# SOCIOECOLOGY OF THE GUIANAN BEARDED SAKI, *CHIROPOTES SAGULATUS*

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by

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# CHAPTER 1

# INTRODUCTION TO THE STUDY

Fig. 66. Pithecia Satanas, male (from Brehm).

> "With some monkeys the beard is confined to the male, as in the Orang, or is much larger in the male than in the female, as in *Mycetes caraya* and *Pithecia satanas*."
> -Charles Darwin, The Descent of Man, and Selection in Relation to Sex, 1871

## A Brief History of Studies of Bearded Sakis

Bearded sakis were first described by Humboldt and Bonpland two centuries ago (1812), yet they remain among the least known New World primates; only their sister genus, the uakaris, has received less attention (only three long-term studies have been conducted on uakaris: Ayres 1986; Boubli 1998; Bowler 2007). Most bearded saki research has been conducted in Brazil, with only one study conducted in Guyana (although another was occurred in 2008-09) and a few in Suriname and Venezuela (Table 1.1). However, few studies of free-ranging bearded sakis were conducted in continuous forest, and instead took place on islands and in forest fragments, and the majority of studies were doctoral or Master's thesis research. Certainly the difficulties of studying bearded sakis have influenced this dearth of information. Their preference for the upper canopy and tall trees has contributed to both low visibility and the difficulty of distinguishing individuals. Most bearded sakis studies are ecological, focusing on feeding ecology or ranging patterns (all of those listed in Table 1.1); only a few have focused on social behavior (Peetz 2001; Veiga et al. 2005, but see Table 4.1). Thus, our understanding of social interactions, group and sub-group structure, and sexual behavior is very preliminary.

**Table 1.1.** Previous studies of free-ranging bearded sakis.

| Species | Study country | Study site | Year of study | Length of study (mon.) | Type of forest (size, ha) | Reference |
|---|---|---|---|---|---|---|
| *C. albinasus* | Brazil | Aripuanã Parq. Nac. | 1977-79 | 17 | Continuous | (Ayres 1981; Ayres 1989)[1] |
| | Brazil | Tapajós | 2004-06 | 11 | Continuous | (Pinto 2008)[1] |
| | Brazil | Mato Grosso | 1913-14 | ? | Continuous | (Miller in Allen 1916) |
| *C. chiropotes* | Venezuela | Lake Guri | 1991-92 | 15 | Island (180) | (Peetz 2001)[1] |
| | Venezuela | Lake Guri | 1991-92 | 17 | Island (180) | (Norconk 1996) |
| | Venezuela | Lake Guri | 1989-90 | 5 | Island (180) | (Kinzey and Norconk 1993) |
| *C. sagulatus* | **Suriname** | **Brownsberg Nature Park** | **2008-09** | **13** | **Continuous** | **Present study**[1] |
| | Suriname | Brownsberg Nature Park | 2005-06 | 5.5 | Continuous | (Gregory 2006)[2] |
| | Suriname | Brownsberg Nature Park | 2008 | 1.5 | Continuous | (Nederbiel 2009)[3] |
| | Brazil | Fazenda Esteio | 1980-81 | 3 | Fragment (10) | (Ayres 1981)[2] |
| | Suriname | Raleighvalen-Voltzberg | 1976-78 | 28 | Continuous | (van Roosmalen et al. 1981) |
| | Suriname | Raleighvalen- Voltzberg | 1986-87 | 6 | Continuous | (Norconk and Kinzey 1994) |
| | Brazil | Reserva do Km 41 | 1987-88 | 12 | Fragment (1,100) | (Frazão 1992)[2] |
| | Guyana | Multiple | ? | ? | ? | (Muckenhirn et al. 1975)[4] |
| *C. satanas* | Brazil | Trilha 4 | 2001 | 7 | Peninsula (1,300) | (Santos 2002)[2] |
| | Brazil | Ilha Su | 2002 | 6 | Island (16.3) | (Silva 2003)[2] |
| | Brazil | Trilha 4 | 2002 | 6 | Peninsula (1,300) | (Silva 2003)[2] |
| | Brazil | Maranhão | ?? | 3 | Fragment (63) | (Porto-Carvalho 2002)[2] |
| | Brazil | Trilha 4 | 2003-04 | 12 | Peninsula (1,300) | (Veiga 2006)[1] |
| | Brazil | Ilha do João | 2003-04 | 12 | Island (19.4) | (Veiga 2006)[1] |
| | Brazil | Km 41, Cabo Frio | 2003-06 | 18 | Continuous | (Boyle 2008)[1] |

| | | | | | | |
|---|---|---|---|---|---|---|
| | Brazil | 2303, 3304 | 2003-06 | 18 | Fragment (100) | (Boyle 2008)[1] |
| | Brazil | 1202, 2206, 3209 | 2003-06 | 18 | Fragment (10) | (Boyle 2008)[1] |
| | Brazil | 1104, 2107, 2108, 3114 | 2003-06 | 18 | Fragment (1) | (Boyle 2008)[1] |
| | Brazil | Fazenda Amanda | 2000 | 6 | Fragment (1,200) | (Pereira 2002)[2] |
| | Brazil | ? | ? | ? | ? | (Lopes 1993)[2] |
| *C. utahickae* | Brazil | Ferreira Penna | 1996 | 8 (6 sit) | Continuous (33,000) | (Bobadilla 1998)[2] |
| | Brazil | Fazenda Arataú | 1996 | 8 (21 sit) | Fragment (7,500) | (Bobadilla 1998)[2] |
| | Brazil | Germoplasma Island | 2001 | 8 | Island (129) | (Santos 2002)[2] |
| | Brazil | Germoplasma Island | 2003-04 | 6 | Island (129) | (Vieira 2005)[2] |

