sakis in this study did neither. They actually visited fewer feeding trees, visited lower quality food patches, and decreased daily path lengths during the short dry season. This suggests that intragroup feeding competition may not be the primary driver of bearded saki ranging behavior, despite a group size of more than 60 individuals. Sakis appear to mitigate the effects of intragroup feeding competition by breaking into independently-foraging subgroups during periods of maximum resource scarcity. This suggests that the highly fluid grouping behavior of bearded sakis is not dictated by feeding competition but rather adapted to avoid it.

The data presented above show that group spread in bearded sakis is not correlated with patch quality in a 1:1 relationship, i.e., for each individual food patch. The coalescence and fissioning of the group is not dictated by the characteristics of each patch that the group enters. Sakis do not appear to fission when they enter a low quality patch and then coalesce later in the day when they enter a higher quality patch, as would be suggested by optimal foraging theory. Rather, sakis subgroup into smaller groups that are relatively isolated from each other as a general behavioral strategy during the months when food scarcity is highest. During the short dry season, sakis simply divide into smaller groups that forage relatively independent of each other, and thus likely face little intragroup feeding competition. However, the size of these groups appears to be primarily determined by daily and monthly patch quality, rather than individual patch quality. My data indicate that group cohesiveness in bearded sakis is not so tied to ecological conditions that they are making hourly foraging and ranging decisions (i.e. when a patch is sufficiently depleted that the costs of remaining in it are higher than the travel costs of leaving and going to the next one) based on patch quality. Instead, sakis employ subgrouping seasonally as a more general approach to avoiding competition. While subgroup size appears to be primarily determined by daily and monthly patch quality, bearded sakis do not change group size on a patch to patch basis. Subgroup size is relatively stable, with group sizes usually remaining the same for several days.

Comparison with other studies of Chiropotes

Bearded sakis in this study ranged over a larger area, both in terms of home range size and daily path lengths, than virtually any other Neotropical primate and as large an area as any primate of comparable body size. All other studies of the genus *Chiropotes* have shown them to have large home and day ranges. Yet, both the daily path lengths and home range of this study group exceed previous estimates for the genus (Table 6.8). There are several possible explanations for this difference.

Most notably, as mentioned in Chapter 1, almost all previous studies of the genus have been conducted in fragmented or island habitats. These fragments range in size from 1-250 ha, representing the limits of the home range sizes of the groups that inhabit them. In addition, many other aspects of ranging behavior of these groups appear to be affected by their fragmented habitats. Researchers on bearded sakis in these types of habitat report shorter daily path lengths, increased reuse of feeding trees, and more circular movement patterns (e.g., Frazao 1992, Peetz 2001, Boyle et al. 2009). The little continuous forest data that is available on bearded sakis shows that the results of this study are likely representative of the normal ranging behavior for this genus in continuous forest (Boyle 2008, Gregory 2011, Veiga pers. comm.). For example, from only five days of observation Boyle (2008) found that a bearded saki group in continuous forest used over 550 ha. Similarly, Gregory (2011) reported a home range size of at least 600 ha for a group of *Chiropotes sagulatus* in Suriname. Finally, Pinto (2008) estimated *Chiropotes albinasus* in continuous forest used an area of over 1000 ha.

It is also possible that the larger size of the study group compared to previously studied groups of bearded sakis necessitated a larger home range. A positive correlation between group size and home range size has been suggested to be a consistent pattern throughout the primate order (see below). However, in this study, even during months when mean saki group sizes were comparable to those of other bearded sakis (i.e., September through December), home ranges were still very large. In addition, bearded saki daily path lengths did not correlate with group size. These results suggest that larger groups did not need to travel further than smaller groups in order to obtain the same amount of nutrients per individual.

If enormous home ranges and daily path lengths are characteristic of bearded sakis, this raises the question of why they need to range over such large areas. If they are able to exploit such a wide variety of plant parts and species, why can’t bearded sakis subsist in a much smaller supply area? One possibility is that these huge home ranges are simply a result of the extremely large sizes of bearded saki groups. There is an extensive literature suggesting a relationship between primate group sizes and home range size (Schoener 1971, Clutton-Brock and Harvey 1977, Dunbar 1988, Di Fiore 1997, Chapman and Chapman 2000, Sussman et al. 2005). Optimal foraging theory predicts that the addition of individuals to a group means that each animal will receive less food, assuming the total amount of food in the environment is held constant. Therefore, a larger group will have to travel over a larger area than a smaller group if ecological conditions are the same. However, many researchers have challenged the correlation between group size and home range size, both within species at different study sites and across the primate order (Chivers 1991, Dias and Strier 2003, Sussman et al. 2005, Sussman and Garber

2011). As mentioned above, there was not a significant positive relationship between group size and range size (either home or day range) for bearded sakis in this study. In addition, studies of smaller groups of bearded sakis have reported home and day ranges that are much larger than those of most other new world monkeys in similarly sized groups.

The results of this study suggest two other explanations for the huge home range sizes observed in the genus *Chiropotes*. First, bearded sakis must travel extremely far and feed from many different trees during the course of an average day to obtain the proper mix of nutrients from a heavily seed-based diet. Second, having an enormous home range increases the number of trees that will be fruiting at any one time for bearded sakis to access in a highly seasonal environment.

As mentioned throughout this thesis, bearded sakis are characterized by dental specializations for <u>accessing</u> mechanically protected seeds. It is unclear, however, if these dental adaptations are accompanied by a specialized gut morphology adapted to <u>digesting</u> seeds. As mentioned in Chapter 5, seeds often contain high levels of toxins and difficult-to-digest secondary fiber as protective mechanisms to avoid mastication. Unfortunately, there have been very few studies on the gut morphology of any of the pitheciines. What limited data are available suggest that bearded sakis have a relatively generalized gut morphology and have gut passage times similar to those of highly frugivorous primates (i.e., *Ateles*; Norconk et al. 2009). They clearly lack highly specialized adaptations like the sacculated stomachs of old world colobines, the complex small intestine of *Propithecus*, or the enlarged cecum of *Alouatta* (Milton 1984, Davies 1991, Lucas and Teaford 1994, Oats 1994, Norconk et al. 2009).

Bearded sakis may buffer themselves against harmful chemicals by concentrating on immature seeds, the defenses of which are less well developed. In all studies of the genus

Chiropotes, including this one, the monkeys show a strong preference for immature seeds. In addition, the mechanically protected seeds for which sakis demonstrate masticatory adaptations likely contain fewer secondary compounds than seeds lacking mechanical protection. Plants are limited in the energy they can devote to protecting their seeds and generally employ a strategy of either mechanical or chemical protection but rarely both (Esau 1977, Janzen 1978, Bell 1984, Kinzey 1992).

Nevertheless, the limited data available on the nutritional composition of pitheciine foods suggests that they do contain higher percentages of secondary compounds (especially fiber) than fleshy mature fruit (Ayers 1986, Norconk 1996, Norconk et al. 2009, Norconk and Veres 2011). Therefore, bearded sakis likely have to visit many different feeding trees to avoid ingesting too much of any one type of seed toxins/secondary compounds. By visiting the trees of many different species during the course of a single day (up to 26 in this study), they are able to balance their secondary compound load and obtain a sufficient nutrient mix. This hypothesis is supported by the fact that bearded sakis feed from significantly fewer trees during the months when the seed portion of their diet was lowest. This also explains why they do not feed for very long from any single tree or any specific food patch even when there are very high concentrations of seeds or patches are of high quality. The study group frequently left food trees despite there still being a lot of food available. They did not generally leave these trees full of seeds to socialize or rest, which might suggest they were satiated, but instead to travel to the next set of feeding trees. This explanation is consistent with a community ecology perspective, as trees would be unable to reproduce if bearded sakis ate all of their seeds before the fruits were ripe.

Studies of other primate seed predators also support this hypothesis. Most other primate seed predators preferentially select immature seeds (Cartmill, 1974, Kinzey 1974, Whiten et al. 1990, 1991, Daegling, 1992, Dumont 1995, Kitko et al. 1996, Shellis et al. 1998, Altmann 1998, Poulsen et al. 2001, Fashing 2007, Kirkpatrick 2007, Norconk and Veres 2011). This is especially true for non-colobine seed predators, like *Papio* and *Cebus*, which may be less well-adapted to consuming seeds high in secondary compounds (Kinzey 1974, Daegling, 1992, Dumont 1995, Kitko et al. 1996, Altmann 1998, Shellis et al. 1998, Fragaszy et al. 2004, Sterling and McCreless 2006, Visalberghi et al. 2009). While some colobine seed predators concentrate feeding on a few seeds, primates with less specialized gut morphologies appear to avoid consuming too many of any one seed species (Davies 1994, Norconk et al. 2009, Lambert 2011, Swedell 2011, Thierry 2011). Thus, the bearded saki ranging strategy of traveling very large distances and feeding from many individual feeding trees representing many plant species over the course of the day is likely a behavioral adaptation to buffer the effects of seed secondary compounds.

The need for an extremely large day range is partially explained by this need to travel long distances each day. However, it may also be explained as another bearded saki adaptation related to dietary flexibility. As shown in Chapter 5, the bearded saki's ability to eat from a tremendous variety of different plant species buffers them during periods of resource scarcity by providing them with access to fruiting species at all times of the year. Having a home range that incorporates a large number of micro-habitat types with a variety of different plant species increases the likelihood that some species will be fruiting. While tropical rainforest trees show general patterns of fruiting at certain times (e.g., most of the trees at this study site fruit from February to April), different plant species exhibit tremendous variety in phenological patterns, both annually and over the course of many years. Even during the short dry season, when very few plant species are fruiting, sakis have access to fruiting species within their extensive home range. They can simply adjust ranging patterns to more intensively utilize portions of their home range that have fruiting species.

Previous studies of bearded saki populations have suggested a high degree of variability in group cohesiveness across study sites (van Roosmalen et al. 1981, Ayers 1989, Norconk and Kinzey 1994, Ferrari and Lopes 1996, Ferrari et al. 1999, Peetz 2001, Veiga et al. 2006, Boyle 2008, Pinto 2008, Silva and Ferrari 2009, Gregory 2011). Some studies have suggested sakis travel in a relatively cohesive manner but fission upon entering food patches. Other researchers have reported a more regular pattern of subgrouping, with subgroups foraging independently of each other and maintaining their integrity for several days at a time. While all observers of *Chiropotes* have reported a certain amount of group fissioning, the specific pattern of subgrouping sakis exhibit appears to differ across studies. According to Norconk (2011: 139):

> We still do not know what it is about resource availability that affects group fissioning or determines the size of subgroups: Is it the relative abundance of fruit crops, availability of fruit-producing crowns of a particular size, seasonal availability of preferred foods like seeds driving either group dispersion or cohesion, diversity of fruiting species, or absolute (regional) fruit abundance.

The results of this study shed light on the likely reasons for these observed differences and provide a relatively clear picture of how saki cohesiveness varies according to ecological changes.

Norconk and Kinzey (1994) found *Chiropotes sagulatus* groups in Suriname to travel cohesively between “feeding patches,” then fission into subgroups that were up to several hundred meters apart. They contrasted this behavior with that of sympatric *Ateles* groups, which exhibited the typical fission-fusion pattern characteristic of the genus. The authors attributed this difference to the more clumped distribution of the saki feeding trees.

In his comparison of the feeding ecology of *Cacajao calvus* and *Chiropotes albinasus*, Ayres (1989: 711) reported that groups of *Chiropotes* generally foraged as a cohesive unit. He found that “group splitting is not infrequent, but the separation of individuals never exceeds a few hundred meters.” Even when feeding in trees with small canopy areas, groups remained relatively cohesive, with animals waiting in order to feed and individuals removing food and eating it in adjacent trees. Ayres proposed that the ability of *Chiropotes* to eat fruit in several stages of development allowed the monkeys to exploit larger food clumps than *Ateles* and led to their more cohesive pattern of foraging. In one of the only long-term studies of *Chiropotes chiropotes* ranging behavior, Peetz (2001) found sakis exhibited a similar pattern. The group in her study exhibited a foraging pattern of intensively exploiting a small area with several feeding trees for up to five consecutive days then traveling long distances to another food “patch.” When traveling between highly dispersed food patches, individuals generally traveled in single file, and group spread rarely exceeded 100 m.

In contrast, Frazao (1992) suggested a more regular pattern of fissions and fusions in a study of *Chiropotes satanas* in Brazil. Group fragmentation occurred throughout the day, during both travel and in feeding patches, with group spread reaching up to 300 m during travel. Like subgroups of *Ateles* and Pan, the composition and size of bearded saki subgroups varied. Similarly, Veiga et al. (2006) found that groups of *Chiropotes albinasus* and *Chiropotes satanas* were almost continuously fragmenting into two or more subgroups, although subgroup composition was highly variable. The authors concluded that group fusion was influenced by the availability and distribution of *Simarouba amara*, a patchily distributed food species exploited for immature seeds.

Norconk and Kinzey (1994) suggested groups of *Chiropotes sagulatus* traveled cohesively between food patches. Upon entering these patches, the group would spread out and individuals scattered over several hundred meters. They contrasted this behavior with that of sympatric *Ateles* groups, which exhibited the typical fission-fusion pattern characteristic of the genus. The authors attributed this difference to the more clumped distribution of bearded saki feeding trees. However, they did not attempt to quantify either a "food patch" or group spread. The sakis in my study clearly did not show a similar pattern. There are several possible reasons for this. First, it is possible that the pattern Norconk and Kinzey (1994) observed was a response of bearded sakis in Suriname to local ecological conditions that are different from those at my study site. I have already shown that bearded sakis display tremendous flexibility in feeding and ranging behavior in Guyana as ecological conditions change throughout the year. Therefore, it is likely that groups facing different local conditions in different habitat types (i.e., food patches of different quality with different spatial distributions from the ones at this study site) will employ different behavioral strategies. Unfortunately, the authors did not provide a clear definition of how they defined a food patch or estimated group spread so a quantitative comparison of the two studies is impossible. Additionally, the duration of their study was only two months so it is difficult to assess whether the pattern they observed was a temporary response to seasonal food shortages or a more consistent pattern throughout the year.

It is also possible that the pattern observed by Norconk and Kinzey (1994) is a result of the confusion and difficulty in following a large group of animals that are spread over a couple hundred meters or more and traveling over large distances. Group spread is a notoriously difficult measurement to estimate, especially for arboreal animals in a dark, closed canopy tropical rainforest with low visibility. In most previous studies of primate grouping patterns, researchers have simply estimated group spread visually, used nearest neighbor distances to approximate group spread, or used range finders to estimate spread from the approximate center of the primate group (e.g., Ayers 1989, Norconk and Kinzey 1994, Peres 1996, Di Fiore 1997, Veiga 2006).

Given these difficulties, it is possible that the pattern observed in this study could be interpreted as cohesive travel and less cohesive feeding. As the saki group moved in an amoeba-like fashion through their environment, it was often difficult for the lone researcher to perceive movement patterns or assess group cohesiveness. Often, I would be surprised to see field assistants who had originally been 300 m away following animals on the periphery of the group appear next to me 30 minutes later. I was often convinced the sakis had displayed a certain pattern of cohesiveness during a full-day follow, only to find that the group spread data collected by field assistants showed movements of individuals of whose presence I was completely unaware. Therefore, it became clear early in this study that without the aid of three GPS locations surrounding the group, it would be extremely difficult to adequately assess daily changes in group cohesiveness beyond gross estimates.

The other pattern of group cohesiveness reported by Frazao (1992) and Veiga (2006) is consistent with that shown by the study group during the short dry season. However, the sakis in this study traveled as relatively cohesive group of 65+ individuals for much of the year. This is clearly different from these authors’s observations of constant subgrouping throughout the year. It is possible that bearded sakis in fragmented or island habitats employ subgrouping as a response to more frequent food shortages in these disturbed habitats. As shown above, bearded sakis in this study respond to food scarcity, both in terms of overall fruit availability and the quality of visited food patches, by foraging in isolated subgroups that appear very similar to those reported by Veiga. As the habitat at her study site appears to be much less productive, it is not surprising that subgrouping would be much more frequent.

Interestingly, uakaris exhibit a pattern of group fragmentation that appears similar to that exhibited by the study group (Ayres 1986, Heymann 1992, Boubli 1994, Barnet et al. 2005, Bowler and Bodmer 2009). All studies of *Cacajao* have revealed some degree of fragmentation and group sizes for the genus are extremely high (up to 200 individuals). Like the bearded sakis in this study, uakaris appear to adjust group size seasonally, although the relationship between group fissioning and resource availability is unknown. Bowler and Bodmer (2009: 984) wrote:

> We suggest that uakari social “groups” in fact represent aggregations of smaller, stable social units of up to 10 or so individuals that regularly associate with other such units on a flexible short-term basis, forming the group sizes encountered. We furthermore suggest that uakari social units may not have fixed home ranges, but rather may range semi-nomadically over vast areas.

This is an intriguing explanation for the ranging behavior and group fragmentation patterns observed in the bearded saki study group. However, several differences between the study group and the behavior of uakaris indicate that bearded saki social structure does not fit this pattern. Bearded sakis in this study and throughout the UECC did not appear to form groups larger than approximately 65 individuals. This is much smaller than the group sizes reported for uakaris occupying a wide range of habitats. In addition, Bowler and Bodmer (2009) found that group size in uakaris was “highly flexible and did not appear consistent at any level, particularly over the long term.” This contrasts with the behavior of bearded sakis in this study, which appeared to maintain a group size of over 50 individuals for months at a time. Group sizes in this study were highly stable throughout the day and usually for several days at a time, regardless of whether they were large or small. Nevertheless, this short-term aggregation hypothesis for bearded saki social behavior certainly deserves further testing.

Comparison with other primates

The question of how groups respond behaviorally to the decreased foraging efficiency expected during seasonal food shortages is among the most studied in primatology. Researchers have focused on the way frugivorous primates exploiting already patchily distributed resources adjust daily path lengths, time spent traveling, patch occupancy, and grouping patterns when these resources become even more patchily distributed. Many studies have shown that primates buffer themselves from the costs of competition by increasing group spread or subgrouping (Dunbar and Nathan 1972, Ayres 1981, 1986, Pereira et al. 1988, Symington 1988, Chapman 1990, Kinzey and Cunningham 1994, Norconk and Kinzey 1994, Peres 1996, Di Fiore 1997, Jamieson 1998, Garber et al. 1999, Dias and Strier 2003, Veiga et al. 2006, Irwin 2007).

As shown above, establishing standard measurements of group spread have proven to be problematic in these studies. In addition, simplistic definitions of what constitutes a food patch have prevented testing the relationship between group spread and patch quality beyond anecdotes. Primatologists have generally relied on the correlation between the number of animals in a feeding tree with dbh to describe the relationship between subgrouping and food patch size. This method may be sufficient for primates foraging in small, widely dispersed subgroups that generally feed simultaneously from the same feeding tree, like *Ateles* (Symington 1988, Chapman 1990, Stevenson et al. 1994). However, these fission-fusion social systems are probably only one end of a broad continuum of patterns of group cohesiveness in primates. Simply correlating dbh and feeding party size is likely insufficient to properly characterize these other patterns of primate group fissioning. The definition of a food patch as a single feeding tree prevents a complete understanding of the relationship between group spread and patch size when the group is spread out over multiple trees. The results of this study are consistent with the patterns shown above by previous research that demonstrates bearded sakis rely on group fissioning to avoid intragroup feeding competition when optimal foraging theory predicts it would be highest. But the methodology used in this study provides a more quantitative and thorough characterization of how groups adjust cohesiveness according to ecological conditions. By defining patch size on a larger spatial scale and group cohesiveness in three ways, I was able to more fully describe these relationships.

Conclusion

As shown in Chapter 5, the foraging strategy of bearded sakis ensures that they face minimal competition from other primates due to their ability to exploit many plant species that other primates cannot. In addition, because they are able to feed from so many different species, they are not heavily dependent on a small set of patchily-distributed resources. The results presented in this chapter also suggest that bearded sakis in Guyana do not suffer from pervasive intragroup feeding competition, despite living in groups of over 60 individuals. Instead, they exhibit a high degree of flexibility in ranging behavior and a highly fluid social structure that mitigates feeding competition, even during periods of resource scarcity.

During most of the year, the bearded saki group moves through their home range like an amoeba, contracting and expanding group spread throughout the day. These hourly contractions and expansions appear to be unrelated to the quality of individual food patches and are more likely dictated by intragroup social dynamics. The group usually coalesces around dusk, possibly as an anti-predator strategy. During the short dry season, when food is most scarce and food patches are of lower quality, bearded sakis regularly split into subgroups. These groups are often isolated from each other for several days and appear to forage independently of one another. Combined, these results question the applicability of the ECM/optimal foraging theory for explaining bearded saki ranging behavior and group cohesiveness.

Table 6.1. Home range and core area estimates obtained for 4 methods.

Method	Home range (ha)	90% core area (ha)	50% core area (ha)
MCP	1011.26	654.20	254.12
100m Grid	722	NA	NA
Fixed kernel	970.12	770.46	249.57
Adaptive kernel	1021.55	761.67	220.41

Table 6.2. Home range and core areas for 5 two-month periods (fixed kernel method).

Core Area	Jan-Feb	Mar-Apr	May-Jun	Sep-Oct	Nov-Dec
50%	287.07	169.13	181.97	170.03	137.52
90%	794.03	558.71	520.55	468.82	420.59
Home Range	956.25	678.18	643.73	558.39	507.70

Table 6.3. Average daily path length by month and for the whole study period (in meters).

Month	Mean daily path length (n)	Max	Min	Std
January	4435 (4)	6154	3445	1184.72
February	4661 (6)	6454	3836	959.42
March	4446 (5)	5032	3752	530.61
April	3577 (4)	3719	3414	128.10
May	3755 (5)	4564	2797	702.18
June	3289 (4)	3562	3032	252.08
September	4309 (3)	4886	3823	537.31
October	3538 (4)	4258	3021	519.59
November	3454 (5)	4785	2928	768.60
December	3883 (4)	4203	3691	278.74
All Months	**3958 (44)**	**6454**	**2797**	**787.83**

Table 6.4. Measures of group cohesiveness.

Measure	Mean	95% CI	95% CI	Max	Min	Std
Group spread (m)	139.47	131.20	147.87	1386.12	3.91	167.83
Group size	36.13	31.98	40.37	65	8	13.86
# indiv. per scan	16.24	16.06	16.43	46	3	6.72

Table 6.5 Measures of Group Cohesiveness and mean daily path length by month.

Month	**GrpSprd**	**GrpSize**	**Indv/scan**	**DailyPath**
January	133.7868	49.75	16.51	4435.25
February	153.5991	46.5	18.17	4661.667
March	259.0322	43.75	14.96	4446
April		37	16.63	3577
May	117.9614	45.8	15.69	3755.2
June	99.93653	36.33333	9.16	3289
September	134.1101	22.66667	10.08	4309
October	71.87303	26.5	10.68	3538
November	88.59329	19	7.18	3454
December	96.83979	29.66667	9.22	3830.25
H-value	**174.36**	**22.67**	**30.99**	**20.28**
p-value	**< 0.001**	**0.007**	**< 0.001**	**0.016**

Table 6.6. Intermonthly variation in patch use for (A) 100m^2 and (B) 50m^2 patch sizes.

(A)

Month	**#feedTrees**	**Trees/Patch**	**AvgPatches/day**	**AvgPQIdbh**	**AvgPQI**	**PatchOcc**
Jan	48.25	1.87	28.33	193.49	465.57	4.17
Feb	64.83	2.12	34.50	262.92	559.29	3.73
Mar	81.2	2.11	41.33	212.50	527.09	3.96
Apr	75.50	NA	NA	NA	NA	NA
May	77	2.36	34	260.44	598.35	4.35
Jun	82.67	2.82	29.33	229.22	521.66	5.11
Sep	37	1.42	23.67	87.61	211.84	4.10
Oct	35	1.49	25	112.99	330.19	3.91
Nov	45.60	2.01	23.33	153.84	429.03	5.09
Dec	63.33	1.85	29.3	122.04	325.26	3.73
H-value	**27.01**	**19.06**	9.39	**110.34**	**66.67**	4.45
p-value	**0.001**	**0.015**	0.311	**< 0.001**	**< 0.001**	0.815

(B)

Month	**#feedTrees**	**Trees/Patch**	**AvgPatches/day**	**AvgPQIDbh**	**AvgPQI**	**PatchOcc**
Jan	48.25	1.28	41.30	134.10	324.82	2.41
Feb	64.83	1.35	54	166.86	355.56	2.36
Mar	81.20	1.36	64.33	132.43	342.22	2.23
Apr	75.50	NA	NA	NA	NA	NA
May	77	1.39	57.67	142.06	326.37	2.38
Jun	82.67	1.56	53	126.07	286.91	2.84
Sep	37	1.14	29.30	69.82	169.70	2.78
Oct	35	1.19	31.67	88.78	340.86	2.51
Nov	45.60	1.25	37.33	95.07	265.13	2.45
Dec	63.33	1.33	40.33	88.99	237.17	2.52
H-value	**27.01**	**20.70**	**17.55**	**104.90**	**74.83**	13.96
p-value	**0.001**	**0.008**	**0.025**	**< 0.001**	**< 0.001**	0.094

Table 6.7. Results of bivariate regressions between group size and patch quality and individuals per scan and patch quality.

Patch Quality Measure	Group Size	95% CI	Indv/Scan	95% CI
PQI 50m	r = 0.69**	0.47 – 0.87	r = 0.63**	0.22 – 0.91
PQIdbh 50m	r = 0.79**	0.61 – 0.91	r = 0.91**	0.85 – 0.96
PQI 100m	r = 0.65**	0.42 – 0.81	r = 0.78**	0.65 – 0.92
PQIdbh 100m	r = 0.55**	0.45 – 0.88	R = 0.59*	0.46 – 0.93

* indicates significance at the $p < 0.05$ level

** indicates significance at the $p < 0.01$ level

Table 6.8. Home range sizes and daily path lengths for previous studies of bearded sakis compared to those of this study group.

Species	Country, Forest Type	Study Duration	Home Range	Daily Path	Reference
Chiropotes sagulatus	Suriname, Continuous	12 months	600+	3 +	Gregory (2011)
Chiropotes satanas	Brazil, Continuous	5 days	559, 300		Boyle 2008
Chiropotes satanas	Brazil, Fragments	6 months	100, 10		Boyle 2008
Chiropotes albinasus	Continuous	12 months	1000+	3.7	Pinto 2008
Chiropotes satanas	Brazil, Fragments	> 12 months	16-100	2.8 – 4	Silva (2003), Veiga (2006)
Chiropotes utahickae	Brazil, Island	6 months	57	2.5	Veira 2005
Chiropotes chiropotes	Venezuela, Island	15 months	250	3	Peetz (2001)
Chiropotes sagulatus	Suriname, Continuous	2 months	200+	2 – 3	van Roosmalen et al. (1981)
Chiropotes albinasus	Brazil, Continuous	intermittent	200+	1.5 – 3	Ayers (1981, 1989)
Chiropotes sagulatus	**Guyana, Continuous**	**12 months**	**1000ha**	**4 km**	**This Study**

Figure 6.1. Group spread analysis conducted using GIS for May 4th. Each 100X100m quadrat received a group spread value for the mean spread of the study group while they were in that quadrat. Mean group spread is higher for darker quadrats.

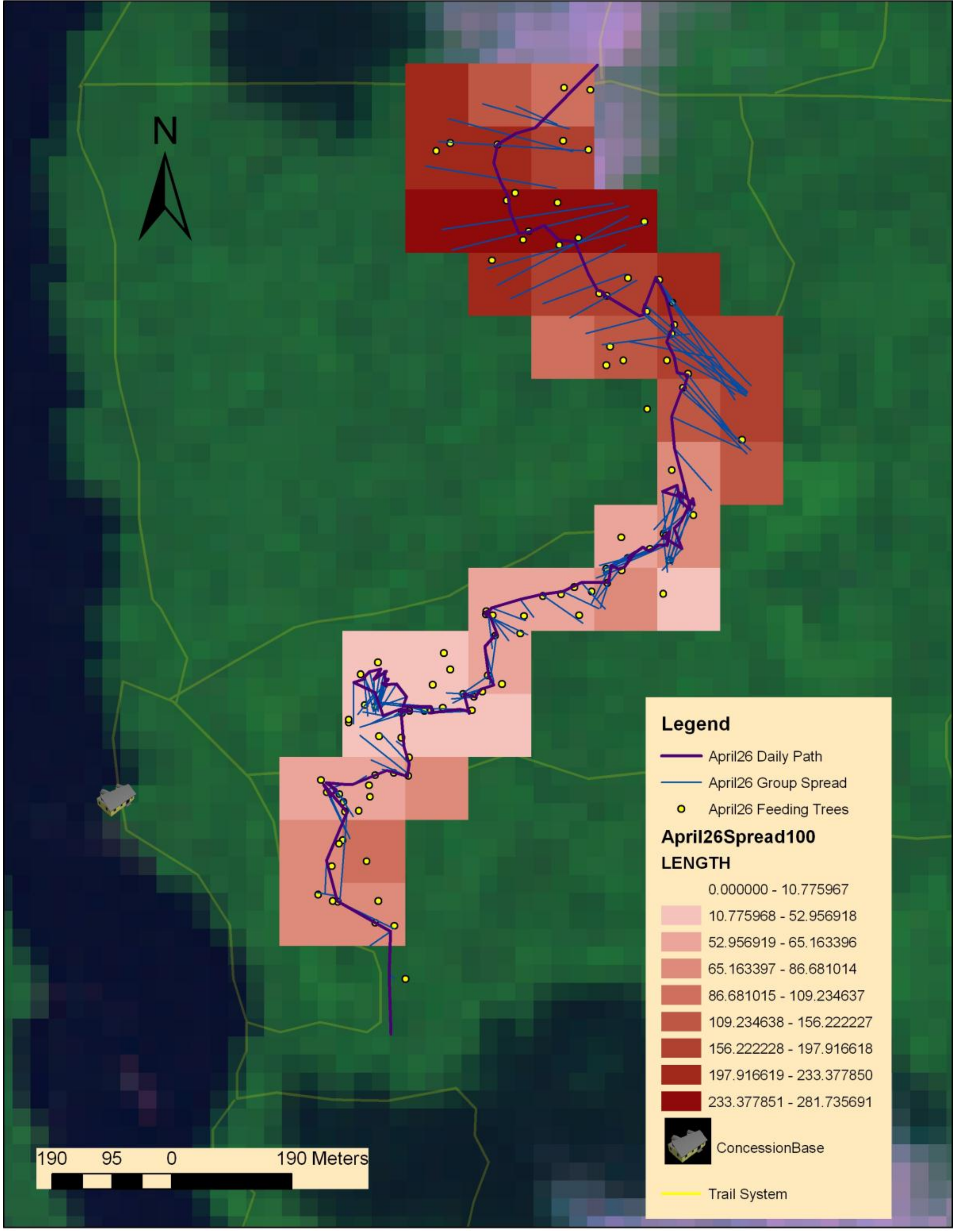


Figure 6.2. GIS analysis correlating group spread with patch quality for May 4th. Darker quadrats represent higher quality food patches and blue lines represent group spread distances at five-minute intervals.

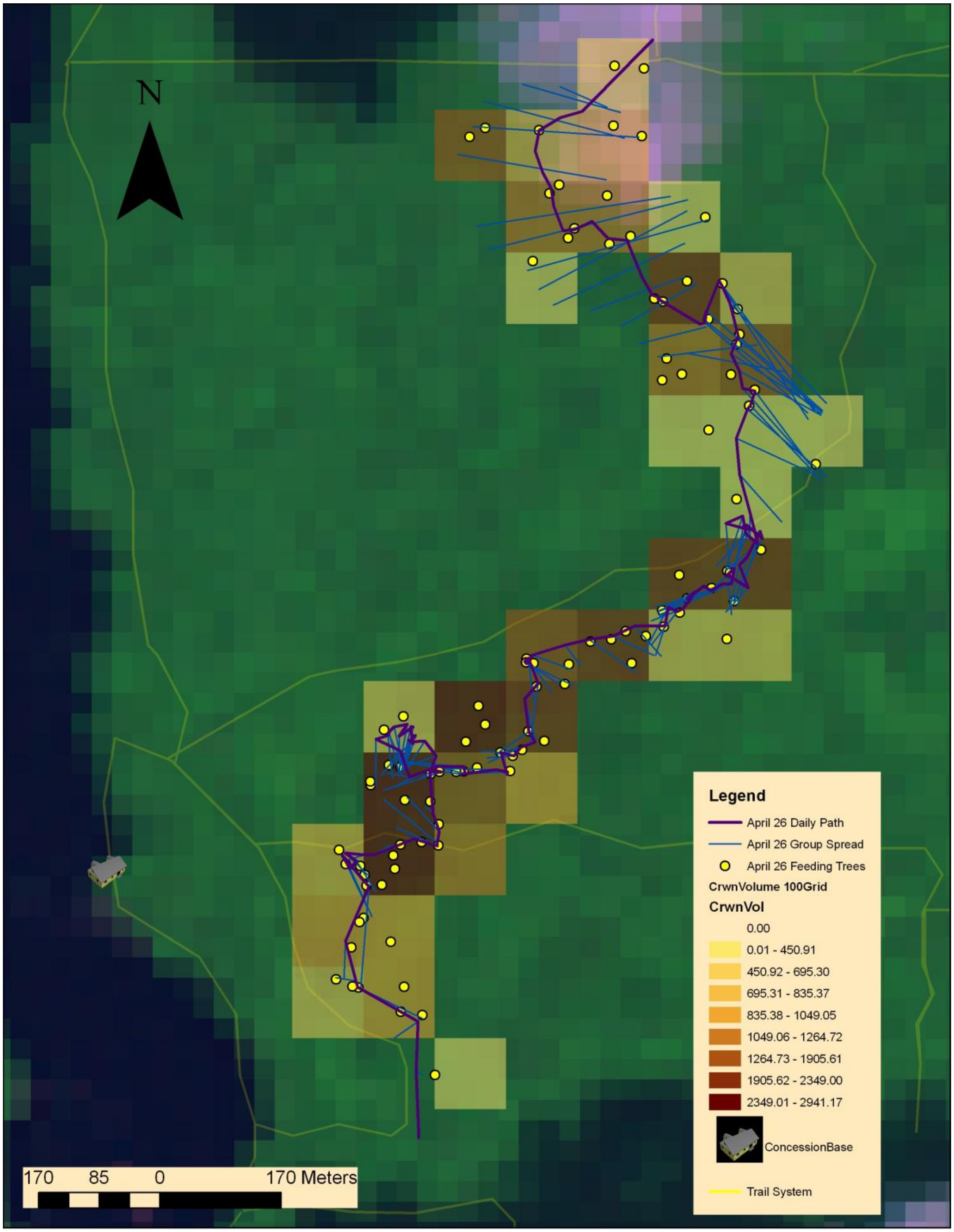


Figure 6.3. Schematic representation of the GIS used to measure the relationship between group spread and patch quality.

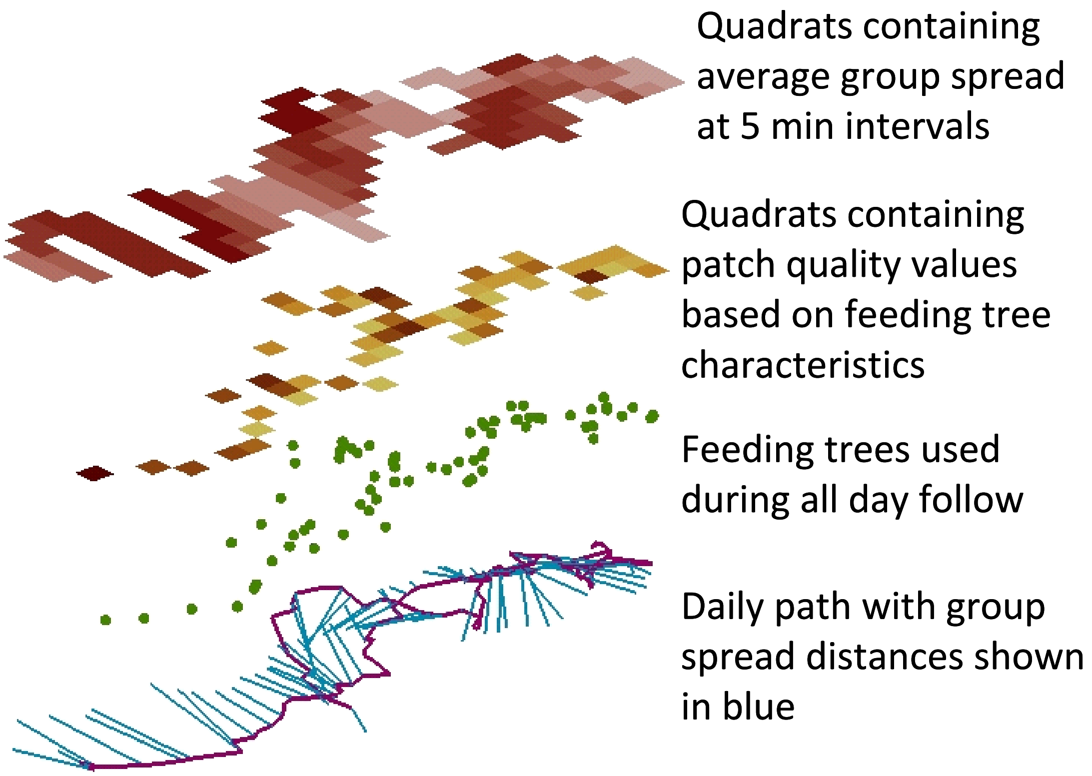


Figure 6.4. Home Range of the study Group using two methods. The minimum convex polygon estimated home range is outlined in orange (1016 ha). The grid method estimated home range ($100m^2$ grids) is shown in red quadrats (722 ha).

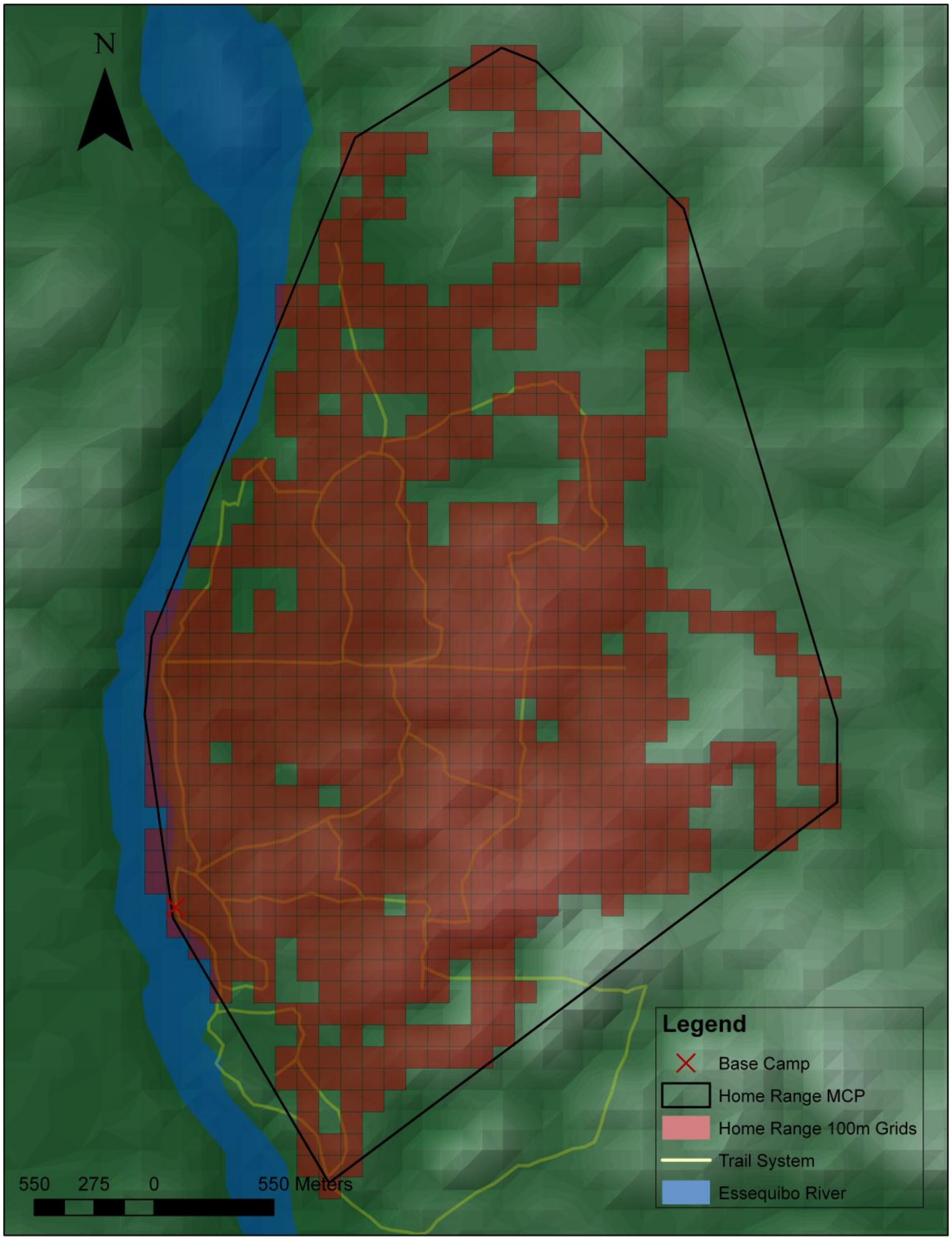


Figure 6.5. Cumulative number of $100m^2$ quadrats entered by the study group each month.

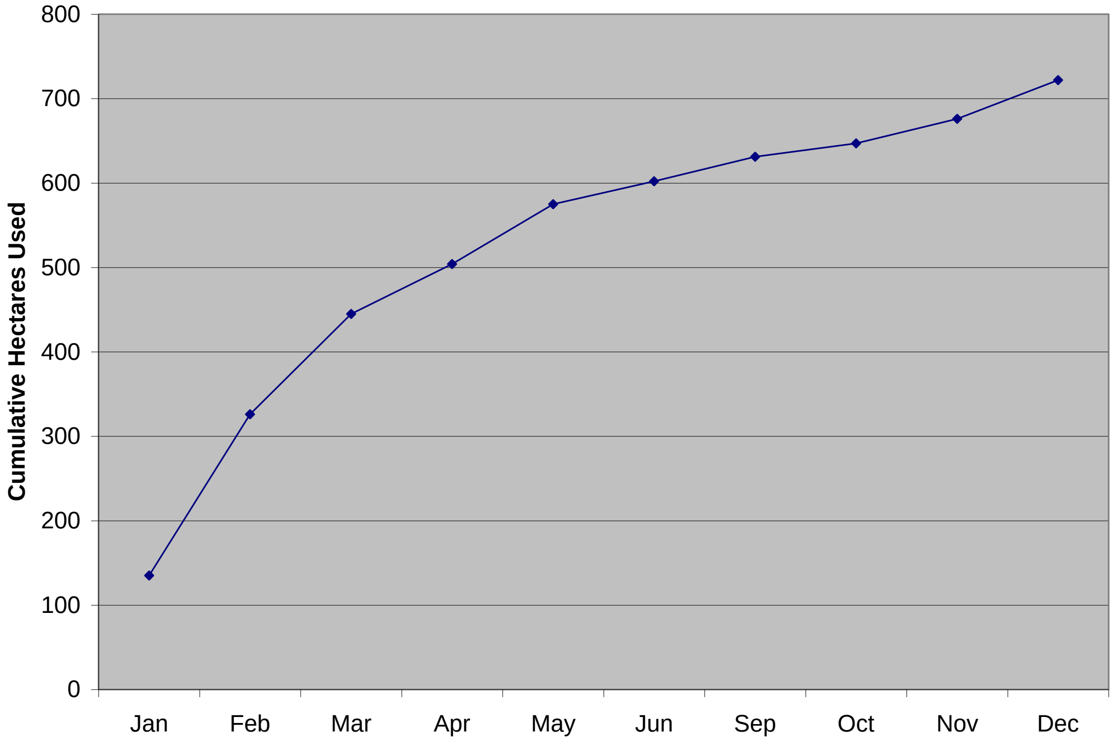


Figure 6.6. Fixed Kernal Density home range estimate compared to home range size obtained by the minimum convex polygon estimate. The lines show the extent of the 50% (249.57 ha), 90% (770.46 ha), and 95% (970.12 ha) core areas.