[1] Dissertation

[2] Master's thesis

[3] Bachelor's thesis

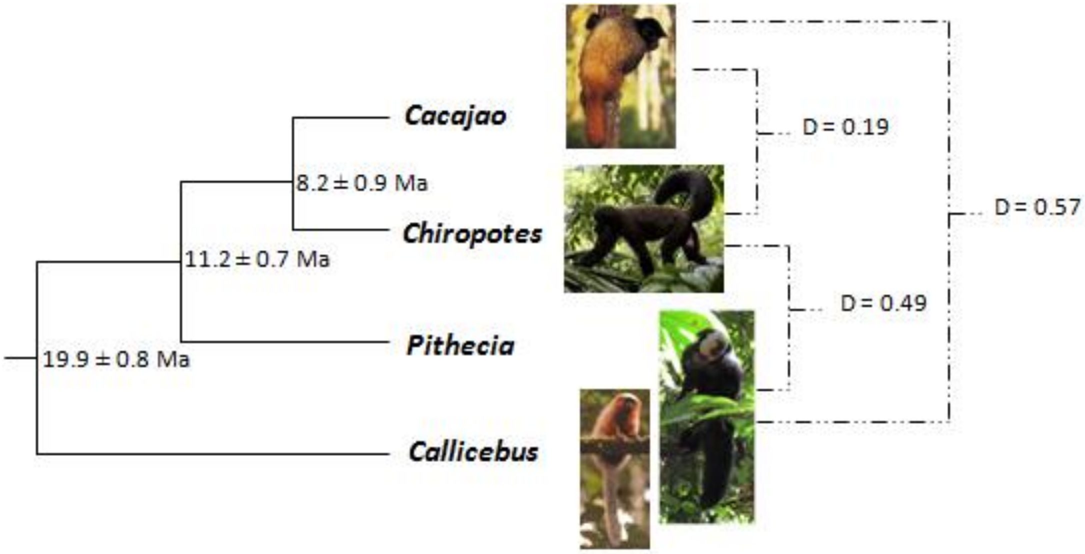
[4] In van Roosmalen et al. 1981, a survey, took place at multiple sites

## The Pitheciines

Bearded sakis (*Chiopotes* spp.) are members of a subfamily of New World monkeys, the Pitheciinae, that includes titis (*Callicebus* spp.), white-faced sakis (*Pithecia* spp.), and uakaris (*Cacajao* spp.) (see Figure 1.1, Kay 1990; Rosenberger 2002). The tribe, Pitheciini includes sakis and uakaris, and excludes titis (Rosenberger 1992). Rosenberger (1992; 2002) includes *Aotus* in the Pitheciinae clade because of morphological data that indicate a sister relationship with *Callicebus*, although other morphological analyses and genetic analyses have grouped *Aotus* with *Cebus* and *Saimiri* (Canaves et al. 1999; Ford 1986; Goodman et al. 1998; Kay 1990; Schneider 2000; von Dornum and Ruvolo 1999). Although there is debate about their relationship to the other 13 genera of platyrrhines, researchers agree that saki-uakaris represent a discrete group (Ford 1986; Horovitz 1999; Kay 1990; Schneider 2000; Schneider and Rosenberger 1996; von Dornum and Ruvolo 1999). The proposed Family Atelidae (pitheciines and atelines, Rosenberger 1992) is estimated to have diverged 23.2 million years ago. Approximately 19.8 million years ago, *Callicebus* split from the pitheciins. This saki-uakari clade (pitheciins) is approximately 11.2 million years old, with divergence of *Pithecia* and the other two genera occurring around 8.2 million years ago (Schneider 2000).

All three genera of saki-uakaris are distinguishable from other platyrrhines based on specializations for seed eating or sclerocarpic seed predation (i.e., they remove a hard seed pericarp with their canines and masticate seeds with their flat posterior teeth, Kinzey and Norconk 1990; Martin et al. 2003) and a preference for unripe fruit. Their dental specializations include procumbent incisors; robust, laterally splayed canines; flat molars with enamel crenulations; and minimal dental sexual dimorphism, and generally only allometric differences are found in dental morphology between the three genera (although *Pithecia* have smaller canines) (Hershkovitz 1985; Hershkovitz 1987; Kinzey 1992; Kinzey and Norconk 1990; Martin et al. 2003; Rosenberger 1992). Up to 90% of the annual diet of these monkeys consists of seeds (Norconk 2011; Norconk et al. 2009).

**Figure 1.1.** The subfamily Pitheciinae, modified from Schneider (2000). Dates represent divergence times estimated using the molecular clock strategy. Genetic distances (D) added (Schneider et al. 1995) for *Pithecia*, *Chiropotes*, and *Cacajao*.



## The Genus *Chiropotes*, Lesson, 1840

In 1985, Hershkovitz identified two species within the genus *Chiropotes*: the monotypic *C. albinasus* and the polytypic *C. satanas*, with three subspecies: *C.s. satanas*, *C.s. chiropotes*, and *C.s. utahicki*. Silva Júnior and Figueiredo (2002) recently revised the genus using morphological and molecular data. They maintain that *C. albinasus* is a separate species and basal to the rest of the species in the genus. They also elevated the three subspecies of *C. satanas* to species status and proposed that the Guianan group (and subject of this study) is a separate species: *C. sagulatus*. According to their analysis, the genus contains five species: primitive *C. albinasus* (white-nosed bearded saki), *C. sagulatus* (Guianan bearded saki), *C. chiropotes* (black saki), *C. satanas* (bearded saki), and *C. utahickae* (Uta Hick's bearded saki) (Figure 1.2). A morphological, karyotypical, and molecular analysis by Bonvicino et al. (2003), identified another species in the Rio Negro region of Brazil, *C. israelita* and found data for *C. sagulatus* to be insufficient. However, other studies have not confirmed *C. israelita* as a separate species.