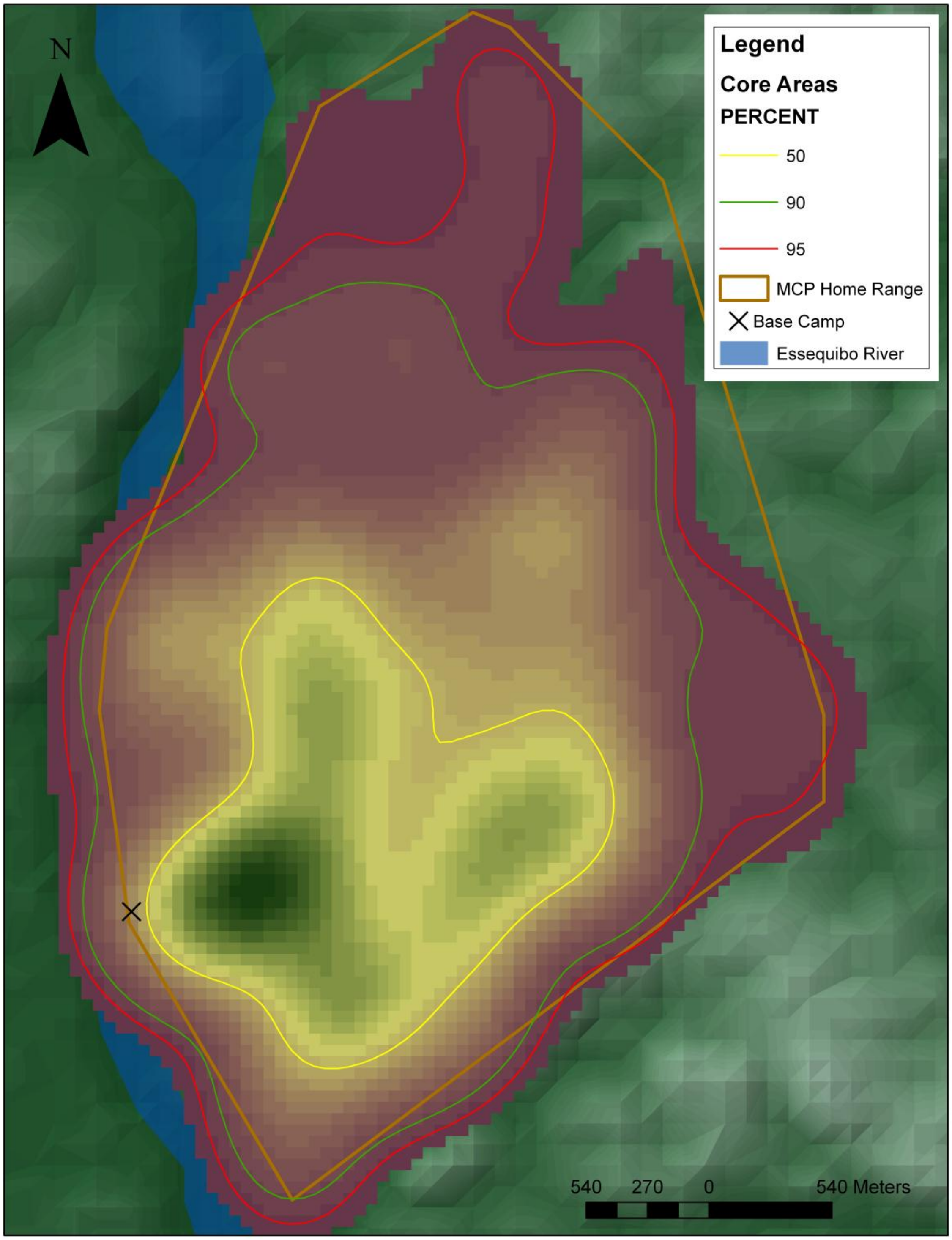


Figure 6.7. Home range and core areas for combined two month periods: Jan-Feb (1), Mar-Apr (2), May-Jun (3), Sep-Oct (4), and Nov-Dec (5). Fixed kernel method

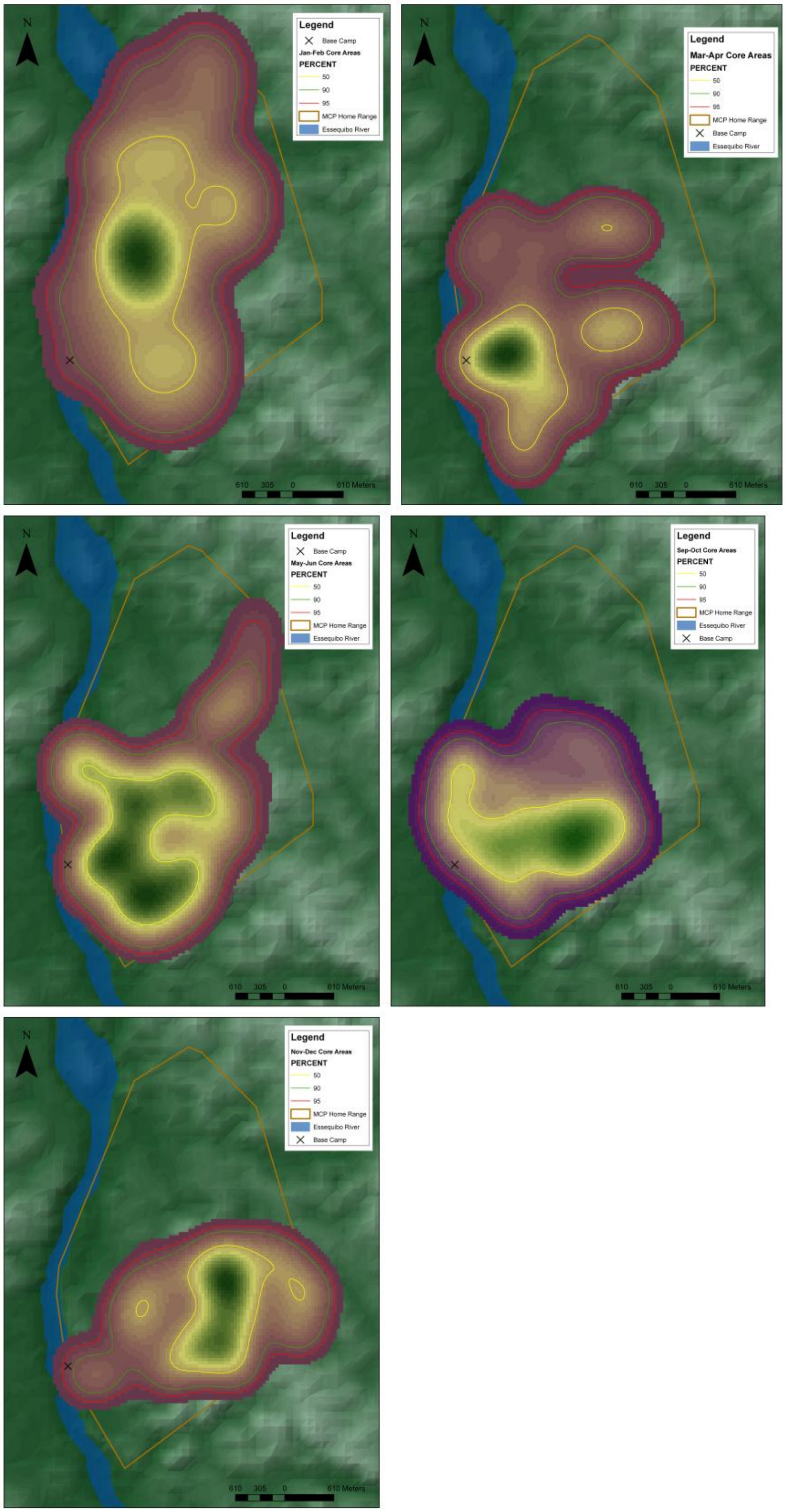


Figure 6.8. Combined Daily Paths for 44 all-day follows during the study period.

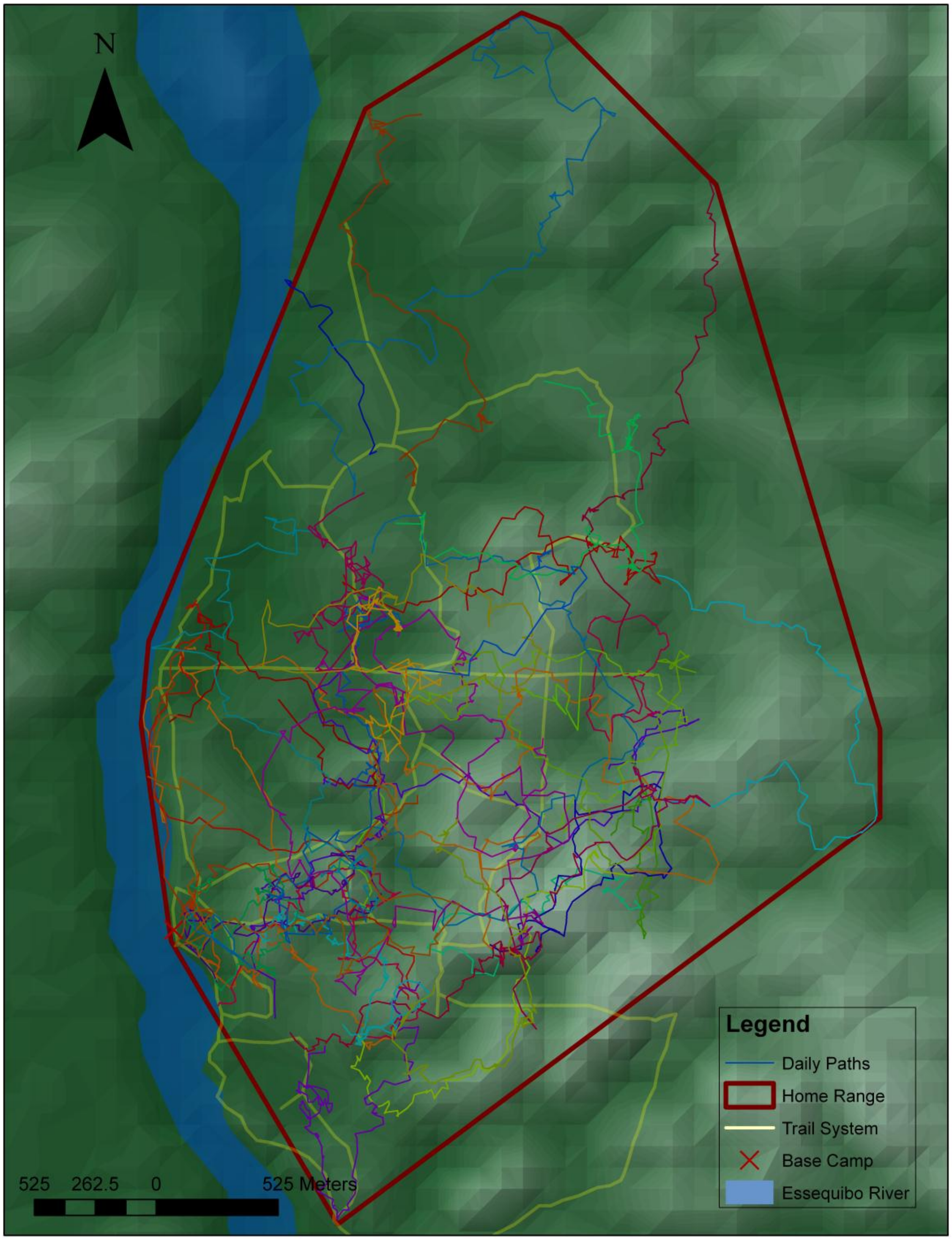


Figure 6.9. Group spread by time of day.

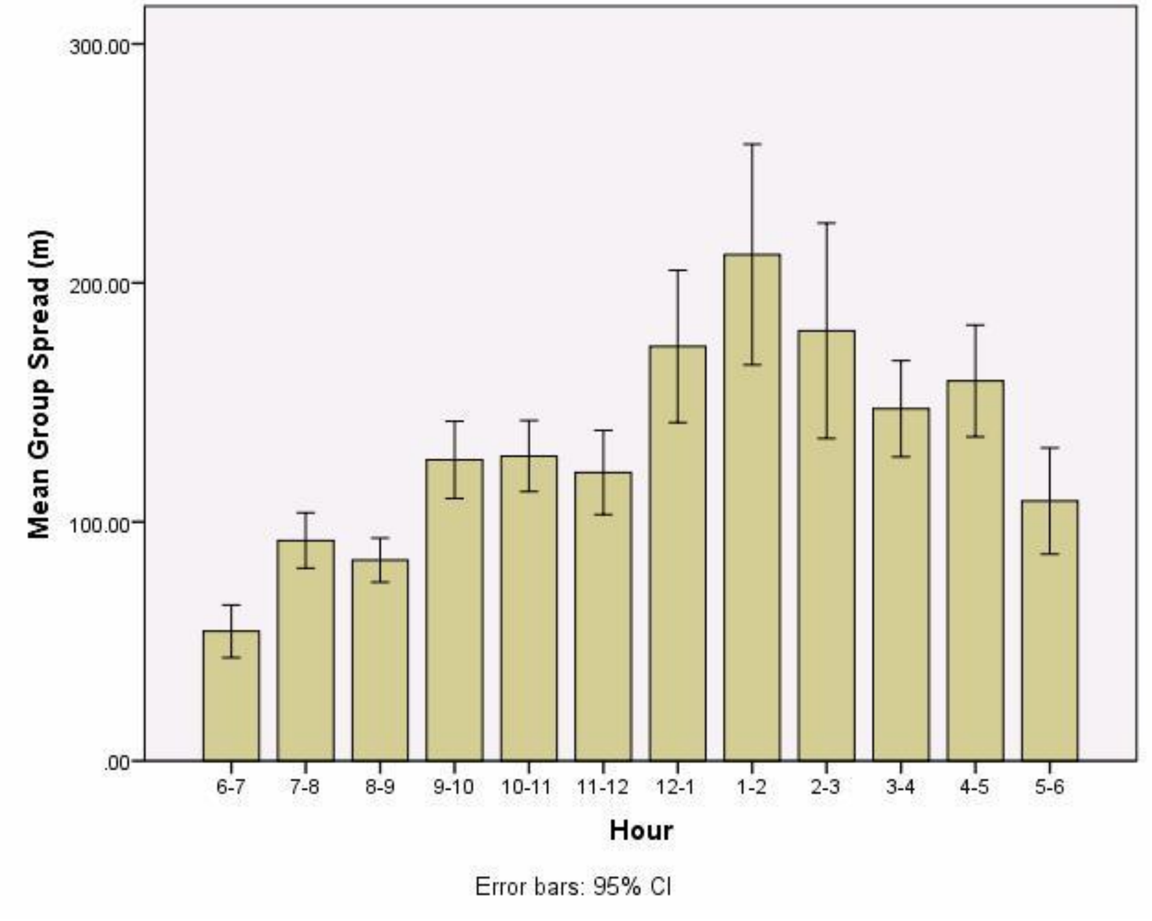


Figure 6.10. Daily path length for November 15 showing the typical pattern of change in group cohesiveness throughout the day that is represented in the graph above. Bearded sakis would generally begin the day in a relatively cohesive group, spread out throughout the day, and coalesce as dusk approached.

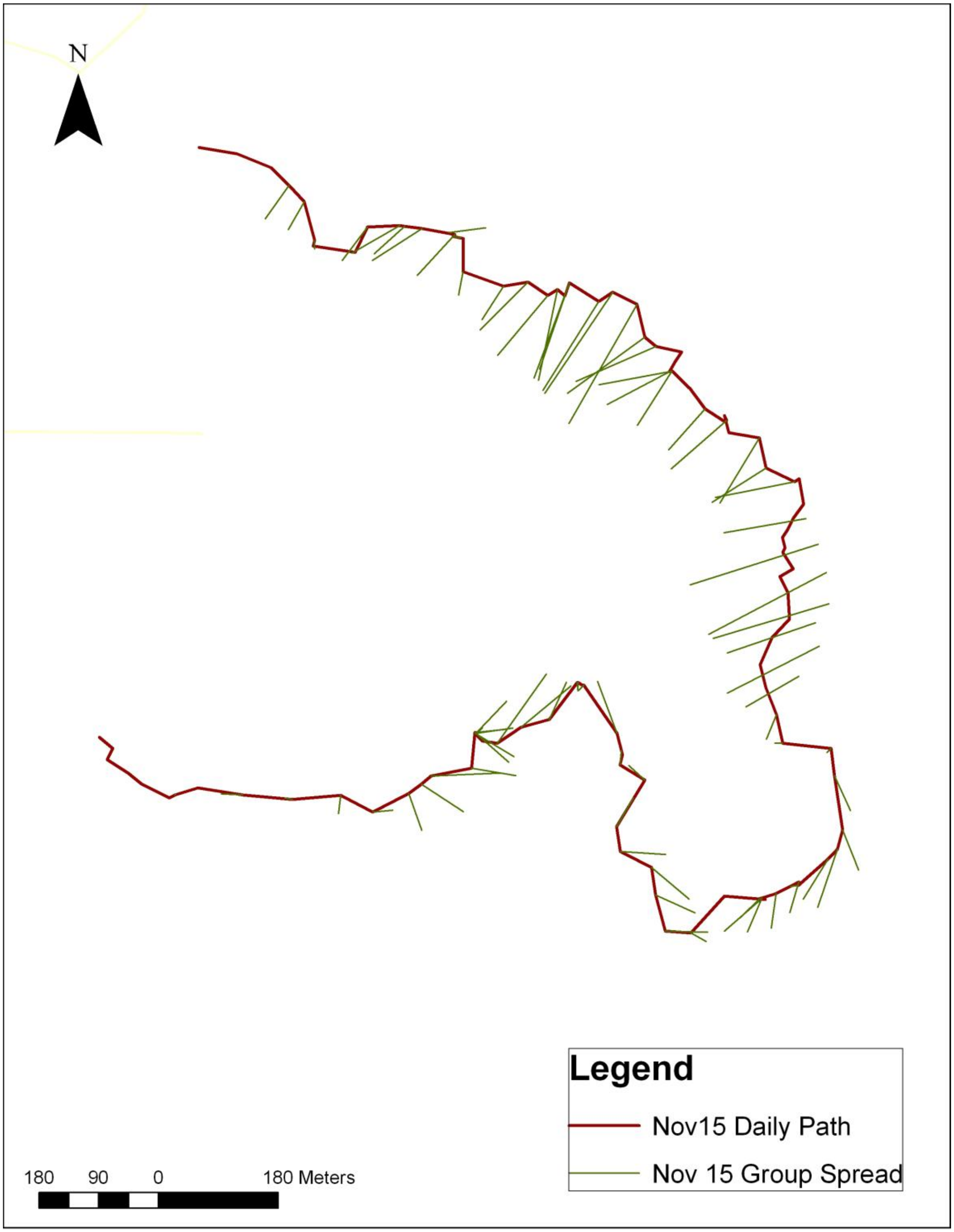


Figure 6.11. Number of five minute scans (Patch occupancy) by mean PQI (Log transformed Data).

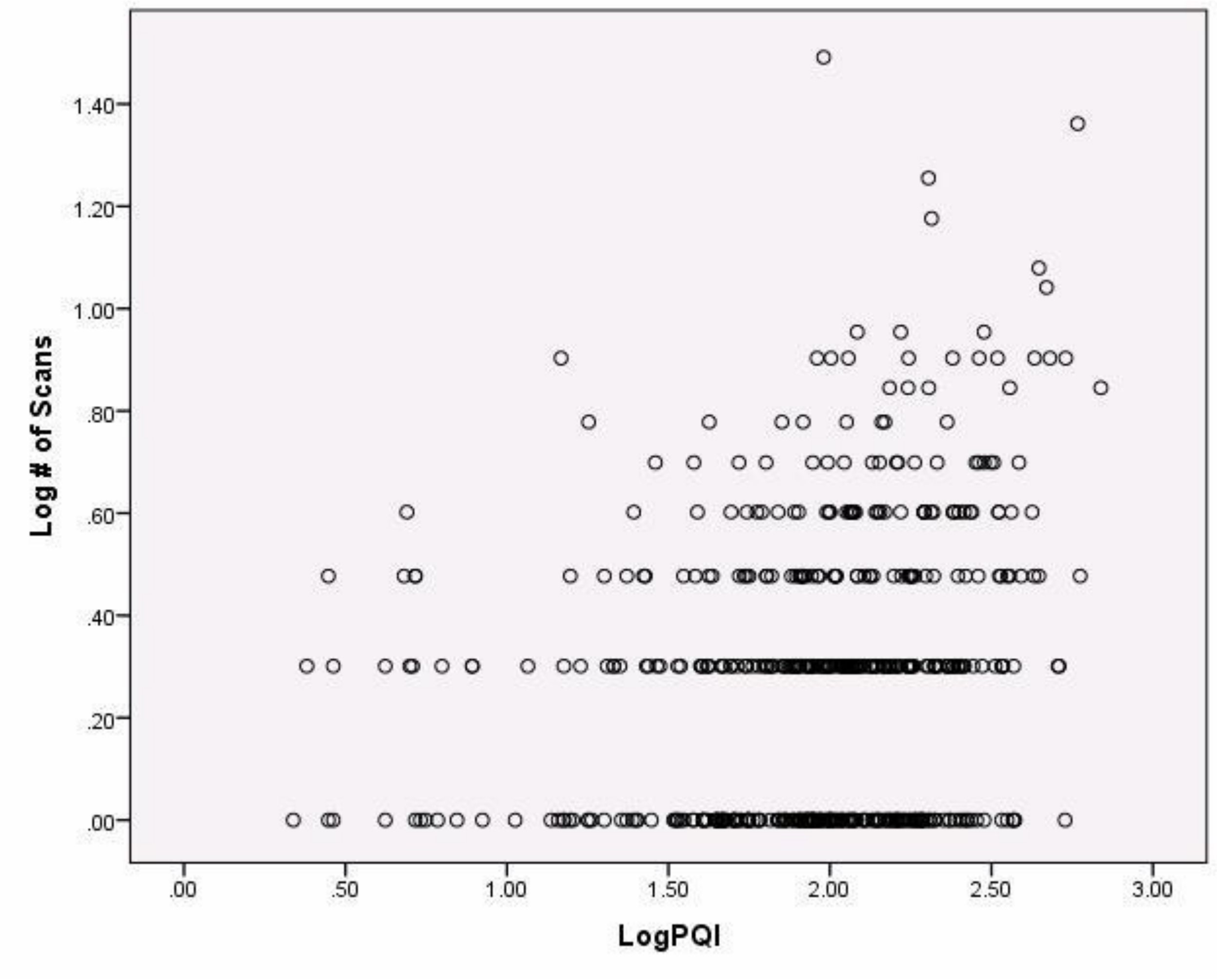


Figure 6.12. Log of mean group spread by Log of mean PQI

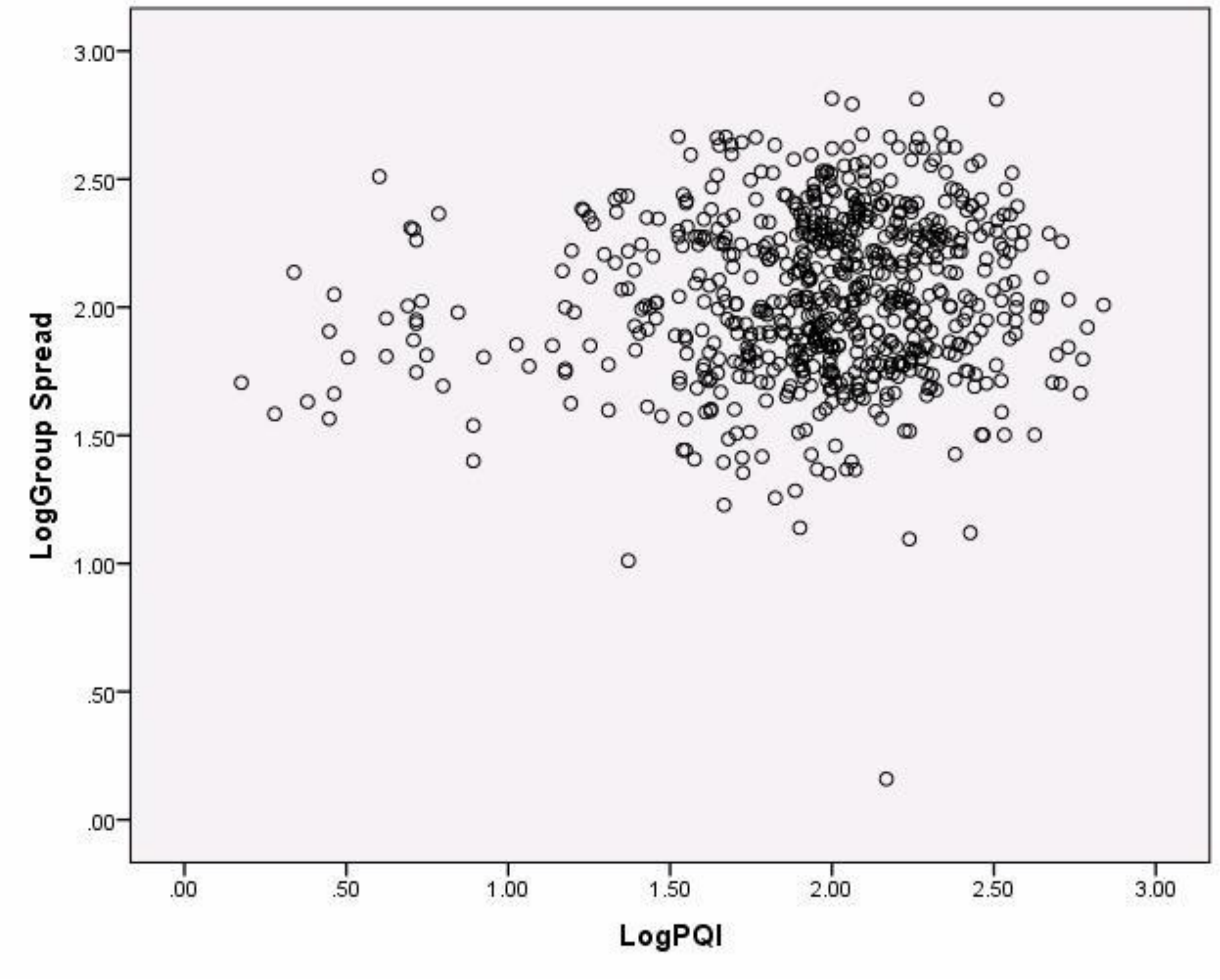


Figure 6.13. Group spread in feeding quadrats versus in quadrats in which no feeding took place.