*Chiropotes* spp. are distributed throughout most of northern South America from French Guiana, to Suriname, Guyana, Venezuela, and Brazil. *C. sagulatus* is the only species found in three of these countries (the exception being Venezuela, Figure 1.3), and three of the other species have very small ranges within Brazil only (*C. albinasus*, *C. satanas*, and *C. utahicki*, and potentially *C. israelita*). The Amazon River seems to be a species barrier, with *C. sagulatus* and *C. chiropotes* to the north, and the other species to the south. By raising all subspecies to species status, there are effectively two *Chiropotes* species listed as threatened by the IUCN: *C. albinasus* is listed in CITES

Appendix I, and *C. satanas* (formerly *C. satanas satanas*) is listed on the 2006 IUCN Red List of Threatened Species (Rylands et al. 2003). The other species are listed in Appendix II: non-threatened.

Morphologically, bearded sakis are slightly smaller than their cousins, the uakaris, and considerably larger than the sakis (*Pithecia*). They show minimal sexual dimorphism in size (body mass: males = 3,100g, females = 2,600g, male:female mass = 1.19: Ford 1994; body length: males = 406mm, females = 369mm; tail length: males = 373.5mm, females = 385.6mm: Hershkovitz 1985). Similar to uakaris (but unlike *P. pithecia*), bearded sakis are sexually monochromatic, with black bodies and black to orange/white upper backs (depending on spp., Figures 1.2, 1.4, and 1.5). Both sexes have distinctive beards, bulbous temporal swellings (more accurately referred to as “circular coronal tufts supported by underlying muscle” by Veiga, pers. com.), and bushy, non-prehensile tails characteristic of the saki clade (van Roosmalen et al. 1981). Bearded saki females have deep pink labia, while male scrotum color varies from white to deep pink in Suriname and at other sites (Figure 1.5, Suriname: pers. obs., Brazil: pers. comm. L. Veiga). Males can usually only be distinguished from females by their slightly larger facial features and pink scrota (Hershkovitz 1985; van Roosmalen et al. 1981). Contrary to Darwin’s comment above in “*Pithecia*” *satanas* (1871), there is only minimal sexual dimorphism in beard size (Hershkovitz 1985).

**Figure 1.2.** Map of the distribution of the five potential bearded saki species. Used with permission from L. Veiga.

Photos: Wolmar Woisiac – Emilio Goeldi Museum Belém Pará Brazil

**Figure 1.3.** Distribution map of the (Guianan) bearded saki (*C. sagulatus*), throughout the Guianas, southern Venezuela, and Brazil, north of the Amazon River. Figure from InfoNatura (2007).

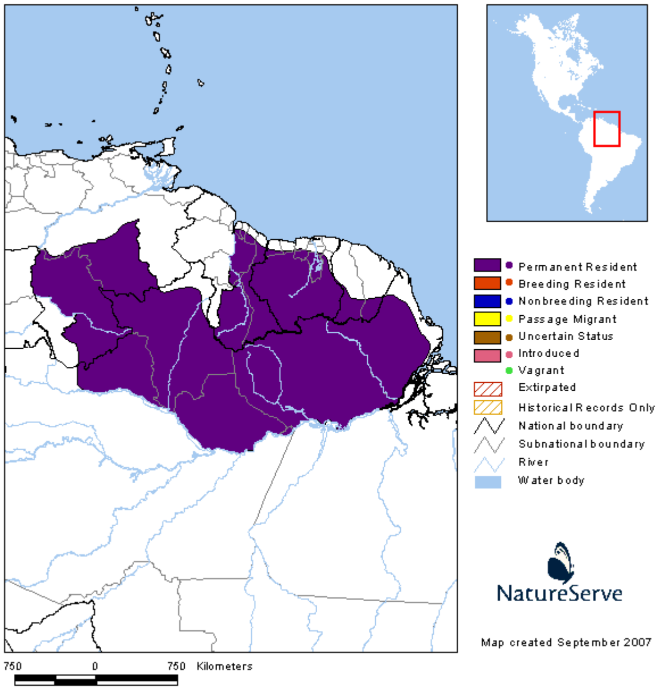


**Figure 1.4.** Adult male bearded saki (*Chiropotes satanas* with darker pelage on the back, compared with the orange upper back pelage of *C. sagulatus* below). Photo by Liza M. Veiga.

**Figure 1.5.** Genitalia of a female (top) and male (bottom) bearded saki at the Paramaribo Zoo in November 2008.

Despite a relative dearth of information about bearded saki behavior and ecology, similar results between studies permit predictions about the genus. Bearded sakis typically live in large groups with multiple males and females (up to 56; see Table 3.1). Even though groups are large, they are frequently characterized by a type of fission-fusion called subgrouping (see Table 3.1). Bearded sakis are above-branch walkers, traveling predominantly though the upper canopies of emergent trees (Fleagle and Mittermeier 1980; Gregory 2006; Walker 2005). Their activity patterns or proportion of the day divided into feeding, resting, and traveling periods are not dramatically different from other platyrrhines (see Tables 4.1 and 4.13), even though they use large home ranges and relatively long day paths (see Tables 4.1 and 4.14). As noted above, they are predominantly seed-eaters, although they also consume fruit pulp, flowers, pith and insects (see Table 4.15). Data on social behavior in bearded sakis, while limited, indicates that male-male relationships are affiliative (Peetz 2001; Veiga et al. 2005), and territorial defense has not been documented.