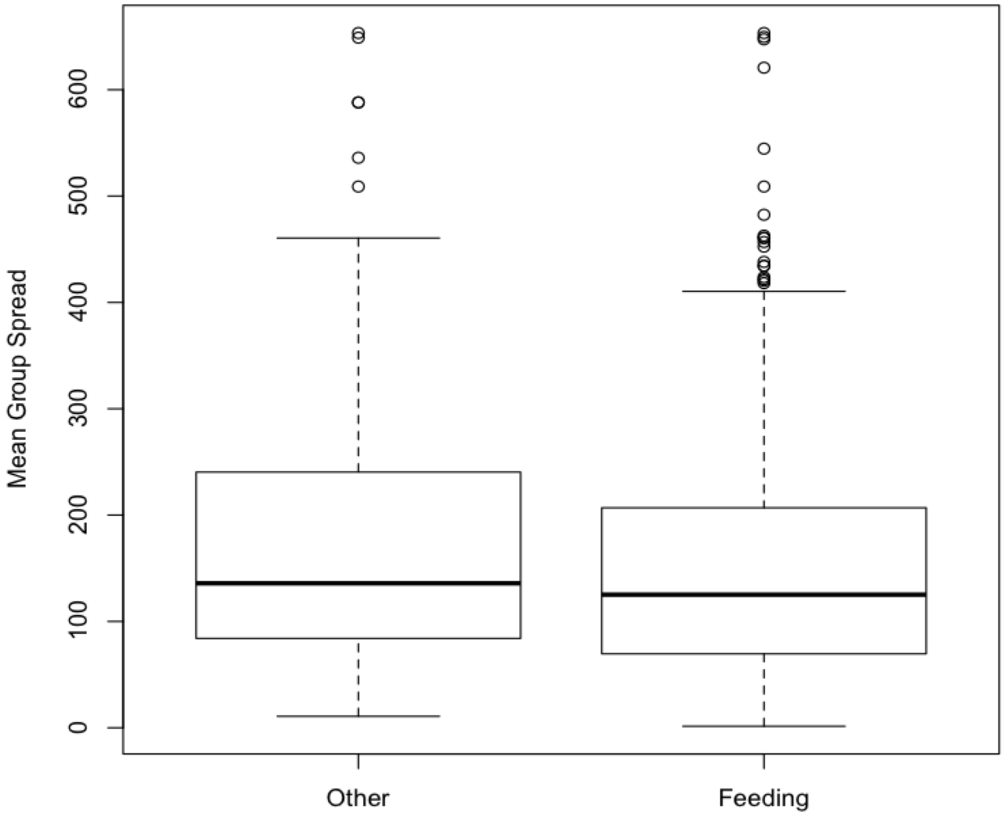
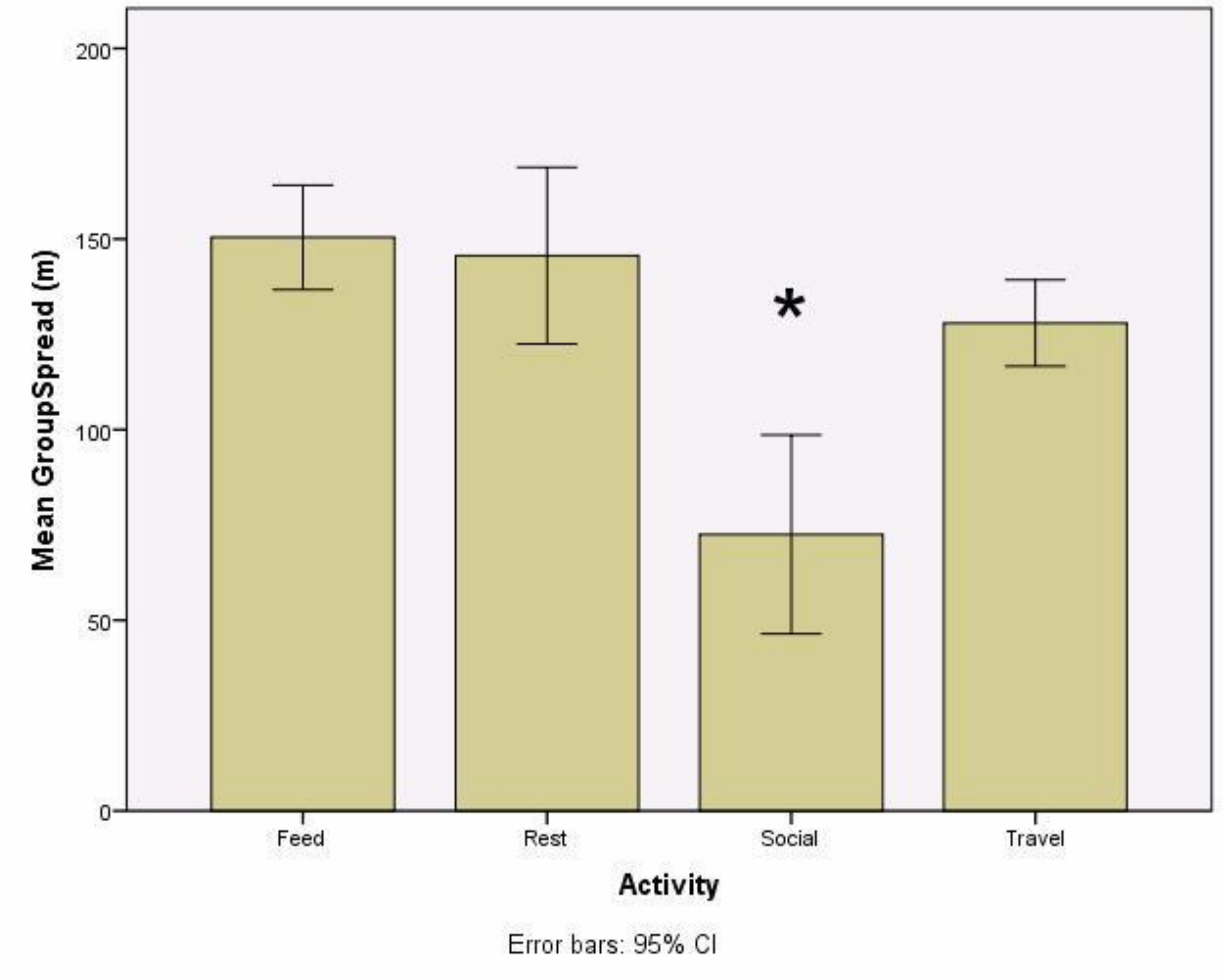


Figure 6.14. Mean group spread by activity



* indicates mean was significantly different from mean for all other activities (T = -5.16; p<0.001)

Figure 6.15. Mean minimum group size by total fruit abundance (RAI).

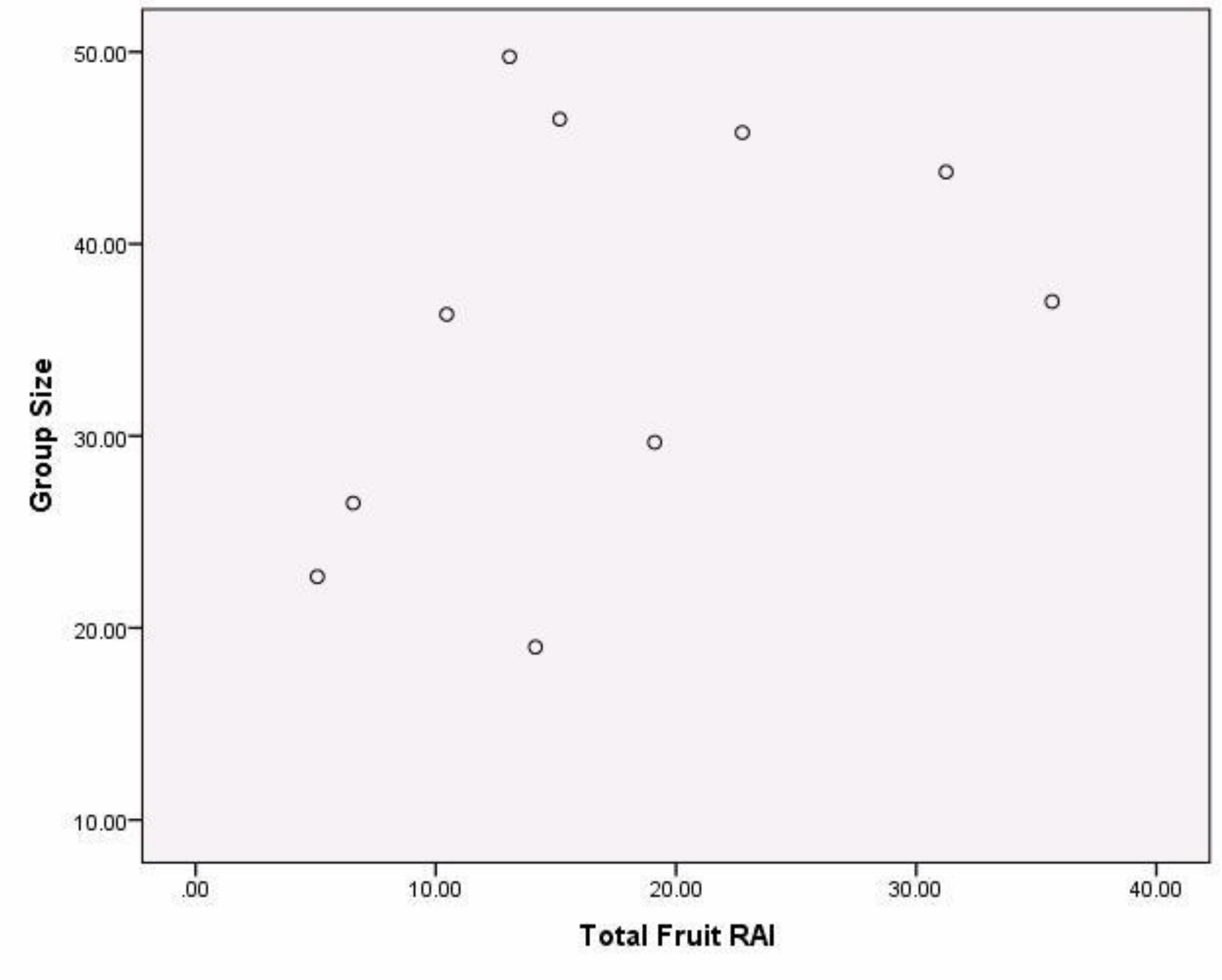


Figure 6.16. Mean minimum group size total fruit abundance (RAI).

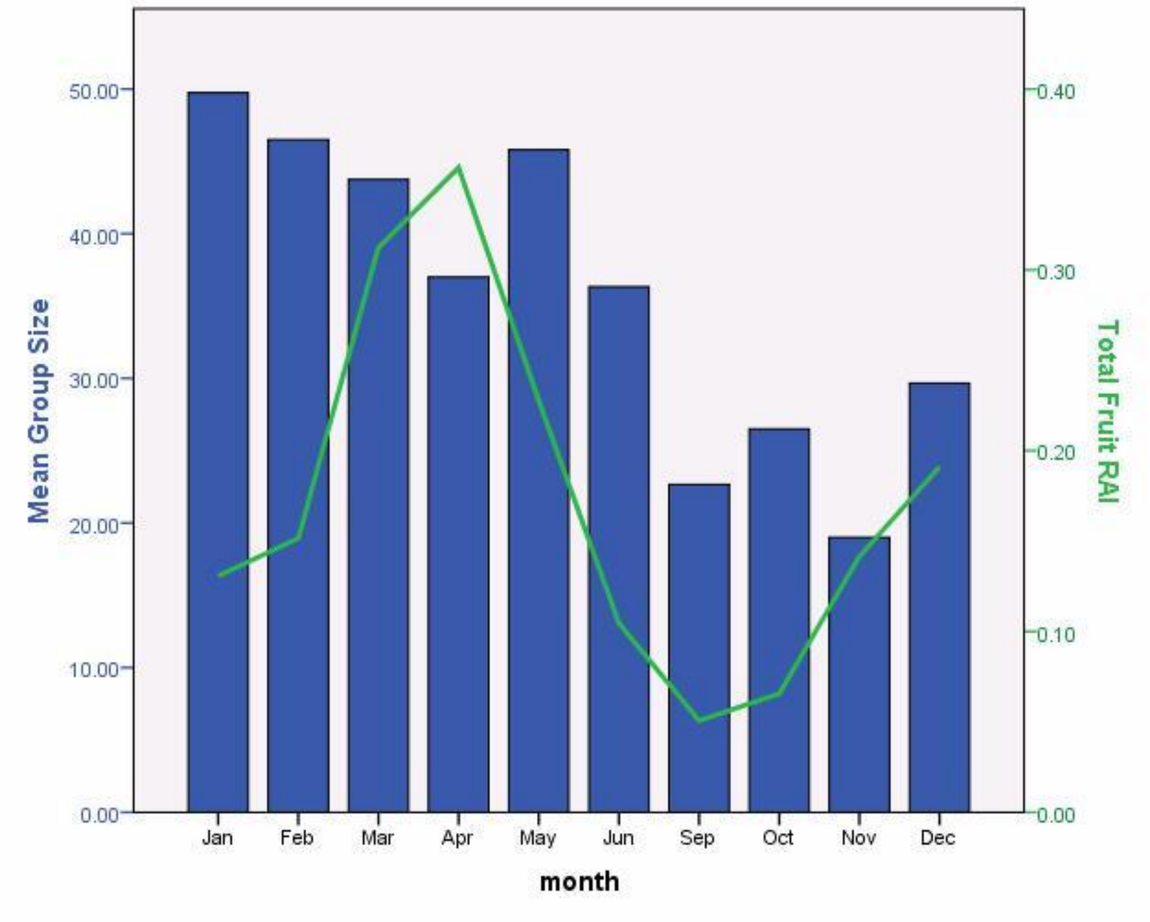


Figure 6.17. Regression between mean minimum group size and mean patch quality (PQIdbh for 50m quadrats).

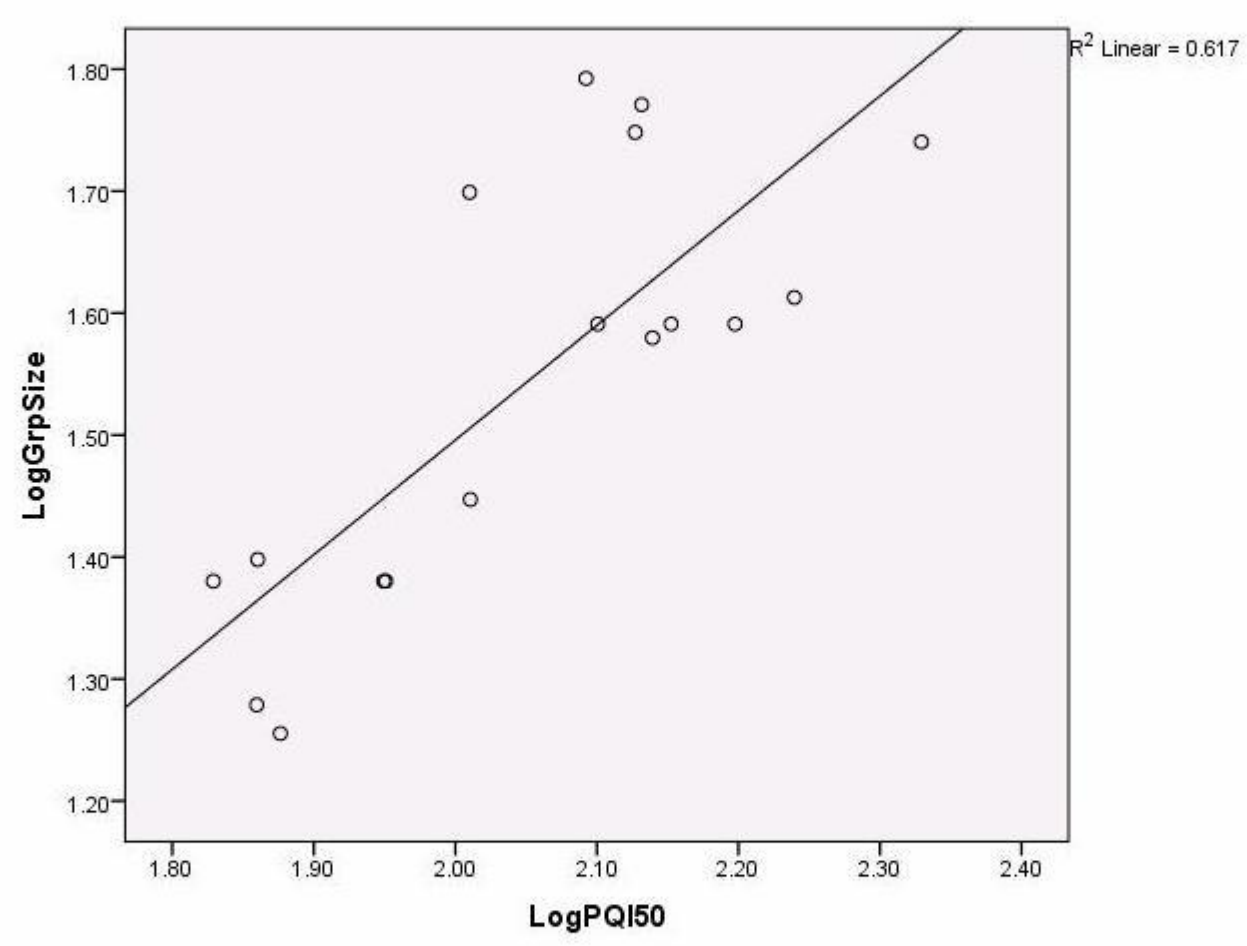


Figure 6.18. Mean minimum group size compared to mean monthly patch quality (PQIdbh).

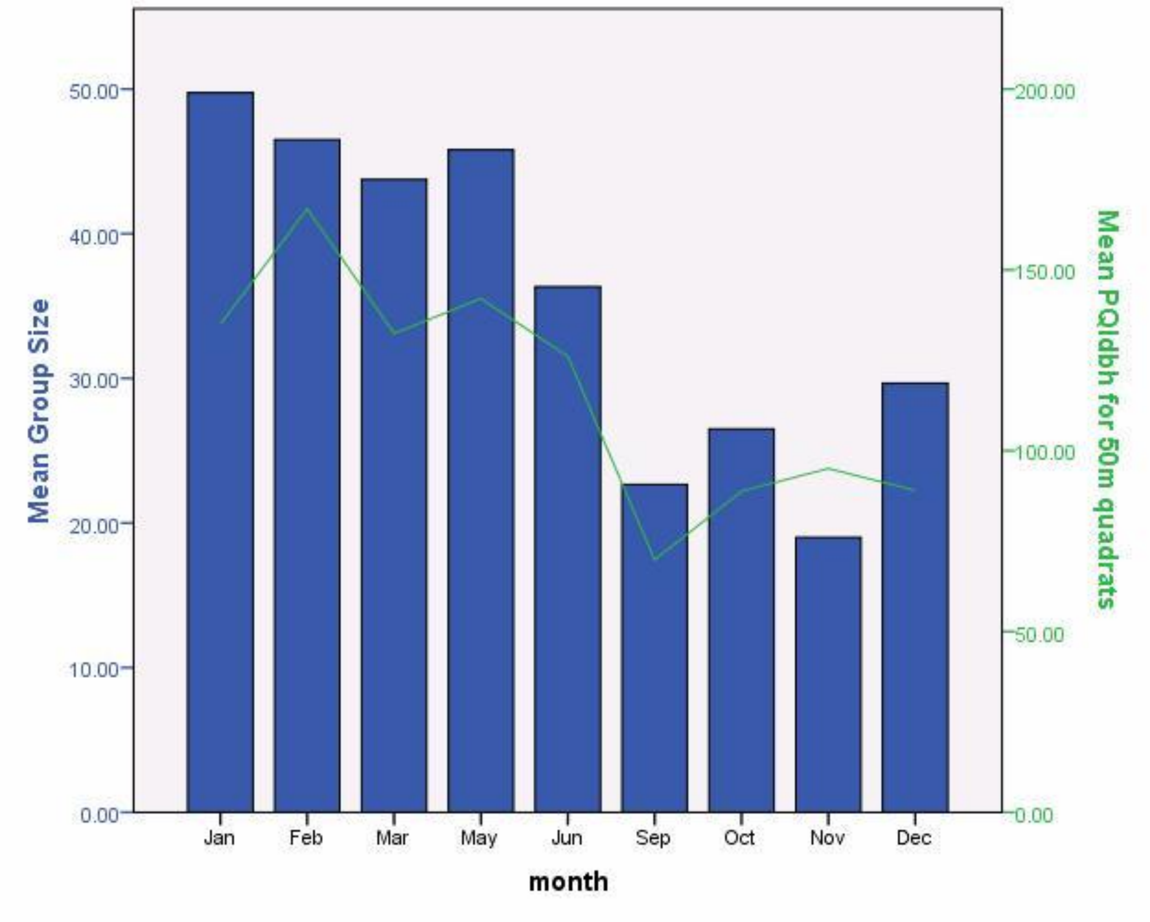


Figure 6.19. Regression between mean number of individuals per scan and patch quality (PQIdbh for 50m quadrats).