## Pitheciin Adaptive Suites

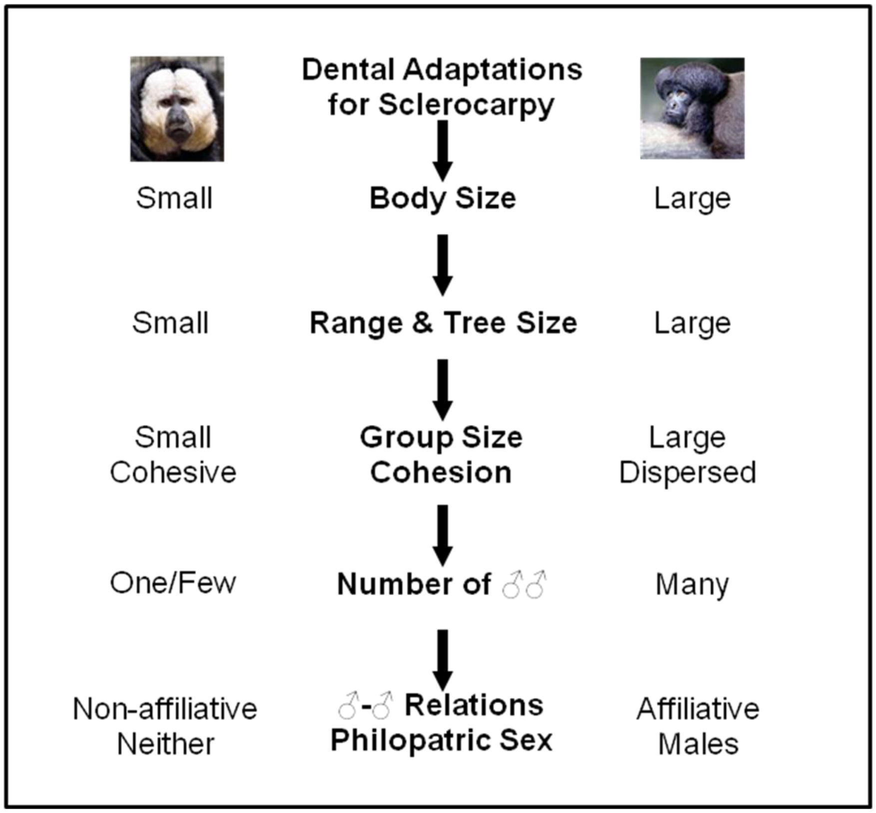
Results of studies of bearded saki and uakari ecology and social behavior (particularly grouping patterns) demonstrate many similarities between these two taxa (see Figure 4.1). In fact, the absence of sympatry between the two genera is potentially a consequence of excessive niche overlap and competitive exclusion. On the other hand, as suggested by Norconk (2011), sakis (*Pithecia*) seem to occupy a sufficiently different niche to allow sympatry in some areas (and see Ferrari et al. 1999 for evidence on distribution variation between areas of allopatry and syntopy in *Chiropotes albinasus* and *Pithecia irrorata*).

Where animals occur in sympatry, there are unique opportunities for understanding niche divergence and evolution, because many ecological variables may be held constant. Therefore, in order to understand bearded saki social behavior within an evolutionary framework, in 2005-2006 a study was conducted to analyze similarities and differences between sympatric white-faced and bearded sakis (Figure 1.6, Gregory 2006).

The white-faced saki adaptive suite of characters is considered to be “basal” to the saki-uakari clade due to the fact that fossil and molecular evidence shows that ancestors resembled smaller-bodied *Pithecia* more than the other two genera (Fleagle et al. 1987; Meldrum and Kay 1997). Despite similar dental adaptations (Kinzey 1992; Martin et al. 2003; Norconk et al. in press), sakis and bearded sakis show little overlap in resource use (perhaps related to differences in habitat use, Gregory 2006; Norconk 1996). Small body size, small groups, preference for the lower levels of the forest, and slow, relatively silent travel in cohesive groups in white-faced sakis contrasts with larger body size, larger troops, and travel in the upper canopy in bearded sakis (Gregory 2006).

The comparison of these species provides preliminary evidence for niche diversification that led to uni- or two-male groups in one species (perhaps the primitive condition) and a derived condition of multimale, male-male-cooperative groups with novel behaviors and morphologies in the other species. As suggested by Rosenberger (1981) it is possible that female dispersal is basal to all atelids (pitheciines and atelines), and within-group male bearded sakis are related. Philopatry and relatedness could signal an important component of their proposed bondedness as seen in chimpanzees (see Chapter 3 for a discussion of social behavior).

**Figure 1.6.** Comparison of adaptive suites of white-faced (left) and bearded sakis (right).



## Hypotheses and Predictions

This study addresses some of the gaps in our knowledge of bearded saki social behavior and ecology. Data on bearded saki social behavior is severely lacking. What is known comes from a study of an island group with only one adult male (Peetz 2001), a preliminary analysis of a data set from a group living in a small, 80ha home range (Veiga et al. 2005), and anecdotal information (see Table 3.1). In this study in continuous forest, the existence of affiliative male-male relationships is explored and described in further detail. Male-male relationships are hypothesized to be affiliative, reflecting intragroup scramble competition for mates and male-male and male-female relationships egalitarian, reflecting high intergroup competition for resources (Chapter 3).