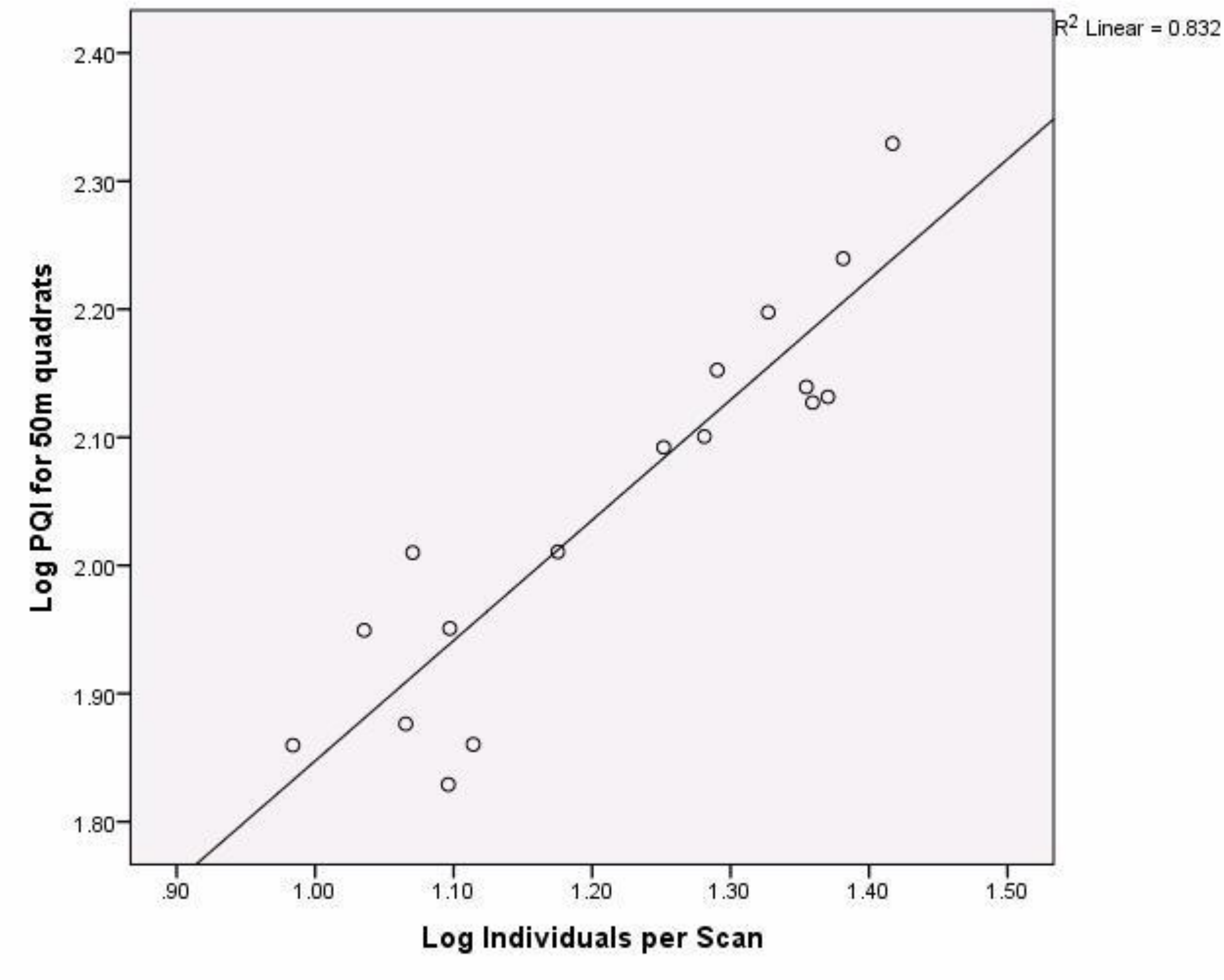
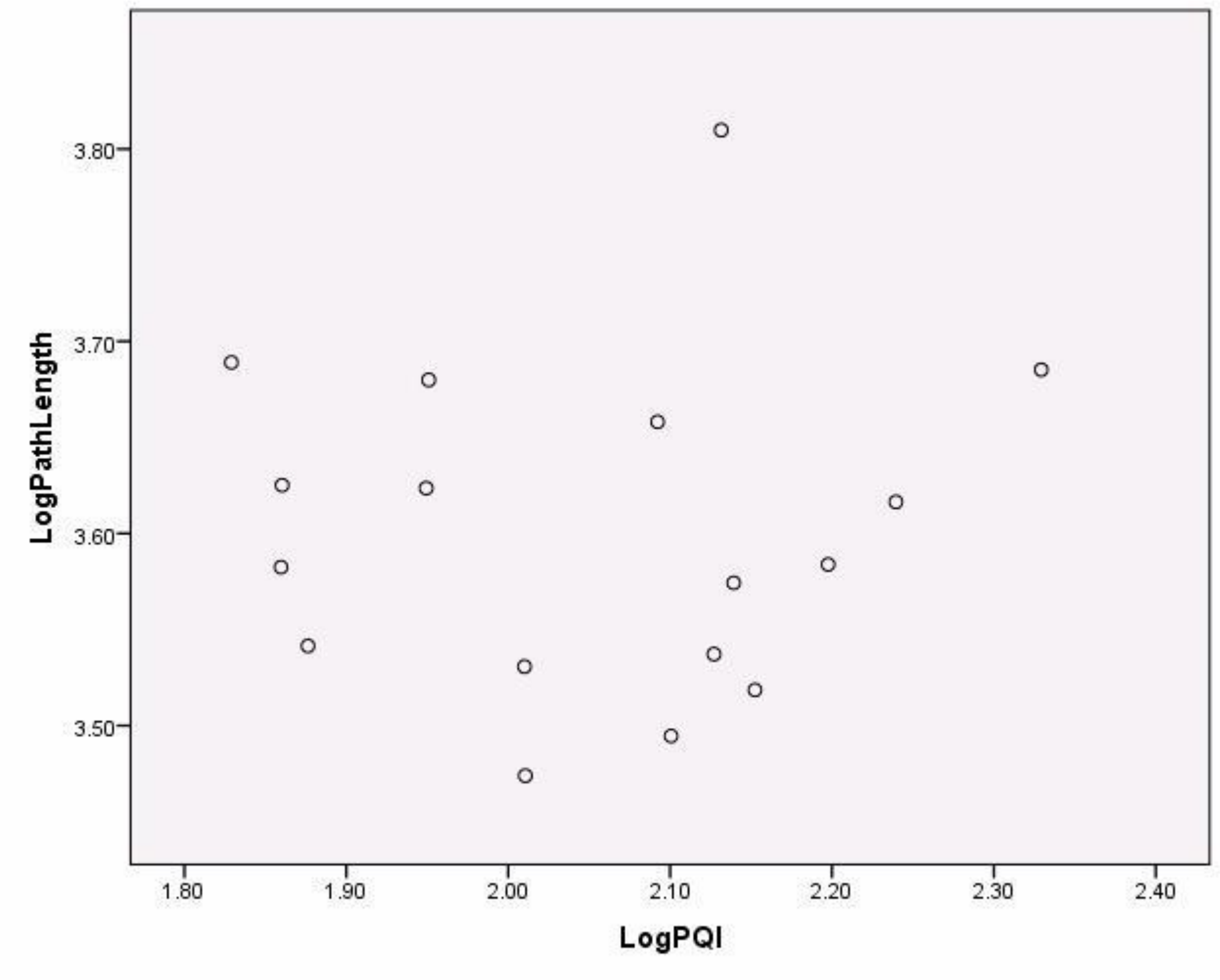


Figure 6.20. Mean daily path length by mean daily patch quality (PQI) (Data are log transformed).



CHAPTER 7 - DISCUSSION

Introduction

This study had three main objectives: (1) to describe the behavioral ecology of the northern bearded saki (*Chiropotes sagulatus*) in an undisturbed and continuous forest, a habitat characteristic of most of its geographic range, (2) assess the influence of intragroup feeding competition on bearded saki behavioral ecology, especially in relation to ranging behavior and patch use, and (3) create better methods for quantifying food patch quality and how it relates to group cohesiveness in primates. I completed the first objective by collecting detailed behavioral data on bearded saki socioecology during my 15-month study in the Upper Essequibo Conservation Concession. In this dissertation, I have described the activity budget and social behavior, feeding ecology, and ranging behavior of *Chiropotes sagulatus* in Guyana and how these vary in relation to seasonal variability in ecological conditions. I completed the second objective by testing the research questions and hypotheses outlined in Chapter 1. I completed the third objective by utilizing a novel, GIS-method for testing hypotheses concerning bearded saki patch use.

In this chapter, I review the hypotheses I presented in the introduction and tested in Chapters 4-6. I then summarize the bearded saki niche as evidenced by the data collected. In addition, I discuss the comparative behavioral ecology of pithecines in light of the insights derived from this study and develop a model to explain bearded saki socioecology. Finally, I discuss important areas for further research revealed in the course of completing this dissertation and address conservation priorities for bearded sakis.

Review of Research Questions and Hypotheses

Hypothesis 1: The bearded saki activity budget—specifically time spent feeding, traveling, and resting—will show significant seasonal variation that will be correlated with seasonal changes in food resource availability.

My data support this hypothesis. Bearded sakis demonstrated significant intermonthly variation in the time spent both feeding and resting. In addition, time spent feeding was significantly correlated with monthly abundance of fruit. These results are consistent with those from several other studies of bearded sakis and support the notion that bearded sakis adjust their activity patterns in response to seasonal ecological changes (Peetz 2001, Boyle and Smith 2009, Gregory 2011).

However, bearded sakis in this study cannot easily be classified as either energy minimizers or maximizers. Rather, they are highly active throughout the year but increase feeding time when resources are most abundant. This strategy may allow them to accumulate fat stores that help buffer them from the detrimental effects of resource scarcity during the short-dry season (Ayers 1986, Di Fiore and Rodman 2001).

Hypothesis 2: Bearded sakis will increase dietary diversity when resources become scarce and will rely more heavily on seeds during these periods.

The results of this study do not support this hypothesis. Bearded saki dietary diversity did not show significant intermonthly variation and bearded sakis actually spent less time feeding on seeds when overall fruit abundance was lowest. Instead, sakis increased the time spent feeding on mature fruit, flowers, and, especially, insects. Flower feeding was significantly correlated with monthly flower availability, indicating that the study group was able to exploit flowers as they became abundant. In addition, bearded sakis increased insect feeding significantly during the short-dry season, when fruit was at its lowest abundance. Finally, the study group did not shift to lower quality "fallback foods" when resources became scarce. Instead, like many other frugivores at this study site, they appeared to utilize *Goupia galba* as a high-quality source of mature fruit and possibly as a keystone resource).

The highly specialized dental adaptations of bearded sakis allow the monkeys to exploit a tremendous variety of plant species when fruit and seeds are most abundant. However, during the short dry season, it is the bearded sakis' ability to exploit a variety of plant parts, rather than their sclerocarpic seed-eating adaptations *per se*, that buffers them from the detrimental effects of resource scarcity. Therefore, it is likely that the craniodental adaptations for seed-eating evolved in bearded sakis to enable them to widen their overall feeding niche and not to provide them with a fallback food.

Hypothesis 3: Bearded sakis will spend more time feeding in higher quality food patches.

My data support this hypothesis, as bearded saki patch occupancy was significantly correlated with patch quality. However, this relationship was not very strong, with patch quality explaining only 10% of the variation in the time bearded sakis spend in a patch. Therefore, while it is possible that higher intragroup feeding competition in lower quality food patches dictates that bearded sakis leave these patches earlier, patch quality does not appear to be the primary determinate of the length of time sakis spend in a patch.

Hypothesis 4: Bearded sakis will increase group spread when feeding in lower quality patches.

This hypothesis was not supported by the results of this study. Mean group spread was not significantly correlated with any measure of patch quality for either spatial scale. This suggests that the coalescence and fissioning of the group is not determined by the characteristics of individual patches that the group enters. Bearded sakis do not appear to fission when they enter a low quality patch and then coalesce later in the day when they enter a higher quality patch, as would be suggested if intragroup feeding competition was driving daily foraging decisions.

This pattern of variability in group spread is somewhat different from reports of previous research on bearded sakis. However, the lack of quantification of both group spread and patch quality in these previous studies may be responsible for the observed differences.

Hypothesis 5: Bearded sakis will be less cohesive during periods of resource scarcity.

My data support this hypothesis. While group spread did not vary by month, my other two measures of group cohesiveness, group size and number of individuals per scan, were highly significantly correlated with patch quality and group size was significantly correlated with total fruit abundance. During the short dry season, when fruit was most scarce, bearded sakis commonly foraged in subgroups. These subgroups appeared to forage completely independently of one another and were isolated by several kilometers, which is well out of auditory range for contact calls. Therefore, the ability to form subgroups seasonally is likely an important behavioral adaptation in bearded sakis that mitigates intragroup feeding competition.

Hypothesis 6: Bearded sakis will increase group spread during feeding and decrease group spread during traveling

This hypothesis was not supported by the results of this study, as group spread showed no significant difference between the two activities. This is consistent with the notion that intragroup feeding competition is not driving changes in bearded saki group cohesiveness throughout the day. Instead, the group moves like an amoeba through the environment expanding and contracting according to changes in intragroup social dynamics rather than due to intragroup feeding competition. The group begins each day as a relatively cohesive unit, group spread fluctuates throughout the day, and then the group coalesces as dusk approaches. Social cohesion is maintained by contact calls and the upper limit to group spread is likely determined by the distance contact calls can be heard by conspecifics.

Hypothesis 7: Bearded sakis will increase daily path length during months of resource scarcity or when feeding on lower quality patches.

The data presented in this dissertation do not support this hypothesis. Bearded saki path lengths did not show significant intermonthly variation and path length was not correlated with monthly fruit abundance, patch quality, or group size. These results suggest intragroup feeding competition is not determining daily path length in the study group. Instead, bearded sakis travel long distances throughout the year, independent of group size or resource quality. I suggest that long daily path lengths are a necessary component of the bearded saki sclerocarpic seed predator niche. The apparent lack of highly specialized gut adaptations may require bearded sakis to visit numerous different tree species each day to avoid accumulating any one type of toxin or secondary compound. Thus, daily ranging behavior is not dictated by either the abundance of resources in patches or the decreased energy per individual when group sizes are large, but rather by the need to obtain a proper nutrient balance when exploiting resources high in secondary compounds.

The Bearded Saki Niche

Synthesizing these results provides a summary of the ecological niche occupied by bearded sakis in the Upper Essequibo Conservation Concession in Guyana. Bearded sakis are sclerocarpic seed predators with a highly specialized dental morphology adapted to accessing and masticating mechanically protected seeds. Consistent with these dental adaptations, they rely on seeds, both immature and mature, for a vast majority of their diet. However, they do not additionally possess a gut morphology specialized for digesting secondary compounds and toxins commonly associated with seeds. Therefore, bearded sakis must range over large distances each day and throughout the year to exploit a tremendous variety of plant species (an average of 50 per month and more than 215 during the course of the study) to avoid consuming too many toxins from any one species. Their ability to consume plant parts from virtually any tree species, including some of the most abundant species, as well as their huge home range that includes a variety of habitat types, buffers bearded sakis from intragroup feeding competition during most of the year. The bearded saki group moves fluidly through its home range, expanding and contracting throughout the day but coming together at night. These group expansions and contractions are independent of changes in patch quality and are likely related to intragroup social dynamics.

When resources become scarce during the short dry season, bearded sakis exhibit several behavioral strategies that mitigate intragroup feeding competition. First, they divide into independently foraging subgroups. Second, they become food item generalists, incorporating high percentages of mature fruit, insects, and flowers in their diet. Finally, bearded sakis may be buffered by the presence of fat stores accumulated by increasing foraging effort during periods of resource abundance.

It is important to note that, like Sussman and Garber (2011), I am not suggesting that intragroup feeding competition has not played an important role in shaping the behavioral ecology of bearded sakis. Minimum group size in saki appears to be primarily determined by the quality and number of food patches and subgrouping is clearly an adaptation for mitigating intragroup feeding competition when resources are most scarce because food patches are fewer and of poorer quality. But it is precisely this ability to temporarily adjust group size, as well as adjust activity patterns and increase the types of resources exploited, that prevents intense intragroup feeding competition throughout the year.

Due to the stability of the forest and associated ecological community at this study site, intragroup feeding competition is unlikely to be currently driving evolutionary changes in bearded sakis (Fuentes 2011, Sussman and Garber 2011). The data outlined throughout this dissertation show that bearded sakis are extremely well adapted for avoiding feeding competition despite the seasonally variable ecological condition in the UECC. Therefore, unless the ecological conditions change drastically (e.g., forest fragmentation, change in the ecological community structure from hunting or disease), intragroup feeding competition will not function as a selective pressure driving evolutionary change in *Chiropotes sagulatus* at this study site.

The results presented above and elsewhere in this dissertation provide important insight into a poorly known topic: the foraging strategy and behavioral ecology of bearded sakis in continuous forest. In addition, these results suggest the behavior of bearded sakis in many previous studies of the genus *Chiropotes* may not be species-typical behavioral patterns (van

Roosmalen et al. 1981, Ayers 1989, Norconk and Kinzey 1994, Ferrari and Lopes 1996, Ferrari et al. 1999, Peetz 2001, Boyle 2008, Silva and Ferrari 2009). Data from previous research on the genus *Chiropotes* differs from that of the present study in several ways. While some of this variation is likely due to species differences or the different plant composition at the study sites, I suggest that the primary explanation for these differences is the fragmented nature of these habitats. Bearded sakis in most of the previous studies may be exhibiting behavioral responses to resource scarcity year round because of the marginality of these habitats. This marginality may explain why previous reports of bearded saki group sizes are much smaller than that of my study group. In several studies, researchers have shown a clear relationship between the size of the forest fragment inhabited by *Chiropotes* and their group size (Veiga 2006, Boyle 2008, Silva and Ferrari 2009, Boyle and Smith 2010). In addition, day range lengths and ranging patterns appear to be highly affected by forest fragmentation in bearded sakis. Finally, group cohesiveness is almost certainly affected by fragmentation and anthropogenic disturbance. The data presented in Chapter 6 indicate that bearded saki group size is strongly related to food patch quality. It is probable that patch quality in fragmented habitats is lower throughout the year, necessitating correspondingly small group sizes. More data from bearded saki populations living in continuous forest is necessary to assess the extent to which these differences represent species typical variation or behavioral responses to anthropogenic disturbance.

Comparative Ecology of the Pitheciines

The pitheciines are united by their specialized anterior dentition adapted for sclerocarpic foraging. All three genera show this highly derived dental morphology and exhibit a correspondingly high reliance on seeds in their diet (van Roosmalen et al. 1988, Soini 1986, Ayers 1989, Kinzey and Norconk 1993, Peres 1993, Setz 1993, Norconk 1996, 2007, Homburg 1997, Aquino 1998, Boubli 1999, Defler 1999, Peetz 2001, Barnett et al. 2005, Veiga 2006, Veiga and Ferrari 2006, Bowler 2007, Norconk et al. 2009, Palminteri et al. 2009, Boubli et al. 2010). Bearded sakis and uakaris appear to consume a higher percentage of seeds than any other primates (Norconk et al. 2010).

The seed-eating niche currently occupied by *Chiropotes*, *Pithecia*, and *Cacajao* appears to have a long history in South America. In fact, one of the first shared-derived adaptations to appear in the neotropical primate fossil record is specialized anterior dentition associated with seed eating (Kay and Takai 2008). The first evidence of this adaptation appears in the middle Miocene (12-15 Ma) in Colombia and Argentina. Fossils from these areas show remarkable similarities to the modern saki/uakaris and suggest that the titi monkey clade had separated from pitheciines before15 ma (Kay et al. 2008, Kay and Takai 2008). The fossil record from the middle Miocene also contains a family of extinct species called Soriacebidae that have anatomical adaptations consistent with those used for seed eating. However, they are distinct from pitheciines and may have occupied the seed predator niche independently from but concurrent with the pitheciines.

All pitheciines show a preference for slowly maturing fruit and seeds available in the dry season. This may account for their ability to live in oligotrophic species-poor forests or flooded forests (Boubli et al. 2008, Norconk 2010). The ability to consume a diet composed primarily of seeds has been suggested to somewhat insulate the pitheciines from seasonal shortages of food resources (Ayers 1989, Kinzey and Norconk 1993, Peetz 2001, Bowler 2007, Norconk 2007). Seeds have a much longer temporal availability than ripe fruit and are an important source of protein, lipids, and fiber (Kinzey and Norconk 1993). The results of this study are consistent with the hypothesis that the ability to exploit various types of slowly maturing and dry fruits is central to the bearded saki niche. Bearded sakis in this study appear to have an abundance of resources they are able to exploit during the long-dry season, a period when primates in many other forests are experiencing maximum resource scarcity. While this was the period of greatest mature fruit availability at this study site, these mature fruits were, for the most part, not fleshy fruits that could be exploited by other primates. A majority were dry fruits like pods, pyxidium, and legumes that do not provide nutrients to animals that are unable to access their seeds. Thus, while overall fruit availability was highest at this time, non-pitheciine primates may have faced resource scarcity.

Seed eating adaptations make the pitheciines extremely well adapted to the forests of the Guianan Shield and northern Brazil. Many species of plants that produce dry fruits with mechanically protected seeds are highly abundant in the ancient Guiana Shield forests (Mori 1989, ter Steege and Zondervan 2000, ter Steege et al. 2006). Several botanical surveys have shown that legumes (especially those in Caesalpiniaceae and Fabaceae), as well as plants in Lecythidaceae and Chrysobalanaceae, are much more abundant and species diverse in the forests of the Guiana Shield than those of western Amazonia (ter Steege 2000, ter Steege et al. 2006). These families are characterized by dry dehiscent and indehiscent fruits and pods and feature prominently in the diets of all three genera of Pitheciini at every site they have been studied (Norconk 2007). These families are much less well represented in western Amazonia, where families that are rare in the Guiana Shield (e.g., Moraceae and Bombacaceae) are dominant. Seven of the top ten genera in the Guiana Shield are legumes while none of the top ten in Western Amazonia are (ter Steege et al. 2006). The ten most abundant Guiana Shield genera (*Carapa*, *Lecythis*, *Aldina*, *Pentaclethra*, *Alexa*, *Dicorynia*, *Eperua*, *Catostemma*, *Mora*, and

Dicymbe) are some of the most important genera in the diet of the Pitheciini, especially uakaris and bearded sakis (Norconk 2007). Many Lecythidaceae species appear to have originated in the Guiana Shield and only recently expanded their range to parts of the Amazon Basin (Mori 1989).