While grouping patterns have been described in many studies, the relationship between group size plasticity and seasonality has not been explored. Here, fluctuation in group size is analyzed within and between seasons to understand how group size flexibility may be an adaptation for reducing intragroup feeding competition. Because resource availability fluctuates over the course of the year, it is hypothesized that shifts in bearded saki group size will reflect changes in the availability of resources (Chapter 2).

The majority of bearded saki studies have focused on ecology. However, many of these studies were performed in geographically limited areas (e.g., islands, peninsulas, forest fragments), and the size of the area available to animals is likely to affect ecology. In this study, various aspects of bearded saki ecology were examined, and many analyses explored seasonal patterns in behavior. Traveling, activity, and feeding patterns were analyzed by season and compared to results at other sites. Although sakis may not experience dramatic shortages in food availability over the course of the year because of a specialized but flexible diet (Norconk et al. 2009), they are nonetheless predicted to change their behavior (Chapter 4).

Bearded saki spatial ecology was also studied to explore strategies the monkeys may use to navigate the mountainous terrain of Brownsberg Nature Park. As observed in primates and other taxa, bearded sakis are predicted to make use of topographic features in order to reduce the energetic cost of navigating the landscape (Chapter 5).

# CHAPTER 2

# GENERAL METHODS

## Study site: Brownsberg Nature Park, Suriname

Suriname, along with eastern Venezuela, Guyana, French Guiana, northern Brazil, and eastern Columbia, lies in the 2.3-million-square-kilometer geomorphologic region of northern South America called the Guiana Shield (Hammond 2005a). This area comprises 13% of the South American continent and has been called one of the Earth's "good news" areas for conservation (Myers et al. 2000). As stated by Hammond, the Guiana Shield "could be described as a land of old rock, poor soils, much water, extensive forests, and few people" (2005a:1). The 2009 United Nations World Population Prospects report showed Suriname's population density to be among the World's lowest (total population = 520,000, 3.2 people per km$^2$) in the range of Canada (3.4/km$^2$), Iceland (3.1/km$^2$), and Australia (2.9/km$^2$) (UN 2009). In 2005, the Food and Agriculture Organization of the United Nations (FAO 2005), documented that Suriname has the highest percent forest cover of any country in the world (14,776,000 ha of a total area of 15,603,000 ha = 94.7%), followed by neighboring French Guiana (91.8%) and Micronesia (90.6%). Furthermore, 96% of the forested areas in Suriname contain primary forest (FAO 2005).

Formed during the Precambrian Period, around 1.7 billion years ago, the Guiana Shield is one of the three cratons (a rigid, stable portion of the Earth's crust) forming the

South American Tectonic Plate and is made up of metamorphic lava called greenstone(Hammond 2005b). After millions of years of erosion, the Shield is now characterized by laterite-bauxite outcroppings (Hammond 2005b).

Brownsberg Nature Park (BNP) is located between 04°45’46’’N and 05°59’44’’N and between 55°07’58’’W and 55°15’23’’W, Zanderij datum (Figures 2.1 and 2.2) in northeastern Suriname, South America, approximately 100 km south of the capital of Paramaribo. BNP’s main geomorphological feature is a 500-meter-high laterite-bauxite plateau, one of the outcroppings described above. The plateau is 34 km long, 13.5 km wide, and covers approximately 27,000 ha. The top of the plateau encompasses 1,400 ha and is characterized by a ferro-bauxite crust, which protects the underlying soil from erosion (De Dijn et al. 2007; Hammond 2005b).

The eastern edge of the park is bordered by Lake Brokopondo (or the Prof. Dr. Ir. W.J. van Blommensteinmeer), a reservoir formed in the late 1950s-early 1960s during the construction of the hydroelectric Afobaka Dam. The western boundary of the park is the main course of the Mindrineti Creek and the Atjonipasi Road. Adjacent to the northern edge of the park is Brownsweg, a village of approximately 3,500 Saramaccan inhabitants who were refugees from seven communities upriver, displaced by the construction of the dam and flooding of the reservoir.

**Figure 2.1.** A Google Earth Image of Brownsberg Nature Park from the southern edge of the park looking northward, with the Atlantic Ocean in the distance (~100km north of the park). The Brownsberg Plateau courses down the spine of the mountain, with the town of Brownsweg to the north of the plateau, the Brokopondo Reservoir on the eastern side, and the Ajonipasi Road on the western side. Artisanal (now illegal) gold mining takes place primarily on the eastern edge of the reservoir. The elevation was exaggerated in Google Earth by a factor of three for better visibility. The image is tilted to illustrate the topography of the plateau.