Another characteristic of the forests of the Guiana Shield and northern Brazil that distinguish them from western Amazonian forests and is likely of extreme importance to the Pitheciini is that they are composed of trees with much larger seeds (ter Steege 2000, ter Steege et al 2006). According to ter Steege et al. (2006: 445), "average community seed mass increases by more than an order of magnitude along the main compositional gradient from southwest Amazonia to central Guyana. The increase…is driven by an increase in seed mass of both legumes and non-legumes." They reported that legumes had a 20% higher average seed mass than non-legumes in the Guiana Shield but were similar in size to non-legumes in western Amazonia. Larger seeds are particularly common in the seasonally flooded, black-water *igapo* habitats that make up much of the range of *Cacajao*. Several studies have shown that pitheciines, especially bearded sakis and uakaris, prefer larger seeded species (Ayers 1986, Norconk 1996, Bowler and Bodmer 2010, Norconk and Veres 2011). For example, Ayers (1986) found that uakaris preferentially selected larger seeds and that lipid content was correlated with seed mass. Thus, large seeds and the presence of certain plant families appear to determine habitat suitability for the pitheciines, especially bearded sakis and uakaris.

In a study of the geographic distribution and abundance of the Pitheciini, Stevenson (2001) found that fruit abundance alone did not predict pitheciine biomass or the number of pitheciine species present at 30 neotropical field sites. Instead, the abundance of pitheciines was strongly related to the abundance of trees in the genus *Eschweilera* (Lecythidaceae).

In conjunction with the results of this study, these findings suggest that seed eating evolved in the pitheciines as a way of exploiting the most common fruit species in their habitats throughout the Guiana Shield. The monkeys' ability to exploit mechanically protected seeds, especially those of legumes and species of Lecythidaceae, allows them to take advantage of abundant resources that most other primates in these forests cannot exploit. However, during the months when these resources become scarce, the pitheciines rely on their behavioral flexibility instead of their extreme seed eating adaptations. In addition to being seed-eating specialists, the pitheciines also appear to be behavioral generalists, relying on behavioral and dietary flexibility to subsist during periods of resource scarcity. The limited data available for the genus *Cacajao* shows that, like bearded sakis, they are able to supplement their seed-based diet with a variety of food items, including mature fruit, insects, flowers, nectar, leaves, and pith (Ayers 1986, 1989, Boubli 1999, Aquino and Encarnacion 1999, Barnett et al. 2005, Bowler et al. 2009). In addition, uakaris appear to adjust group size seasonally, not unlike the bearded sakis in this study (Ayers 1986, 1989, Defler 2003, Bowler et al. 2009).

Pithecia, the most studied genus of the Pitheciini, also shows the greatest amount of behavioral variability. *Pithecia* spp. incorporate a high percentage of leaves in their diet in almost all studies, and the genus appears to have several morphological adaptations for folivory (Peres 1993, Norconk 1996, 1998, 2006, 2007, Homburg 1997, Norconk et al. 2003, Setz et al. 2008, Norconk et al. 2009). Sakis also exhibit high levels of flower feeding in some studies and supplement their diet with insects, wasp nests, and nectar as well (Norconk 2007).

Despite their common adaptations for sclerocarpic seed eating, the Pitheciini show considerable variability in their geographic ranges, social behavior, and ranging patterns. *Cacajao* shows the most restricted geographic range, while *Pithecia* shows the broadest

(Norconk 2007). As shown above, the abundance of legumes, Lecythideae, and other plant families that produce dry fruits appears to be a determining factor in the geographic ranges of the pitheciines. Because they are the most specialized of the pitheciines, *Chiropotes* and *Cacajao* appear to be the most dependant on these plant families. The fact that bearded sakis are restricted to forest of the Guiana Shield is consistent with this hypothesis. Similarly, the geographic distribution of *Cacajao* may be limited by the presence of Lecythidaceae, with the western migration of Lecythidaceae genera setting the extent of uakari distribution into western Amazonia (Ayers 1986, Norconk 2007). As species of Lecythidaceae slowly migrated toward western Amazonia, the geographic range of *Cacajao* likely followed. The lack of overlap in the ranges of *Chiropotes* and *Cacajao* probably reflects competitive exclusion, given their extremely similar feeding ecology, locomotion, use of vertical space, and perhaps, according to the results of this study, ranging behavior (Ayers 1986, Boubli et al. 2008, Boubli and Lima 2009). While the two genera do coexist in one area of central Amazonia (Ayers 1986), outside of this small forest their ranges completely abut each other. A recent model of the geographic distribution and niches of *Cacajao* and *Chiropotes* by Boubli and Lima (2009) indicate that geographical barriers (i.e., rivers) do not explain the separation between the genera.

In contrast, *Pithecia* coexists with either *Chiropotes* or *Cacajao* in virtually all areas. They also show the largest geographic range and are found throughout the Guiana Shield, central Amazonia, and western Amazonia. Dietary flexibility and a less specialized dental morphology may make *Pithecia* less limited by the availability of legumes and Lecythidaceae species. The ability of *Pithecia* to incorporate a high percentage of leaves in their diet may contribute to their more flexible habitat requirement. In addition, the flexibility in use of vertical space exhibited by *Pithecia* may have allowed them to disperse across seasonally dry habitats and xeric, scrubby forests. These environments appear to have prevented the migration of bearded sakis into French Guiana. Interestingly, in the absence of sympatric *Chiropotes* or *Cacajao* species, western Amazonian *P. albicans* show larger body sizes, larger home ranges, and a preference for higher-canopy travel than other *Pithecia spp*. (Peres 1993, Norconk 2007). Norconk (2007) suggested this may represent competitive release and is consistent with the Pitheciini radiating out of the Guiana Shield and occupying western Amazonia more recently.

Several studies suggest that, despite dental morphology that is similar to the larger Pitheciini, the seed-eating adaptations of *Pithecia* are quite different. *Chiropotes* and *Cacajao* lump together and both differ considerably from *Pithecia* in several aspects of their dental morphology, including having more robust mandibles, condyles that are longer in an anteroposterior dimension (related to jaw opening ability, load resistance, and/or the need to house enlarged and procumbent anterior teeth), smaller molar areas, and less developed shearing crests (Norconk 1996, Wright 2004, Norconk et al. 2009). Consistent with these differences, bearded sakis show a preference for fruits with much larger breadth and thickness (Norconk et al. 2009). In addition, the gut transit time of *Pithecia* is much longer than that of *Chiropotes* or *Cacajao*. While bearded sakis and uakaris have transit times of about five hours, among the shortest of any platyrrhine, *Pithecia pithecia* and *Pithecia monachus* have transit times in excess of 15 hours. In fact, the only platyrrhine genus with a longer transit time is *Alouatta*. This dramatic difference suggests that *Pithecia* is much better adapted to exploiting resources that are high in secondary compounds like leaves and, possibly, chemically protected seeds.

These differences in morphology between *Pithecia* on the one hand and *Cacajao*/*Chiropotes* on the other suggest that, despite their shared adaptations for seed predation, these two groups are adapted to exploiting slightly different resources. The bearded saki/uakaris are the most specialized sclerocarpic seed predators and are morphologically adapted for exploiting mechanically protected seeds. However, they may be limited in their ability to exploit chemically protected seeds. *Pithecia*, while also adapted for sclerocarpic foraging, appears to be more limited in their ability to exploit mechanically protected seeds. However, they appear to possess a combination of dental and gut specializations that allow them to exploit leaves, and possibly, more chemically protected seeds. Consistent with these adaptations, Norconk et al. (2009) found that *Pithecia* consume a diet high in lipids but also high in dietary fiber. The estimated energy value of their diet was much lower than that of *Cacajao* and *Chiropotes*.

In addition to possibly contributing to their more restricted geographic range, the more highly derived dental morphology of bearded sakis and uakaris (vis-à-vis *Pithecia*) may also explain the extreme differences in group size and ranging behavior between the two groups. I suggest that the large home and day ranges of *Cacajao* and *Chiropotes* are necessary parts of their highly specialized sclerocarpic seed-eating adaptations. The need for balancing the effects of seed toxins and other secondary compounds may require they visit many feeding trees each day. The large group sizes of these two genera may also contribute to the need for large ranges. The positive relationship between group size and day and home range size does not appear to hold true for all primates (Sussman and Garber 2011). The results of several studies of bearded sakis, including this one, indicate that daily group size may not be related to day range length (Boyle and Smith 2010, Gregory and Norconk 2011). Nevertheless, it is certainly possible that these large groups simply need a larger supply area to feed all the individuals appropriately.

Towards a Model of Bearded Saki Socioecology

According to the results of this study, *Chiropotes sagulatus* in Guyana lives in large, multimale-multifemale groups in excess of 60 individuals. Data from the few other studies of *Chiropotes* in continuous forest suggest that large groups are characteristic of the genus, with smaller reported group sizes probably representing a behavioral response to resource scarcity (Boyle 2008, Pinto 2008, Silva and Ferrari 2009, Gregory 2011). If this is the typical group size for bearded sakis, two important questions are raised: how do they avoid the detrimental effects of intragroup feeding competition living in such large groups, and why do they form such large groups? The results presented in this dissertation provide an answer to the first question and offer several possible explanations for the second.

I suggest that bearded sakis at the study site are actually experiencing little intragroup feeding competition because they have evolved a number of morphological and behavioral responses to mitigate its effects. These include flexible activity patterns, an ability to exploit a wide variety of food parts and plant species, and a highly fluid social structure. Not surprisingly, the results presented in this dissertation, which are from a study conducted in a forest where bearded sakis have lived for hundreds of thousands of years, show that they are extremely well adapted to living in this ecological community.

Why then, do these primates form such large groups, especially when other members of the Pitheciini, specifically *Pithecia*, live in extremely small groups? One explanation suggested by the results of this study is protection and vigilance from predation. The bearded sakis at this study site appear to be under high predation pressure from a suite of avian and mammalian predators. I witnessed four attempted attacks by predators, a notoriously rare observation for primate researchers. In addition, the bearded saki group appeared to be constantly vigilant for predators and would often respond skittishly to obviously benign birds (e.g., macaws, which are easily distinguished from any potential avian predator by calls, appearance, flight pattern, and group size). While predation is poorly studied in primates (but see Hart 2000, Gursky and Nekaris 2007, and Ferrari 2009), studies of harpy eagle nest remains also suggest that bearded sakis are an important avian prey species and a successful harpy attack of a bearded saki has been observed (Rettig 1978, Martins et al. 2005).

Bearded sakis seem to preferentially form larger groups when resources allow them to (i.e., during periods of resource abundance and in larger forest fragments). In addition, bearded sakis in this and other studies appear to prefer dense vegetation for resting and socializing, even in areas where they are well habituated (Peetz 2001, Veiga 2006, Silva and Ferrari 2009). Similarly, bearded sakis in this study selected sleeping sites that were lower in the canopy rather than in emergent trees as many neotropical primates do (Milton 1980, Strier 1986, Di Fiore 1999). Sakis also coalesced before dusk and slept in a relatively cohesive group. All of these behaviors suggest predation risk may be quite high for the monkeys.

In contrast, *Pithecia* relies on cryptic behavior to avoid predation. Except for male white-faced sakis, *Pithecia* is among the most cryptically colored neotropical primates (Hershkovitz 1968, Ferrari 2009). All other *Pithecia* individuals exhibit a mottled gray pelage, a variation of the agouti pattern in which “alternate light-dark banding of the hairs results in a fuzzy visual effect, which may be especially effective in complex environments such as that of the tropical forest” (Ferrari 2009: 257). *Pithecia* species are characterized by their preference for the lower levels of the forest canopy and understory, rarely traveling into the middle or upper canopy (Fleagle and Mittermeier 1980, Fleagle and Meldrum 1988, Walker 1996, Norconk 2007). In addition, sakis are notoriously cryptic and difficult to observe, exhibiting periods of rapid travel followed by long periods where they remain motionless in dense vegetation (Norconk et al. 2003, Norconk 2006, Norconk 2007, Setz et al. 2008, Ferrari 2009).

Perhaps one explanation for the differences in behavior observed in the Pitheciini is that the more extreme seed eating specializations of *Cacajao* and *Chiropotes* require them to travel further and be more active to obtain the proper nutrient balance from an extremely seed based diet. This high level of activity and need to be constantly on the move may expose them to predation more and make crypticity an untenable anti-predator strategy. In addition, the high percentage of the day bearded sakis and uakaris spend in the upper parts of the canopy may make them particularly vulnerable to avian predators. Few other neotropical primates, especially of comparable body size or smaller, are as highly arboreal as *Chiropotes* and *Cacajao*. *Chiropotes* and *Cacajao* appear to spend a higher percentage of their time in the highest levels of the canopy than any other platyrhinnes. The only new world primates that show similar vertical stratification preferences, like *Ateles*, *Lagothrix*, and *Brachyteles*, are much larger than the saki/uakaris (Ferrari 2009, Di Fiore et al. 2011).

Pithecia spend most of their time in the understory, where attack from avian predators is much less likely. As mentioned above, *Chiropotes* and *Cacajao* are the most highly specialized of the pitheciines and appear to be so highly tied to seed eating that their geographic range is limited by the presence of certain plant families. Therefore, it may be that long day ranges, large home ranges, a high activity level, and large group sizes represent a suite of adaptations that complement being a highly specialized seed eater.

While protection from predation provides a functional benefit to group living in primates, recent research suggests that individuals may be expected to form groups, even when the functional benefits of doing so are minimal (Johnson et al. 2002, Sussman et al. 2005).

According to the resource dispersion hypothesis (RDH), “if resources are heterogeneous in space or time, group living might be less costly than previously thought, regardless of whether individuals gain direct benefits from group membership” (Johnson et al. 2002). These researchers argue that if resources are patchily distributed and relatively abundant in an area occupied by a single animal, there will be an excess of resources some or all of the time in that area, and these excess resources are sufficient to sustain additional animals.

> The smallest territory that will support a primary pair might also support additional individuals at minimal cost to the primary occupants and without any requirement for cooperation between them. This is because where resource patches are heterogeneous (in space and/or time), primary animals will have to defend a relatively larger area to include sufficient potential resource patches to guarantee some critical probability of encountering enough usable patches over time. (Johnson et al. 2002)

As the resources exploited by primates are almost always patchily distributed in space and time, the RDH provides a potentially powerful explanation for primate grouping behavior. In combination with the functional benefit of increased vigilance from predators, the RDH provides an explanation for the large groups formed by *Cacajao* and *Chiropotes* that does not invoke feeding competition as the driving force.

The results of this and previous studies of bearded sakis can be synthesized to produce a model of bearded saki socioecology (Figure 7.1). This model explains the large home and day ranges and large group sizes of *Chiropotes* as behavioral adaptations necessitated by their seed predator niche. According to this model, the bearded saki sclerocarpic seed predator niche requires them to range over large distances each day to obtain a proper nutrient mix and balance the effects of seed secondary compounds. The need for large daily path lengths, as well as the correspondingly high percentage of the day spent traveling and preference for the highest levels of the canopy (combined with small body size), exposes bearded sakis to high predation risk, especially from avian predators. This high predation risk causes bearded sakis to preferentially form large groups, as more individuals allows for increased vigilance and facilitates mobbing as an anti-predator strategy. These large groups, in turn, contribute to the need for large home and day ranges.

Therefore, I suggest that bearded saki group size is not dictated by intergroup feeding competition, infanticide protection, or territorial defense, but by the need for increased vigilance from predators in a highly active, highly arboreal, small-bodied seed predator. The lack of evidence for intragroup feeding competition during most of the year, the numerous behavioral adaptations that bearded sakis exhibit to mitigate intragroup feeding competition, and the predictions of the RDH indicate that feeding competition does not set the upper limit for bearded saki group size. Instead, the maximum number of animals in bearded saki groups is likely dictated by the ability of group members to maintain social cohesion. Bearded sakis may simply not be able to maintain contact with each other and coalesce at the end of the day if group sizes exceed a certain level (perhaps 60-70 animals).

This model may also explain the similar ranging behavior, large group sizes, and group fissioning patterns of the genus *Cacajao*. As shown above, uakaris appear to have extremely similar morphological adaptations and dietary preferences to bearded sakis. In addition, they exhibit extremely large home and day ranges similar in size to those of the bearded sakis in this study. Further, they are also highly active, prefer the upper levels of the canopy, and are even more conspicuously colored than bearded sakis. Unfortunately, there is even less data on the behavioral ecology of uakaris than for bearded sakis. Therefore, the applicability of this model to uakari socioecology is difficult to assess.

This model does appear to account for the behavioral differences exhibited by *Pithecia*. The different seed-eating niche occupied by *Pithecia* (ability to consume more chemically protected seeds and leaves) means they do not require as large of a supply area and do not have to travel as far per day as the bearded saki/uakaris. This allows them to be much less active and rely on crypticity to avoid predation. The lack of predation risk makes small group sizes possible.

The lack of data from long-term studies of the genus *Chiropotes*, especially in continuous forests that possess a healthy community of avian predators, make currently testing this model difficult. However, this model provides a context for understanding the socioecology of the genus given what limited data is currently available. In addition, it provides a framework for generating testable hypotheses in future studies of bearded sakis and the other pitheciines.

The Role of a Primate Seed Predator in the Wider Ecological Community

Bearded sakis and the other pitheciines are generally referred to as seed predators because they destroy the seeds that they consume. Most primates, on the other hand, are important seed dispersers, playing a critical role in the maintenance of forest communities (Terborgh 1983, Garber 1998, Lambert et al. 1998, Chapman 2007). This contrast raises an interesting question: what is the role of a primate seed predator within the wider ecological community? Are bearded sakis a sort of rainforest “freeloader,” destroying the embryos of trees while providing them no benefit?

There is an extensive literature on the role that seed predators play in ecological communities (Janzen 1971, Waller 1979, Dirzo and Dominguez 1986, Smythe 1986, Bodmer 1991, Peres and Baider 1997). One of these roles is increasing the heterogeneity of forests by limiting the abundance of certain plant species (Paine and Beck 2007, Lewis and Gripenberg 2008, Ferreira et al. 2010). For example, Paine and Beck (2007) found that post-dispersal seed predation by small mammals significantly increased plant species richness in a neotropical forest via disproportionately intense predation on common and large-seeded species. Most of the research on the effect of seed predation on forest composition has focused on either insect predators or post-dispersal seed predators, like ungulates and rodents. There is almost no data on the extent to which primate seed predators might play this role in rainforests. However, the results of this study show that bearded sakis heavily exploit the seeds of some of the most dominant tree species (e.g., Wamara, Wallaba). In addition, like the seed predators in the study by Paine and Beck (2007), bearded sakis and uakaris preferentially consume large seeds. It is possible, therefore, that sakis play some role in increasing habitat heterogeneity.

In addition to acting as pre-dispersal seed predators, bearded sakis appear to be important facilitators for post-dispersal seed predators like fish, terrestrial ungulates, and some bird species. Post-dispersal seed predators include a variety of fungi, insects, small and large mammals, birds, and fish in flooded forests (Janzen 1971, Bodmer 1991, Paine and Beck 2007, Anderson et al. 2009). Bearded sakis in this study were extremely messy feeders, dropping many fruits in various stages of processing during almost every feeding bout. I was unable to assess the extent to which this behavior was intentional (i.e., whether fruits were discarded because they were deemed nutritionally poor or too im-/mature). However, it appeared that in most cases, individuals were simply grabbing fruits haphazardly. The large quantities of fruit dropped during bearded saki feeding frequently attracted post-dispersal seed predators, including peccaries (*Tayassu tajacu* and *T. pecari),* brocket deer (*Mazama americana*), tapir (*Tapirus terrestris*), terrestrial birds (like the black curassow, *Crax alector*), and many species of fish when the study group fed in inundated portions of their home range. Groups of collared peccaries (*T. tajacu*), were especially commonly observed under bearded saki feeding trees. As these terrestrial and aquatic seed predators are unable to access immature seeds of most tree species (fruit fall does not occur until fruits are mature), they may be highly dependent on the messy feeding behavior of bearded sakis.

Finally, I suggest that, in addition to being highly specialized seed predators, bearded sakis may actually be important seed dispersers as well. Norconk et al. (1998) argued that pitheciines may disperse seeds by manipulating them in ways that enhance germination (assuming those seeds are subsequently discarded) and by swallowing small seeds intact and then dispersing them through defecation. I was unable to assess the extent to which bearded sakis might disperse seeds by the latter method as I did not measure the size of small seeds ingested during mature fruit consumption. While Norconk et al. (1998) suggested dispersal by the former method was rare in pitheciines, evidence from this study suggests that the feeding behavior of bearded sakis may be an important dispersal mechanism for several plant species.

As shown in Chapter 5, many of the fruits eaten by the study group were indehiscent pods or capsules, meaning they do not open at maturity and rely on other mechanisms, like decay or the action of seed predators, to expose their seeds. Many post-dispersal seed predators serve this function, and some plant species with indehiscent fruits are so dependent on seed predators for dispersal that the plants cannot survive without them (Peres and Badier 1997, Asquith 1999). As discussed above, bearded sakis in this study were tremendously messy feeders, dropping large quantities of fruits and seeds in all stages of mastication. Individuals would often open pods and drop several of the contained seeds unharmed. Because they were constantly on the move and often ate while traveling, bearded sakis would frequently drop fruits and seeds quite far from the parent tree (as much as 1 km!). Therefore, it is quite possible that sakis were increasing the probability of germination for these seeds not only by opening indehiscent pods but also by carrying the seeds away from the seed shadow of their parent tree. This foraging behavior may also facilitate dispersal of large fruits (like *Pouteria speciosa*) whose seeds were left intact and whose size and pericarp toughness made dispersal by other animals unlikely. Finally, the messy feeding behavior of bearded sakis may help disperse seeds through the actions of secondary dispersers. Intriguingly, Anderson et al. (2009) found that three common frugivorous fish species in Amazonia were seed dispersers for 35% of tree and liana species that fruited during the flooding season. The large groups of fish gathered below the feeding trees that bearded sakis exploited in flooded portions of their home range suggests the monkeys may contribute to dispersal by providing the fish with more fruit to disperse. While anecdotal, these observations indicate that seed dispersal in bearded sakis is certainly deserving of future research.

Future Directions

The results of this study reveal several important avenues for future research on the behavioral ecology of bearded sakis. In addition, the methodology utilized in this dissertation to quantify food patches and group spread through GIS has important applications for future studies of primate behavioral ecology.

Perhaps most importantly, more research into the nutritional properties of the seeds eaten by the bearded sakis in this study and those in other studies is necessary to test the hypothesis that ranging behavior is related to the need to avoid the accumulation of any specific secondary compound. In addition, nutritional information is important for understanding why bearded sakis exploit so many individual trees even when they appear to have an abundance of fruits to eat and why they appear to frequently leave feeding trees full of fruits.

The subgrouping behavior of bearded sakis also requires more research, especially the extent to which bearded saki subgroups coordinate their activities. If these subgroups are independently foraging units that are out of vocal range from each other, how do they subsequently coalesce? Is coalescence accidental or are individuals in different subgroups communicating with each other through some other means? Is the ranging behavior of each subgroup truly independent or are they somehow coordinated?

Additionally, nothing is known about the dispersal patterns of bearded sakis. Questions about which sex disperses from their natal groups, at what age individuals begin to disperse, and to what extent male affiliation is related to relatedness between males are currently impossible to answer in bearded sakis because no researchers have been able to identify individual animals.

Further, more studies of the different species of *Chiropotes* in continuous forest are necessary to determine the extent to which observed populational differences in behavioral ecology are a result of species/habitat differences or represent responses to anthropogenic disturbance.

The role of bearded sakis within the wider ecological community is also poorly understood. The results of this study suggest that bearded sakis play many roles in their ecological community, including changing forest composition through seed predation, increasing access to immature seeds for post-dispersal seed predators, and dispersing the seeds of plant species with indehiscent fruits. More data are needed to detail the extent to which bearded sakis fulfill these roles. The dietary overlap of bearded sakis with the other primates in their community was not addressed in this study. Therefore, documenting the niches of the other seven primates in the UECC is necessary to further elucidate the ecological place of bearded sakis. As shown in Chapter 5, macaws appear to belong to the same ecological guild (seed predators adapted to sclerocarpic feeding) as bearded sakis at this study site. Exploring the extent to which these two taxa compete for resources is another interesting direction for future research. The Concession preserves a remarkably complete ecological community, with a full compliment of sympatric primates, other seed-predators, and predators. It is, therefore, the perfect place to study the community ecology of a Guiana Shield lowland rainforest.

Finally, the methodology used in this study to quantify food patches using GIS has important applications for future studies of the relationship between primate behavioral ecology and the spatial distribution and quality of food patches. While GIS have been increasingly utilized by primatologists in the past decade, their use has generally been restricted to population level research questions or the calculation of home and day ranges (Boyle et al. 2008, but see Gregory 2010). While these are excellent uses of the technology, GIS represents a powerful tool for answering any research question that includes a spatial component. Primatologists have traditionally analyzed behavioral and ranging data separately. However, every behavioral data point also has a spatial component (i.e., every observed behavior is affected by the spatial context in which it occurs). GIS allows the researcher to simultaneously analyze these two types of data, providing a much more powerful data analysis for primate behavioral ecology.

As shown in this study, GIS can be used to quantify food patches and group spread, two notoriously difficult variables to measure. The concept of food patches is central to most models of primate socioecology yet researchers have struggled to find a suitable definition for what constitutes a patch. While there are certainly deficiencies in the way patches were defined in this study, I attempted to improve on previous definitions by using two spatial scales and defining patches in a way that incorporates more than one feeding tree. The fact that patch quality as defined in this study explained between 50% and 80% of the variation in bearded saki group size indicates this is an extremely robust method for defining patch quality. I intend this definition to be merely a starting point that allows for future improvements and species-specific applications. Possible future directions include adding a component that incorporates the nutritional quality of each plant species and quantifying patches for non-plant food items like insects.

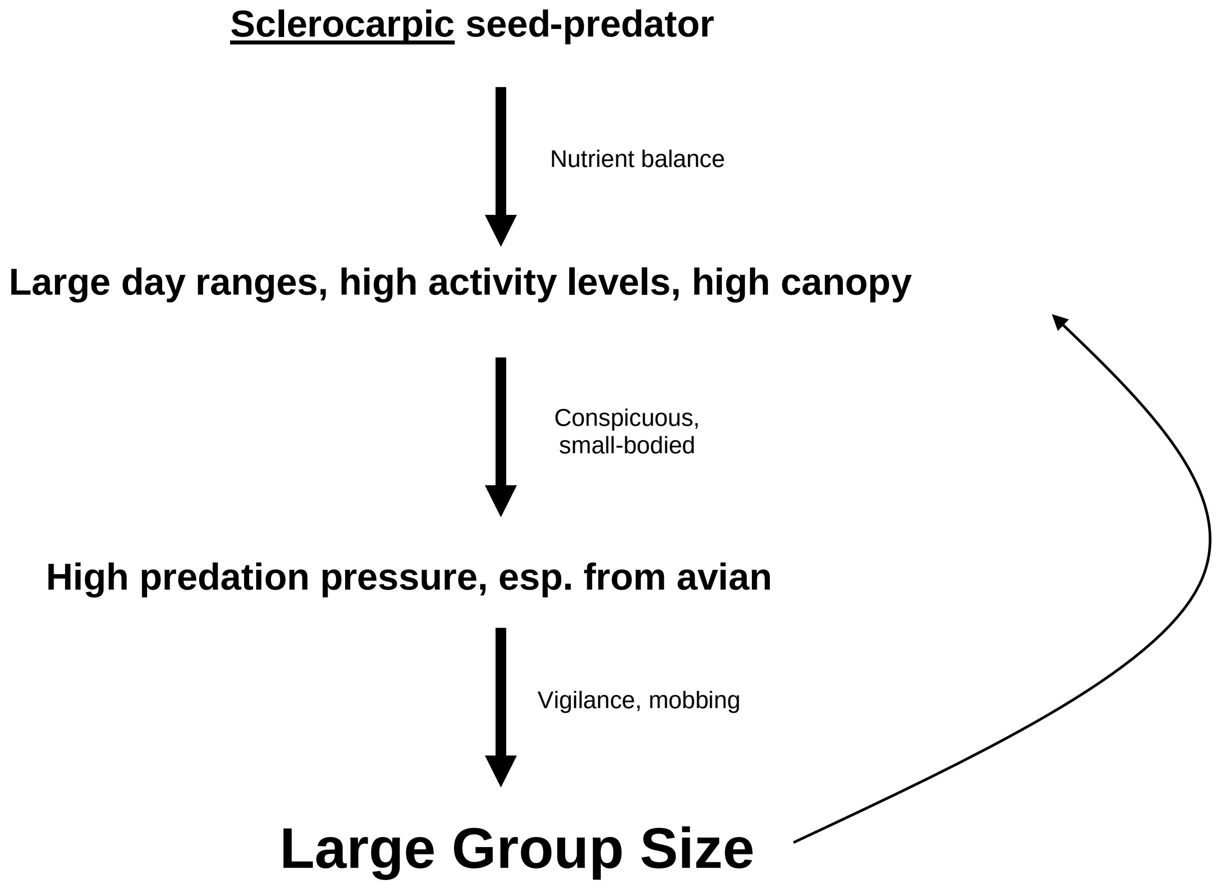
Conservation

Of the five species currently recognized in the genus *Chiropotes*, three (*Chiropotes satanas*, *C. albinasus*, and *C. utahickae*) are listed by the IUCN red list as threatened or endangered (Veiga et al. 2008). These species show more restricted ranges than the other *Chiropotes* species and are threatened primarily by forest fragmentation. *C. sagulatus* is listed as "least concern", predominantly due to the presence of vast tracts of primary forest throughout much of its' geographic range (Suriname and Guyana). Understanding how primates respond to forest fragmentation is critical for primate conservation as fragmented habitats are an unfortunate reality for most primates (Ferraz et al. 2003, Marsh 2003, Boyle and Smith 2010). Obviously, protecting the primates that have been made endangered by fragmentation is of the utmost priority.

However, equally important is protecting those species that are not currently endangered because they are still present in vast tracts of continuous forest. Protecting these continuous forests is critical, even if most of the species they harbor are not yet endangered. This is especially true for animals like bearded sakis that appear to require large areas of continuous forest. While island and fragment studies have shown that bearded sakis can inhabit forest fragments that are only a fraction of their typical home range (even 1 ha), recent data suggests that the long-term viability of these populations is questionable. For example, the behavior of bearded sakis in some of these landscapes suggests they are under considerable food stress (Silva and Ferrari 2008, Boyle and Smith 2010). Also, Boyle and Smith (2010) found that there had not been a successful birth in at least 3.5 years in either of two bearded saki groups occupying 10 ha forest fragments.

In addition, because of their extremely large home ranges, the conservation of bearded sakis facilitates the conservation of many other less wide-ranging species. Unfortunately, many of these vast tracts of continuous forest are imperiled. In 2010, the Guyanese government granted a logging concession that surrounds the UECC on three sides, including upriver (GFC 2010). While the logging company, a United States based company called Simon and Shock International, has promised to execute a careful environmental impact study before extracting any timber, it is unclear how much longer these forests will remain continuous without intervention. It is, therefore, critical that conservation strategies target the few continuous forest tracts that remain in the neotropics before these forests become highly fragmented, when it may already be too late for many species.

Figure 7.1. Proposed model of bearded saki socioecology.



APPENDIX 1 – ETHOGRAM AND DEFINITIONS OF OTHER BEHAVIORAL VARIABLES

DEFINITIONS OF BEHAVIORS

Behavioral categories used in this study were *feed*, *move*, *travel*, *rest*, *social*, and *other*. These categories were mutually-exclusive. Definitions were derived from observations during the habituation period and previous research of bearded sakis, especially Ayers 1968, Peetz 2001, and Boyle 2008.

Feed

The active ingestion of a food item or the manipulation of a food item prior to ingestion. This category included the action of picking food items off branches and any obvious searching for insect prey (i.e. searching through dead leaves or dried fruit pods). Whenever this category was recorded, the type of food item, its maturational state, and the species (if it was a plant) were also recorded.

Food Types

Fruit – Either the entire fruit (including the seed) was eaten or the pericarp, mesocarp, and or aril were eaten and the seed discarded.

Mature Fruit – The fruit had reached the apex of maturity, indicated by color, size, and hardness.

Immature Fruit – The fruit was still in the process of developing

Seed – Either the whole seed, or part of the seed (i.e. cotlydon, endosperm, embryo, or seed coat) was ingested

Mature Seed – A seed from a mature fruit (see above)

Immature Seed – A seed from an immature fruit.

Flower – The flower (all or part) was ingested. This category did not include the ingestion of nectar without eating any part of the flower. Nectar feeding was not observed in this study.

Insect – The ingestion of or process of searing for invertebrates.

Pith – The central meristem of a plant.

Water – Drinking water directly from a tree cavity or a bromeliad.

Other – Any food type not listed above

Unknown – I was unable to ascertain the type of food item being consumed.

Move

Vertical or horizontal movement within a single tree crown that was not food oriented. Moving was distinguished from travel in that it was confined to a single tree.

Travel

Movement from one tree crown to another. If an individual moved from one crown to another and then quickly returned, this was still classified as travel.

Rest

To be stationary; either asleep, lying or sitting, or passively examining the environment.

Social

To be engaged in one of the behaviors listed below. Social behavior could be an event or a state. An attempt was made to determine the exact length of social interactions that were states but, as social behavior was not the focus of this study, and the study group was difficult to observe, these were only recorded ad libitum.

Social Rest – To rest in extremely close proximity to each other, usually touching.

Groom – to deliberately manipulate the fur of another animal, picking or brushing.

Animals would clearly seek out other individuals to rest next to.

Huddle – To line up in a group of two to six (most commonly a group of two or three). Animals would rub their bodies together and appeared to synchronize the wagging of their tails, in addition to vocalizing with soft whistles that were not heard at any other time.

Play – to engage in animated behaviors (including wrestling, chasing, and grabbing) with no evidence of threatening behavior or aggression.

Displace – to approach another animal within 2 m and have that animal retreat.

Chase – to rapidly approach another animal in an obviously threatening manner (as opposed to play), usually accompanied by an aggressive facial display or vocalization.

Copulation – to mount another animal in a sexual manner and thrust rhythmically.

Grab – to physically grab another animal in an obviously threatening manner (as opposed to play)

Attack – to physically attack (i.e. bit, hit) another animal in an obviously threatening manner

Other

To engage in any other behavior than those listed above. The *Other* category consisted almost entirely of vocalizations.

DEFINITIONS OF AGE-SEX CLASSES

Because of the difficulties involved in observing bearded sakis, only four age-sex categories were used in this study. These categories were mutually exclusive.

Adult Male – A full grown male with typical bearded saki secondary sexual characteristics (i.e. larger body size than females, more developed temporal swellings, larger beard, and testicles [if these could be observed])

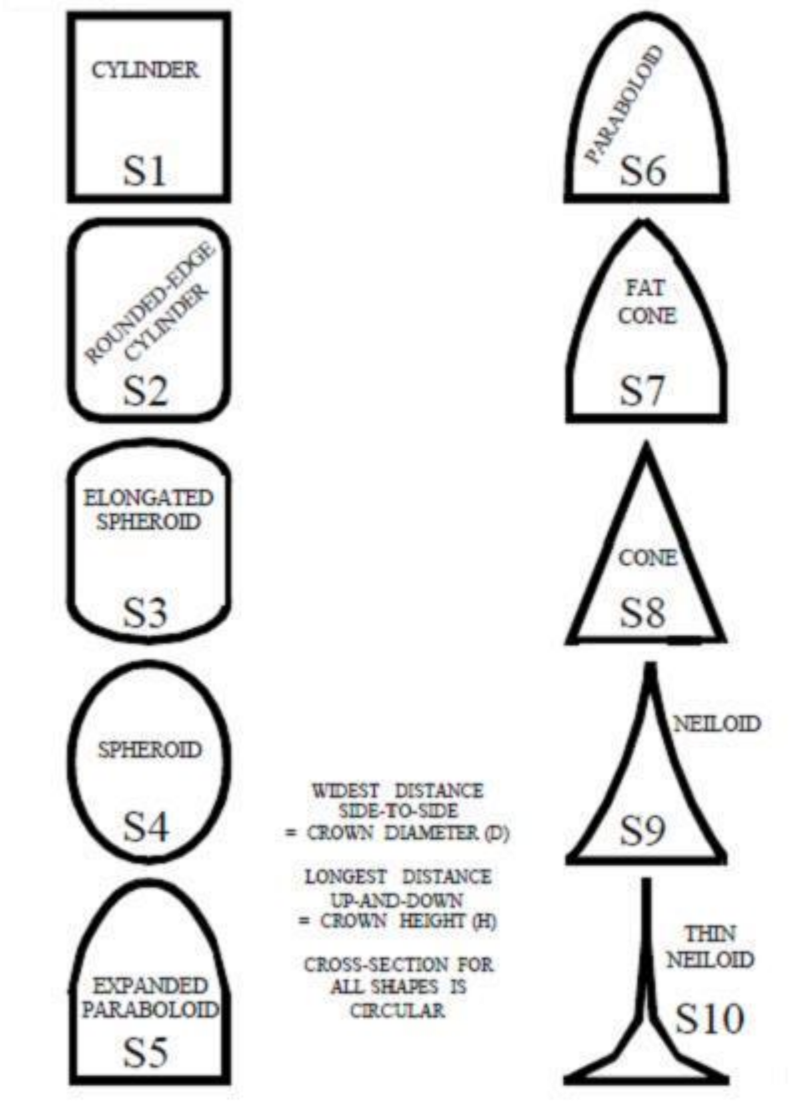
Adult Female – A full grown female. Females were distinguished from adult males because they lacked the secondary sexual characteristics listed above and were slightly smaller than males. They were easily distinguished from juveniles because of their beards and temporal swellings. Despite females having smaller beards and temporal swellings than males, these characteristics were almost completely absent in juveniles.

Juvenile – An immature individual that was not fully grown and lacked a prominent beard or temporal swellings but spent time foraging and traveling on its own. Juveniles were occasionally carried by their mothers during travel. The sex of juveniles was virtually impossible to determine.

Infant – An immature individual that was always carried by its mother and was never observed locomoting independently.

APPENDIX II. CROWN VOLUME SHAPES AND FORMULAE (MODIFIED FROM CODER 2000).

Crown Shapes



Crown Volume Formulae

Shape	Shape Value	Shape Formula	Shape Name
S1	8/8	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.7854)	Cylinder
S2	7/8	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.6872)	Rounded-edge Cylinder
S3	3/4	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.5891)	Elongated Spheriod
S4	2/3	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.5236)	Spheriod
S5	5/8	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.4909)	Expanded Paraboloid
S6	1/2	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.3927)	Paraboloid
S7	3/8	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.2945)	Fat Cone
S8	1/3	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.2619)	Cone
S9	1/4	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.1964)	Neiloid
S10	1/8	$(\text{Crown Diameter})^2$ x (Crown Height) x (0.0982)	Thin Neiloid

APPENDIX III. ALL PLANT SPECIES RECORDED IN BOTANICAL TRANSECTS DURING THE STUDY PERIOD.

Common Name	Scientific Name	Family	% basel Area	# of Indv	% of Indv
Wamara	Swartzia leiocalycina	Fabaceae: Papilionaceae	6.54%	23	5.19%
Wadara	Couratari guianensis	Lecythidaceae	5.11%	14	3.16%
Mora	Mora excelsa	Fabaceae: Caesalpiniaceae	4.59%	14	3.16%
Wallaba	Eperua falcata	Fabaceae: Caesalpiniaceae	3.90%	13	2.93%
Mahicaballi	Phyllanthus spp.??	Euphorbiaceae	3.17%	19	4.29%
Hiawaballi	Tetragastris altissima	Burseraceae	3.15%	10	2.26%
Kauta	Licania alba	Chrysobalanaceae	3.00%	14	3.16%
Black Kakerelli	Eschweilera sagotiana	Lecythidaceae	2.52%	13	2.93%
Crabwood	Carapa guianensis	Melastomataceae	2.48%	10	2.26%
Sheu	??	??	2.45%	12	2.71%
Sand Baromalli	Catostemma fragrans	Bombacaceae	2.37%	11	2.48%
Asepoko	Pouteria guianensis	Sapotaceae	2.35%	14	3.16%
Maporokon	Inga alba	Fabaceae: Mimosaceae	2.24%	12	2.71%
Wina	Eschweilera corrugata	Lecythidaceae	2.04%	11	2.48%
Manaca	Euterpe edulis	Palmae	1.81%	14	3.16%
Pear Leaf Silverballi	Ocotea spp.	Lauraceae	1.72%	1	0.23%
Sincona	Geissospermum sericeum	Apocynaceae	1.70%	7	1.58%
Dukaliballi	Brosimum parinarioides	Moraceae	1.69%	4	0.90%
A	Prieurella spp.	Sapotaceae	1.57%	3	0.68%
Hiariballi	Alexa wachenheimii	Fabaceae: Papilionaceae	1.57%	3	0.68%
Asashi	Rheedia spp.	Guttiferae	1.56%	13	2.93%
Maho	Sterculia rugosa	Sterculiaceae	1.48%	6	1.35%
Red Ruri	Chaetocarpus schomburgkianus	Euphorbiaceae	1.37%	6	1.35%
Kaditiri	Sclerolobium guianense	Fabaceae: Caesalpiniaceae	1.31%	4	0.90%
Tibikushi	Brosimum guianense	Moraceae	1.15%	5	1.13%
Aromata	Clathrotropis macrocarpa	Fabaceae: Papilionaceae	1.10%	8	1.81%
Simarupa	Quassia simarouba	Simaroubaceae	1.08%	2	0.45%
Wild Cashew	Anacardium giganteum	Anacardiaceae	1.07%	1	0.23%
Marishiballi	Licania densiflora	Chrysobalanaceae	1.05%	7	1.58%
Ulu	Trattinickia demerarae	Burseraceae	1.03%	2	0.45%
Baromalli	Catostemma commune	Bombacaceae	1.00%	6	1.35%
Ballata	Manilkara bidentata	Sapotaceae	0.99%	3	0.68%
Glasswood	??	??	0.95%	4	0.90%
Asepokoballi	Pouteria caimito	Sapotaceae	0.88%	4	0.90%
Silverballi	Ocotea wachenheimii	Lauraceae	0.86%	5	1.13%
Guavaballi	??	??	0.78%	6	1.35%
Buruma	Pourouma guianensis	Moraceae	0.75%	2	0.45%
Lu	Oenocarpus bacaba	Palmae	0.71%	4	0.90%
Purpleheart	Peltogyne paniculata	Fabaceae: Caesalpiniaceae	0.68%	2	0.45%
Swamp Locust	Hymenaea spp.	Fabaceae: Caesalpiniaceae	0.67%	1	0.23%
	Unkown spp. 4		0.62%	3	0.68%
White Kaditiri	Sclerolobium micropetalum	Fabaceae: Caesalpiniaceae	0.59%	2	0.45%
Hiponi	Parkia nitida	Fabaceae: Mimosaceae	0.57%	1	0.23%
Duru	Apeiba spp.	Tiliaceae	0.57%	1	0.23%
Konoko	Licania majuscula	Chrysobalanaceae	0.55%	2	0.45%
Kukritiballi	Pouteria cuspidata	Sapotaceae	0.54%	3	0.68%