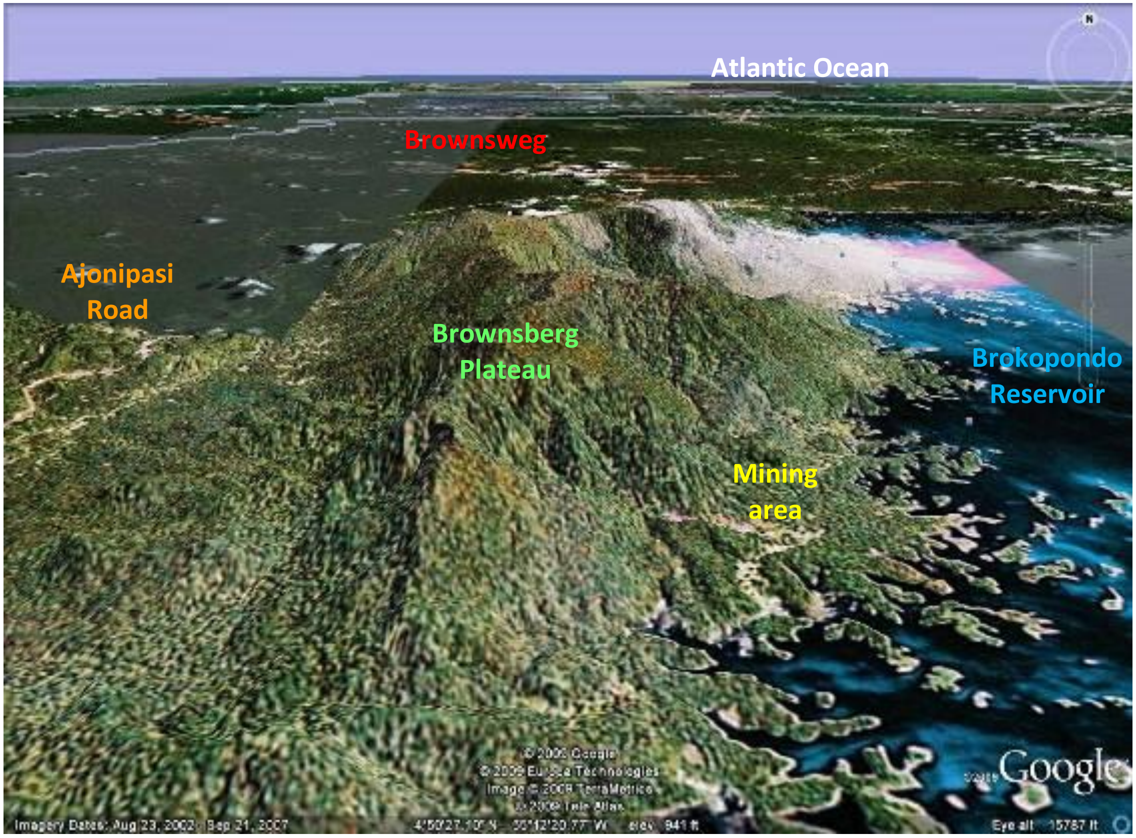
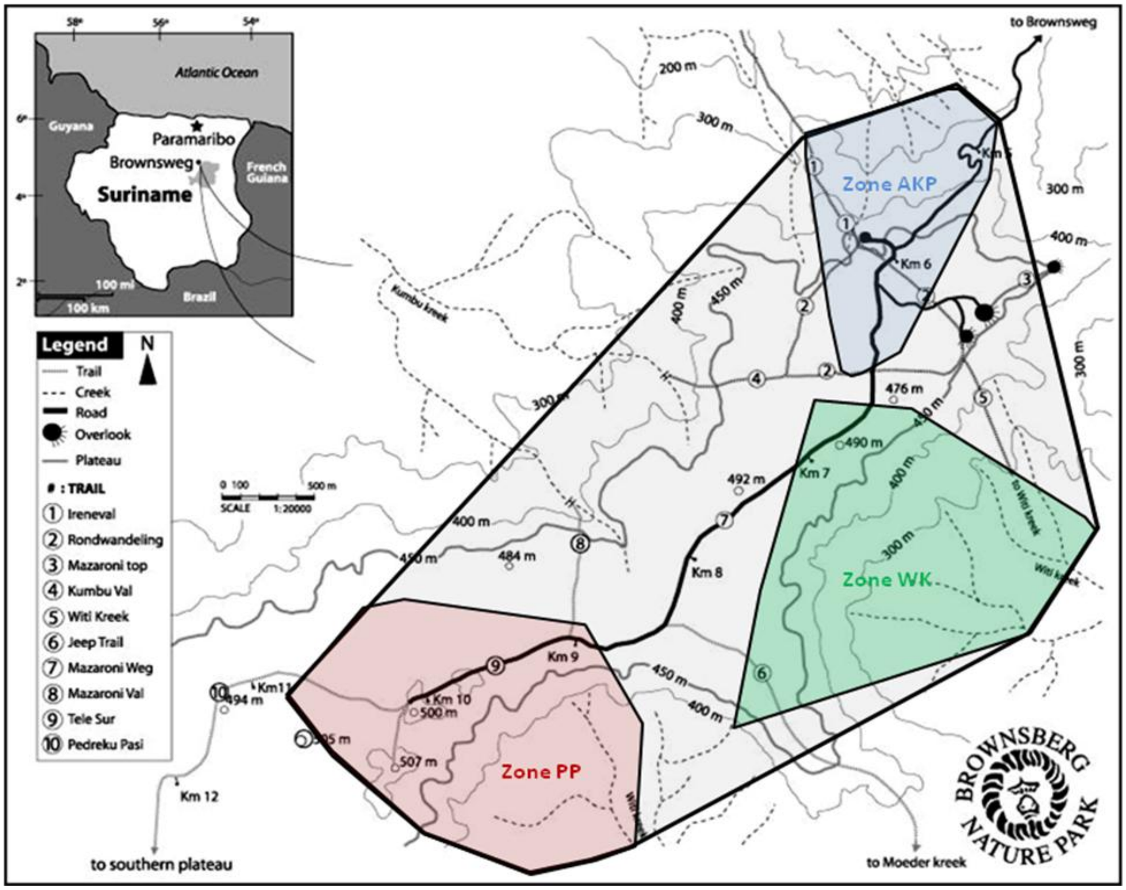


**Figure 2.2.** Map of Brownsberg Nature Park (map by E. Bailey after Fitzgerald et al., 2002). Mazaroni Weg (7) is a road on the plateau. The solid dark line forming a polygon indicates the research area. Groups of bearded sakis were studied in three zones in this area.