Congo Pump	Cecropia spp.	Moraceae	0.54%	2	0.45%
Wayaballi			0.53%	5	1.13%
Baruma	Pourouma minor	Moraceae	0.52%	2	0.45%
Itikiboraballi	Swartzia benlhamiana	Fabaceae: Papilionaceae	0.49%	2	0.45%
Kokrite	Attalea regia	Palmae	0.43%	1	0.23%
Morua	Protium spp.	Burseraceae	0.42%	2	0.45%
Yarridan	Tachigalia spp.	Fabaceae: Caesalpiniaceae	0.42%	3	0.68%
Kurukai	Protium decandrum	Burseraceae	0.42%	3	0.68%
Araridan	Licania spp.	Chrysobalanaceae	0.42%	3	0.68%
Hill Corkwood	Pterocarpus rohrii	Fabaceae: Papilionaceae	0.39%	1	0.23%
Rough Skin Arara	Unonopsis spp.	Annonaceae	0.38%	2	0.45%
Hill Dalli	Virola michelli	Myristicaceae	0.37%	2	0.45%
High bush kiriti		Lauraceae	0.37%	3	0.68%
Red Kuyama	Xylopia nitida	Annonaceae	0.35%	2	0.45%
Burada	Parinari campestris	Chrysobalanaceae	0.31%	1	0.23%
Unknown Sap	??	Sapotaceae	0.31%	2	0.45%
Kirikawa	Iryanthera lancitolia	Myristicaceae	0.30%	2	0.45%
Brown Kaditiri	Sclerolobium spp.	Fabaceae: Caesalpiniaceae	0.29%	1	0.23%
Kabukalli	Goupia glabra	Goupiaceae	0.27%	1	0.23%
Marua		Burseraceae	0.27%	1	0.23%
Huruasa (Soap Tree)	Huarusa	Fabaceae: Mimosaceae	0.25%	1	0.23%
Kamakuti	Bombax flavillorum	Bombacaceae	0.24%	2	0.45%
Futi	Jacaranda copaia	Bignoniaceae	0.23%	1	0.23%
Parakusan	Swartzia schomburgkii	Fabaceae: Papilionaceae	0.23%	1	0.23%
Iguai			0.22%	1	0.23%
Karahuru	Schefflera morototoni	Araliaceae	0.21%	1	0.23%
Bowawa	Astronium ulei	Anacardiaceae	0.21%	1	0.23%
Inga	Inga capitata	Fabaceae: Mimosaceae	0.20%	1	0.23%
Charcoal/Barabara	Diospyros guianensis	Ebenaceae	0.19%	1	0.23%
Maniriballi	Pithecellobium corymbosum	Fabaceae: Mimosaceae	0.17%	1	0.23%
Kribianda			0.16%	1	0.23%
Shibidan	Aspidosperma vargasii	Apocynaceae	0.16%	1	0.23%
Kiriti		Lauraceae	0.15%	1	0.23%
Monkey Syrup			0.14%	1	0.23%
Suya like	Pouteria spp.	Sapotaceae	0.14%	1	0.23%
Watapa Wallaba	Eperua rubiginosa	Fabaceae: Caesalpiniaceae	0.14%	1	0.23%
Swamp Dalli	Virola surinamensis	Myristicaceae	0.14%	1	0.23%
Monkey Pot	Lecythis davisii	Lecythidaceae	0.14%	1	0.23%
Kamarakua(Hiariballi)	Sweetia nitens	Fabaceae: Papilionaceae	0.13%	1	0.23%
Rough Skin Arara (broad Leaf)	Guatteria spp.	Annonaceae	0.13%	1	0.23%
Table Tree		Burseraceae	0.13%	1	0.23%
Duru	Apeiba echinata	Tiliaceae	0.12%	1	0.23%
Kamacushi		Bombacaceae	0.12%	1	0.23%
Munuridan	Ruizterania albiflora		0.12%	1	0.23%
Suya	Pouteria speciosa	Sapotaceae	0.12%	1	0.23%
Darina	Hymenolobium spp.	Fabaceae: Papilionaceae	0.12%	1	0.23%
Guava			0.12%	1	0.23%
Dukuria	Sacoglottis guianensis	Humiriaceae	0.11%	1	0.23%
Yarula	Aspidosperma excelsum	Apocynaceae	0.11%	1	0.23%
Yellow Silverballi	Aniba spp.	Lauraceae	0.11%	1	0.23%

Smooth-Leaf Kakerelli	Eschwilera decolorans	Lecythidaceae	0.11%	1	0.23%
Tatabu	Diplotropis purpurea	Fabaceae: Papilionaceae	0.11%	1	0.23%
Kurihikuyuku	Anaxagorea dolichocarpa	Annonaceae	0.11%	1	0.23%
Adalidan			0.10%	1	0.23%
Ikaribianda			0.10%	1	0.23%
Smooth Skin Arara	Unonopsis guatterioides	Annonaceae	0.10%	1	0.23%
Kork	Ormosia coutinhoi	Fabaceae: Papilionaceae	0.10%	1	0.23%
Sada	Peltogyne venosa	Fabaceae: Caesalpiniaceae	0.10%	1	0.23%
Taparoo	Myrciaria vismeifolia	Myrtaceae	0.10%	1	0.23%
Yari Yari	Duguetia spp.	Annonaceae	0.10%	1	0.23%
Arara (3rd Type)	Malmea spp.	Annonaceae	0.10%	1	0.23%
Awara	Astrocaryum vulgare	Palmae	0.10%	1	0.23%
Kakarelli	Eschweilera chartacea	Lecythidaceae	1.00%	4	0.90%
Liquorice	Pradosia schomburgkiana	Sapotaceae	0.50%	3	0.68%
Kakarelli	Eschweilera delionert	Lecythidaceae	0.80%	3	0.68%
	Swartzia spp.1	Fabaceae: Papilionaceae	0.40%	3	0.68%
	Pradosia spp.2	Sapotaceae	0.35%	2	0.45%
	Clathrotropis brachypetala	Fabaceae: Papilionaceae	0.30%	2	0.45%
	Unknown spp.2		0.25%	2	0.45%
	Unknown spp.1		0.24%	1	0.23%
	Unknown spp.5		0.24%	1	0.23%
	Unknown spp.3		0.23%	1	0.23%
	Unknown	Unknown	1.98%	12	2.71%

APPENDIX IV. PLANT FAMILIES REPRESENTED IN BOTANICAL TRANSECTS

Family	% of Basel Area
Fabaceae: Caesalpiniaceae	12.70%
Lecythidaceae	11.72%
Fabaceae: Papilionaceae	11.48%
Sapotaceae	7.76%
Burseraceae	5.41%
Chrysobalanaceae	5.32%
Moraceae	4.65%
Euphorbiaceae	4.54%
Bombacaceae	3.73%
Fabaceae: Mimosaceae	3.44%
Lauraceae	3.22%
Palmae	3.05%
Melastomataceae	2.48%
Apocynaceae	1.97%
Guttiferae	1.56%
Sterculiaceae	1.48%
Anacardiaceae	1.28%
Annonaceae	1.27%
Simaroubaceae	1.08%
Myristicaceae	0.82%
Tiliaceae	0.69%
Goupiaceae	0.27%
Bignoniaceae	0.23%
Araliaceae	0.21%
Ebenaceae	0.19%
Humiriaceae	0.11%
Myrtaceae	0.10%
Unknown	9.25%

APPENDIX V. ALL PLANT SPECIES EATEN BY BEARDED SAKIS DURING THE STUDY PERIOD.

Common Name	Scientific Name	Family	Percent of Diet	Fruit Type	Parts Eaten
Ballata	*Manilkara bidentata*	Sapotaceae	11.55%	Drupe	Sd, MF, IF
Wamara	*Swartzia leiocalycina*	Fabaceae: Papilionaceae	11.48%	Pod, dehiscent	Sd
Sheu	*??*	??	7.49%	Capsule	Sd
A	*Prieurella spp.*	Sapotaceae	7.10%	Berry	Sd, MF, IF
Sincona	*Geissospermum sericeum*	Apocynaceae	5.60%	Drupe	Sd, MF, IF
Kokritiballi	*Pouteria cuspidata*	Sapotaceae	4.56%	Berry	Sd
Kabukalli	*Goupia glabra*	Goupiaceae	3.51%	Berry	MF
Marishiballi	*Licania densiflora*	Chrysobalanaceae	3.17%	Drupe	Sd
Black Kakerelli	*Eschweilera sagotiana*	Lecythidaceae	2.79%	Pyxidium	Sd
Dukaliballi	*Brosimum parinarioides*	Moraceae	2.74%	Pseudo	Sd
Maporokon	*Inga alba*	Fabaceae: Mimosaceae	2.69%	Pod, indehiscent	MF
Buruma	*Pourouma guianensis*	Moraceae	2.51%	Drupe	Sd, MF
Tibikushi	*Brosimum guianense*	Moraceae	2.25%	Pseudo	Sd, MF
Wina Kakerelli	*Eschweilera corrugata*	Lecythidaceae	1.79%	Pyxidium	Sd, Fl
Mora	*Mora excelsa*	Fabaceae: Caesalpiniaceae	1.67%	Pod, dehiscent	Sd
Mahicaballi	*Phyllanthus spp.*	Euphorbiaceae	1.30%	Capsule	Sd
Hiawaballi	*Tetragastris altissima*	Burseraceae	1.24%	Drupe	Sd
Smooth Leaf Kakerelli	*Eschweilera decolorans*	Lecythidaceae	1.15%	Pyxidium	Sd, Fl
Wadara	*Couratari guianensis*	Lecythidaceae	1.11%	Pyxidium	Sd
Kauta	*Licania alba*	Chrysobalanaceae	1.02%	Drupe	Sd
Suya	*Pouteria speciosa*	Sapotaceae	0.96%	Berry	MF, IF
Baboon Inga	*Inga cinnamonea*	Fabaceae: Mimosaceae	0.79%	Pod, indehiscent	Sd
Arrowpoint Tree	*??*	??	0.75%	Aggregate	Sd
Kokrite	*Attalea regia*	Palmae	0.72%	Nut	MF, IF
	Brosimum rubescens	Moraceae	0.67%	Pseudo	Sd, MF
Kaditiri	*Sclerolobium guianense*	Fabaceae: Caesalpiniaceae	0.64%	Pod, indehiscent	Fl, Sd
Asepoko	*Pouteria guianensis*	Sapotaceae	0.62%	Berry	Sd, Fl
Konoko	*Licania majuscula*	Chrysobalanaceae	0.54%	Drupe	Sd
	??	??	0.50%	Capsule, indehiscent	Sd
	Moutabea guianensis	Polygalaceae	0.49%	Drupe	Sd
	Sloanea acutiflora	Elaeocarpaceae	0.48%		Sd
Dukali	*Parahancornia fasciculata*	Apocynaceae	0.46%	Berry	Sd
Wallaba	*Eperua falcata*	Fabaceae: Caesalpiniaceae	0.44%	Pod, indehiscent	Sd
Kakerelli	*Eschweilera chartacea*	Lecythidaceae	0.43%	Pyxidium	Sd, Fl
	??	??	0.41%	Berry	Sd, MF
Rubber	*Hevea guianensis*	Euphorbiaceae	0.41%	Capsule	Sd
	Eschweilera simiorum	Lecythidaceae	0.38%	Pyxidium	Sd
	Helicostylia tomentosa	Moraceae	0.35%	Pseudo	Sd, MF
		Burseraceae	0.35%	Drupe	Sd
Kuyama	*Xylopa nitida*	Annonaceae	0.33%	Apocarp	Sd
Liquorice	*Pradosia schomburgkiana*	Sapotaceae	0.32%	Berry	Sd
	Eremoluma sagotiana	Sapotaceae	0.31%	Berry	Sd
Inga	*Inga bourgoni*	Fabaceae: Mimosaceae	0.30%	Pod, indehiscent	Sd

Haiariballi	*Alexa wachenheimii*	Fabaceae: Papilionaceae	0.28%	Pod, dehiscent	Sd
	Adenocalymna inundatum	Bignoniaceae	0.28%	Capsule, indehiscent	Sd
Sand Baromalli	*Catostemma fragrans*	Bombacaceae	0.26%	Capsule	MF, IF
Asepokoballi	*Pouteria caimito*	Sapotaceae	0.24%	Berry	Sd
	Gustavia augusta	Lecythidaceae	0.24%	Capsule, indehiscent	Sd
	Chrysophyllum auratum	Sapotaceae	0.23%	Berry	Sd
	Nemaluma engleri	Sapotaceae	0.23%	Berry	Sd
	??	??	0.21%	Drupe	Sd
	Arrabidaea nigrescens	Bignoniaceae	0.20%	Capsule, indehiscent	Sd
Asashi	*Rheedia spp. 1*	Guttiferae	0.20%	Berry	Sd
Smooth Skin Arara	*Guatteria spp.*	Annonaceae	0.20%		Sd
	Pradosia ptychandra	Sapotaceae	0.19%	Drupe	Sd
Crabwood	*Carapa guianensis*	Melastomataceae	0.19%	Capsule	Sd, Pith
Marishiballi	*Licania spp.1*	Chrysobalanaceae	0.18%	Drupe	Sd
	??	Lecythidaceae	0.16%	Pyxidium	Sd
	Iryanthera sagotiana	Myristicaceae	0.16%	Capsule	Sd
Swamp Corkwood	*Pterocarpus officinalis*	Fabaceae: Papilionaceae	0.15%	Pod, indehiscent	Sd
Congo Pump	*Cecropia spp.*	Moraceae	0.14%	Fruiting spike	IF, MF
	Macrolobium acaciifolium	Fabaceae: Caesalpiniaceae	0.14%	Pod, dehiscent	Sd
Monkey Pot	*Lecythis davisii*	Lecythidaceae	0.13%	Pyxidium, indehiscent	Sd
	Pachyptera kerere	Bignoniaceae	0.12%	Capsule	Sd
	Peritassa compta	Celastraceae	0.12%		Sd
	Schradera surinamensis	Rubiaceae	0.11%		MF
		Euphorbiaceae	0.11%		Sd
	Brosimum lactescens	Moraceae	0.10%	Pseudo	Sd
Inga	*Inga rubiginosa*	Fabaceae: Mimosaceae	0.10%	Pod, indehiscent	Sd
	Neoxythece dura	Sapotaceae	0.10%	Berry	Sd
Maho	*Sterculia rugosa*	Sterculiaceae	0.10%	Capsule	Sd
Huarusa	*Abarema jupunba*	Fabaceae: Mimosaceae	0.10%	Pod, indehiscent	Sd
Burada	*Parinari campestris*	Chrysobalanaceae	0.10%	Drupe	Sd, MF, IF
	Achrouteria pomifera	Sapotaceae	0.10%	Berry	Sd
	Monstera adansonii	Araceae	0.10%	Aggregate	IF, MF
	Odontadenia nitida	Apocynaceae	0.10%	Follicle	Sd
	Odontadenia macrantha	Apocynaceae	0.10%	Follicle	Sd
Manni	*Symphonia globulifera*	Guttiferae	0.10%	Berry	Sd
Duru	*Apeiba echinata*	Tiliaceae	0.09%	Capsule	Sd
Red Kauta	*Licania spp.2*	Chrysobalanaceae	0.09%	Drupe	Sd
	Memora flaviflora	Bignoniaceae	0.09%	Capsule	Sd
Red Ruri	*Chaetocarpus schomburgkianus*	Euphorbiaceae	0.09%		Sd
Nabbi	*Heteropsis jenmani*	Araceae	0.09%	Aggregate	MF, IF
Inga	*Inga pezizifera*	Moraceae	0.09%	Pod, indehiscent	MF
Kurihikuyuku	*Anaxagorea dolichocarpa*	Annonaceae	0.09%		Sd
	??	??	0.09%	Capsule	Sd
Shibidan	*Aspidosperma vargasii*	Apocynaceae	0.08%	Follicle	Sd
	Calycolpus spp.	Myrtaceae	0.08%	Berry	Sd
	Memora schomburgkii	Bignoniaceae	0.08%	Capsule	Sd
	Hyeronima laxiflora	Euphorbiaceae	0.08%	Drupe	Sd

	Pradosia spp. 1	Sapotaceae	0.07%	Berry	Sd, IF
	??	??	0.07%		Sd, FL
	Tetracera spp.	Dillenioaceae	0.07%	Follicle	Sd
	Couma spp.	Apocynaceae	0.07%	Berry	Sd
Hiponi	*Parkia pendula*	Fabaceae: Mimosaceae	0.07%	Pod, dehiscent	Sd
	Vochysia guianensis	Vochysiaceae	0.07%		Sd
	Pradosia spp.2	Sapotaceae	0.06%	Berry	Sd
Maniriballi	*Pithecellobium corymbosum*	Fabaceae: Mimosaceae	0.06%	Pod, indehiscent	Sd
Single Leaf Maho	*Sterculia pruriens*	Sterculiaceae	0.06%	Capsule	Sd
	Protium hostmannii	Burseraceae	0.06%	Drupe	Sd
	Chaetocarpus spp.	Euphorbiaceae	0.06%		Sd
	Macrolobium spp.	Fabaceae: Caesalpiniaceae	0.06%	Pod, dehiscent	Sd
	Dendrobangia boliviana	Icacinaceae	0.06%	Drupe	Sd
	Mabea piriri	Euphorbiaceae	0.06%	Capsule	Sd
	Clathrotropis brachypetala	Fabaceae: Papilionaceae	0.06%	Pod, dehiscent	Sd
	Strychnos mitscherlichii	Loganiaceae	0.06%	Berry	MF
	Cupania scrobiculata	Sapindaceae	0.06%		Sd
	Eremoluma spp.	Sapotaceae	0.06%	Berry	Sd
Bataballi	*Ecclinusa guianensis*	Sapotaceae	0.05%	Berry	Sd, MF
Hill Dalli	*Virola michelli*	Myristicaceae	0.05%		Sd
	Eschweilera spp.2	Lecythidaceae	0.05%	Pyxidium	Sd
			0.05%	Berry	MF
	Strychnos erichsonii	Loganiaceae	0.05%	Berry	MF
Lu	*Oenocarpus bacaba*	Palmae	0.05%	Drupe	MF
	Quassia spp.	Simaroubaceae	0.05%	Drupe	Sd
Greenheart	*Chlorocardium rodiei*	Lauraceae	0.05%		Sd
	Prestonia surinamensis	Apocynaceae	0.05%		Sd
Barukaro	*Ormosia paraensis*	Fabaceae: Papilionaceae	0.04%	Pod, dehiscent	Sd
	Drypetes variabilis	Euphorbiaceae	0.04%	Drupe	Sd
	Coupia spp. 1	Chrysobalanaceae	0.04%	Drupe	Sd
	Swartzia spp.1	Fabaceae: Papilionaceae	0.04%	Pod, indehiscent	Sd
	Dioscorea spicata	Dioscoreaceae	0.04%		Sd
Simarupa	*Quassia simarouba*	Simaroubaceae	0.04%	Drupe	Sd
			0.04%		Sd
Arara	*Unonopsis spp.*	Annonaceae	0.04%		Sd
Curare	*Strychnos spp.3*	Loganiaceae	0.04%	Berry	MF
	Sacoglottis spp.	Humiriaceae	0.04%	Drupe	Sd
		Sapotaceae	0.04%	Berry	Sd
	Securidaca paniculata	Polygalaceae	0.04%	Samara	Sd
		Euphorbiaceae	0.03%	Capsule	Sd
Hiawaballi	*Tetragastris panamensis*	Burseraceae	0.03%	Drupe	Sd
			0.03%	Capsule	Sd
		Bignoniaceae	0.03%	Capsule	Sd
	Pradosia spp. 3	Sapotaceae	0.03%	Drupe	Sd
Kakerelli	*Eschweilera delionert*	Lecythidaceae	0.03%	Pyxidium	Sd
			0.03%	Pod, dehiscent	Sd
		Euphorbiaceae	0.03%	Capsule	Sd
Inga	*Inga spp.2*	Fabaceae: Mimosaceae	0.03%	Pod, dehiscent	Sd
		Sapotaceae	0.03%	Berry	Sd

Koroballi	*Penthaclethra macroloba*	Fabaceae: Papilionaceae	0.03%	Pod, dehiscent	Sd
	Conomorpha spp.	Myrsinaceae	0.03%	Drupe	Sd
			0.03%		FL
Inga	*Inga spp.1*	Fabaceae: Mimosaceae	0.03%	Pod, indehiscent	Sd
Kakerelli	*Eschweilera spp.1*	Lecythidaceae	0.03%	Pyxidium	Sd
	Pithecellobium latifolium	Fabaceae: Mimosaceae	0.03%	Pod, indehiscent	Sd
	Heteropteris multiflora	Malpighiaceae	0.03%	Samara	Sd
	Aniba spp.	Lauraceae	0.02%		Sd
	Salacia spp.	Celastraceae	0.02%		Sd
		Euphorbiaceae	0.02%		Sd
Glasswood			0.02%		Sd
			0.02%		Sd
	Posoqueria spp.	Rubiaceae	0.02%		MF
	Mimosa pigra	Fabaceae: Mimosaceae	0.02%	Pod: Lomentum	Sd
			0.02%	Berry	Sd
	Gnetum urens	Gentaceae	0.02%		Sd
			0.02%	Berry	Sd
			0.02%		Sd
			0.02%	Drupe	Sd
	Inga spp.3	Fabaceae: Mimosaceae	0.02%	Pod, indehiscent	Sd
	Lonchocarpus chrysophyllus	Fabaceae: Papilionaceae	0.02%	Pod, indehiscent	Sd
	Parkia ulei	Fabaceae: Mimosaceae	0.02%	Pod, dehiscent	Sd
	Bactris spp.	Palmae	0.02%	Drupe	MF
			0.02%		Sd
	Duguetia spp.	Annonaceae	0.02%		Sd
	Machaerium quinata	Fabaceae: Papilionaceae	0.02%	Pod, indehiscent	Sd
Fukadi	*Terminalia amazonia*	Combretaceae	0.02%		Sd
Itikiboroballi	*Swartzia spp.*	Fabaceae: Papilionaceae	0.02%	Pod, indehiscent	Sd
			0.02%	Capsule	Sd
			0.02%		Sd
Swamp Inga	*Pithecellobium spp.*	Fabaceae: Mimosaceae	0.02%	Pod, dehiscent	Sd
Swamp Dalli	*Virola surinamensis*	Myristicaceae	0.02%		Sd
			0.02%		Sd
			0.02%		Sd
			0.02%		Sd
	Strychnos spp.1	Loganiaceae	0.02%	Berry	MF
Parakusan	*Swartzia schomburgkii*	Fabaceae: Papilionaceae	0.02%	Pod, dehiscent	Sd
	Protium aracouchini	Burseraceae	0.02%	Drupe	Sd
	Brosimum spp.1	Moraceae	0.02%	Pseudo	Sd
	Inga spp.4	Fabaceae: Mimosaceae	0.02%	Pod, indehiscent	MF
	Pouteria spp.	Sapotaceae	0.02%	Berry	Sd
			0.02%		Sd
			0.02%		Sd
			0.02%		Sd
			0.02%		Sd
Turu	*Jessenia bataua*	Palmae	0.02%	Drupe	MF
			0.02%		Sd
Brown Betty			0.01%		Sd
			0.01%		Sd
			0.01%		Sd

			0.01%		Sd
Wadara	*Couratari spp.1*	Lecythidaceae	0.01%	Pyxidium	Sd
	Dioclea virgata	Fabaceae: Papilionaceae	0.01%	Pod, indehiscent	Sd
	Chaunochiton kappleri	Nyctaginaceae	0.01%	Samara	Sd
			0.01%		Sd
	Dalbergia riedelii	Fabaceae: Papilionaceae	0.01%	Pod, indehiscent	Sd
			0.01%	Berry	MF
Yarula	*Aspidosperma excelsum*	Apocynaceae	0.01%	Follicle	Sd
			0.01%		Sd
	Strychnos spp.2	Loganiaceae	0.01%	Berry	MF
Marishiballi	*Coupia spp. 2*	Chrysobalanaceae	0.01%	Drupe	Sd
	Couratari multiflora	Lecythidaceae	0.01%	Pyxidium	Sd
			0.01%	Berry	?
	Acacia paniculata	Fabaceae: Mimosaceae	0.01%	Pod, dehiscent	Sd
			0.01%	Drupe	?
			0.01%	Berry	?
Asashi	*Rheedia spp.2*	Guttiferae	0.01%	Berry	Sd
Buruma	*Pourouma minor*	Moraceae	0.01%	Drupe	Sd
			0.01%	Drupe	?
Itikiboroballi	*Swartzia benlhamiana*	Fabaceae: Papilionaceae	0.01%	Pod, indehiscent	Sd
	Couratari spp.2	Lecythidaceae	0.01%	Pyxidium	Sd
			0.01%		Sd
			0.01%		Sd
			0.01%		Sd
			0.01%		Sd
			0.01%		Sd

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