Brownsberg Nature Park was created in 1970, named after an American goldminer (John Brown) and is managed by Suriname's Foundation for Nature Conservation (STINASU) under a long-term lease from SURALCO (the Surinamese subsidiary of ALCOA.) The Park was expanded in 2001 from 7,000 ha to 11,800 hectares (Fitzgerald et al. 2002), although the extension has not yet been incorporated into the public sector (pers comm. with STINASU staff).

Despite the fact that Suriname's forests are more intact than most tropical habitats, both legal and illegal gold and bauxite mining, logging, and hunting have affected the park for decades. The park borders are not actively protected by park staff, and based on encounters with hunters, shotgun shells found in the forest, and, at times, daily shots heard, poaching activity seems to be very prevalent (pers. obs.). Discussions with park employees and local people also indicate that hunters use shotgun spring traps created with tree saplings. During the period of the study, there was also evidence of clear cutting for illegal marijuana fields within the park.

The main threat to the park, however, is illegal gold mining. In fact, at least 5% of the park has been devastated by artisanal gold mining since 1997 (reported in De Dijn et al. 2007; Teunissen in prep). Although the local population has engaged in artisanal gold mining for generations, miners have replaced low-impact mining techniques such as panning with high impact water jets that blast soil from the river banks and convert forests to ponds and roads to mud. Gold is extracted with toxic heavy metals. Mercury and silt runoff then drain into the Brokopondo Reservoir. Pellegrom (2004) found lower floral diversity in the mining area and elevated rates of mercury in the fish, and also reduced mammal populations (including bearded sakis). Nonetheless, BNP encompasses over 40 km of walking trails and roads (Figure 2.2) and is a popular tourist destination, with over 10,000 Suriname and international visitors per year (De Dijn et al. 2007).

**Fauna in Brownsberg Nature Park**

Fitzgerald (2003) identified 112 mammal species, 350 bird species, and 106 herpetofaunal species. Of the species endemic to the Guiana Shield, BNP has seven species of mammals (including two primates: *Pithecia pithecia*, white-faced saki monkeys and *Ateles paniscus*, black spider monkeys), 30 species of birds , five reptile species, and 13 amphibian species (De Dijn et al. 2007). The eight-species primate community includes the two species mentioned above, in addition to the Guianan bearded saki monkeys, *Chiropotes sagulatus* (formerly *C. satanas*: see(Silva Júnior and Figueiredo 2002), *Alouatta seniculus*, red howler monkeys; *Cebus apella*, brown capuchin monkeys; *C. olivaceus*, gray capuchin monkeys; *Saguinus midas*, golden-handed tamarins; and *Saimiri sciureus*, common squirrel monkeys.

The range of elevations and diverse habitats may contribute to high population densities of primates at the site (Norconk et al., 2003). A census in 2003 documented three troops of bearded sakis with an average of 32.7 (22-44) members in each in Brownsberg (Norconk et al. 2003). In four subsequent studies, between 2004 and 2007, bearded saki groups have been habituated and researched extensively, and it is clear that there are at least six groups within the park (Gregory and Norconk 2011; Gregory 2006). The three zones designated in this study include plateau and slopes in the northern region of the berg. Steep slopes contribute to better visibility of the monkeys, where they can be observed at nearly eye level when the observer is up the slope (Figure 2.3).

**Figure 2.3.** Female bearded saki at rest on a branch approximately 30m high. Observer is up-slope.

## Vegetation Types and Fauna of BNP

Due to its location on a 500 m lateritic plateau, the forests of Brownsberg extend over a large range of elevations resulting in high diversity of both flora and fauna. The upper slopes of the plateau create a high potential for endemism because the surrounding areas are dominated by low flatlands similar to an island habitat. Because the slopes rise steeply, multiple habitat zones may occur in a small area, also contributing to the area's biodiversity. De Dijn, et al. (2007) identified six vegetation types in Brownsberg (Table 2.1). Bearded sakis were found most often in the mesophytic rainforest on the slopes of the mountain and more rarely on the plateau. Both of these habitats support very tall trees. In a study at BNP that included measuring and identifying all trees > 10 cm DBH (diameter at breast height) in nine, one-hectare diversity plots ter Steege, et al. (2007) found the highest average tree diversity at BNP, followed closely by forests on neighboring mountains and then by lowland forests in Suriname. Using Fisher's α, tree diversity at BNP ranged from 72.1 (plateau forest) to 43.1 (plateau, mountain savannah forest). In general, the Guiana Shield has been found to have lower α tree diversity than central and western Amazonia (ter Steege et al. 2006).

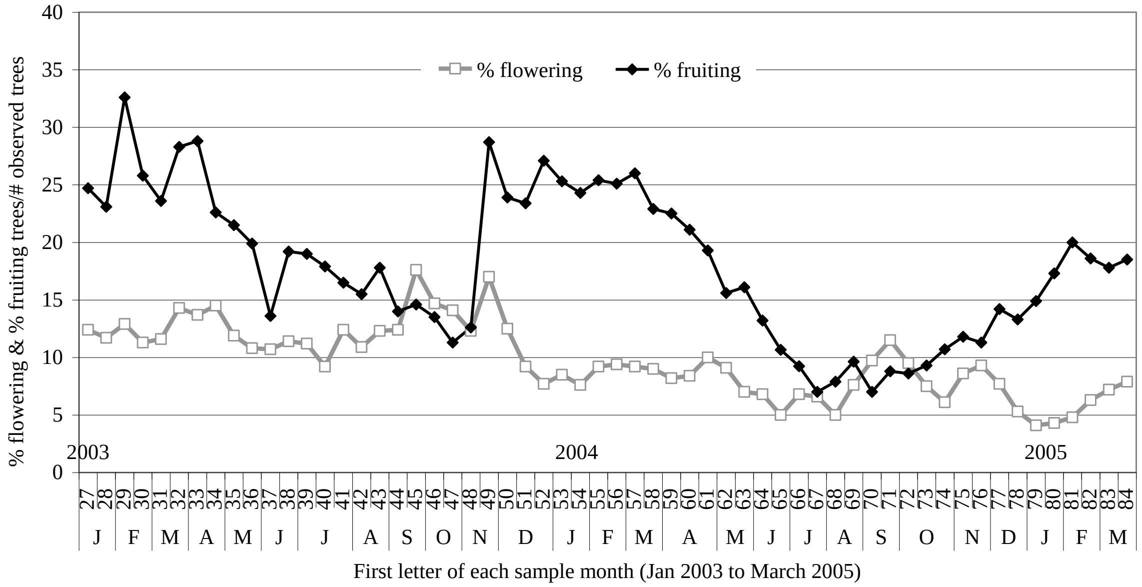
**Table 2.1.** Habitat types of Brownsberg Nature Park with technical descriptions as identified by De Dijn, et al. (2007, see p. 143-144 for full descriptions).

| Habitat Type | Technical Description |
|---|---|
| "Standard" Mesophytic Rainforest | Multi-level forest on deep, well drained soil; canopy high to very high; possibly making up 70-80% of BNP forests |
| Meso-Xerophytic Forest on Partially Ferro-Bauxite-Encrusted Soil | Multi-level forest on encrusted plateaus and caps; lower than "standard" forest |
| Predominantly Xerophytic Low Forest on Heavily Ferro-Bauxite Encrusted Soil | Low, single-level forest in exposed, ferro-bauxite encrusted areas with little topsoil |
| Bamboo/Liana Forest | Low thicket, dominated by lianas and bamboo |
| Marshy Streamside Forest | Similar to "standard" forest but seasonally flooded |
| Swamp-Marsh Forest | Poorly drained, marsh forest dominated by pina palm |

## Weather Patterns at BNP

Ter Steege and Persaud (1991) examined 100 years of phenological records in the forests of nearby Guyana and described a bimodal annual weather pattern (two dry seasons and two wet seasons annually) controlled by the Inter-tropical Convergence Zone (ICZ). Brownsberg demonstrates similar weather patterns. De Dijn, et al. (2007:138) described the four seasons typical of the area as follows: long rainy season—late April-May until mid-August (very reliable); long dry season—mid August until November-December (very reliable); short rainy season—December until January (unreliable, occasionally failing); and short dry season—February-April (transitional and often not very distinct). Variability in the length of the seasons may be due to influences of the Brokopondo Reservoir, a gradual global increase in temperature, and 30-40-year periodic dry-wet phases demonstrated in nearby areas (De Dijn et al. 2007). Furthermore, phenology analyses conducted by STINASU show somewhat erratic fruiting patterns in response to short-term variations in climatic conditions, which suggests considerable inter-annual and inter-seasonal variation in fruiting (Figure 2.4).

**Figure 2.4.** Phenology data for Brownsberg Nature Park for January 2003 through March 2005 (STINASU data, compiled by A. Vreedzaam).



The average annual rainfall at BNP (data from 1972-1985) was 1,985 mm, with a minimum of 1,555mm in 1983 and a maximum of 2,581 mm in 1972 (reported in De Dijn et al. 2007; Reichart 1997 and unpublished Suriname Meteorological Service). The average daily maximum temperature is 30°C and minimum 19°C (STINASU data from the BNP Weather Station between May 2004 and April 2005 (reported in De Dijn et al. 2007; Djosetro et al. 2005). Weather at the top of the plateau is cooler and milder than lowland sites (De Dijn et al. 2007).

During this study, temperature (minimum and maximum) and rainfall (mm) were collected daily at 0630 on top of the plateau. The maximum temperature was 31°C (mean maximum = 27.5±1.6°C) and minimum of 18°C (mean minimum = 20.2±1.0°C, Figure 2.5). Rainfall data demonstrated that the year of the study was abnormally wet, with a total rainfall of 2,896 mm between April 2008-March 2009 (Figure 2.6), 46% more rainfall than the average from 1972 to 1985. As a result, the wet season lasted longer than expected and the short dry season was relatively wet.

### Ecological and Behavioral Data Sampling

The present study took place between March 2008 and April 2009. Three “zones” were used throughout the study during the following periods (see Figure 2.1): Pedreku Pasi (PP) Zone: March-July 2008; Witi Kreek (WK) Zone: June 2008-March 2009; and Aguago Kununu Pasi (AKP) Zone: October 2008-January 2009. In addition to the main camp at the site of the overlooks (Figure 2.1), a satellite camp (7 km south of the main camp) was set up at the beginning of the study and used to collect data in the Pedreku Pasi Zone. Research in the Pedreku Pasi Zone was abandoned in August 2008 and in the Aguago Kununu Pasi Zone in December 2008 due to clear signs of hunters and hunting activity. Methodology specific to ecological and behavioral data collection is included in Chapter 3 (methods for group size and social behavior), and chapters 4 and 5 (sampling methods for ecological data collection).

**Figure 2.5.** Maximum and minimum daily temperature in degrees Celsius between March 22, 2008 and April 30, 2009 at Brownsberg Weather Station.

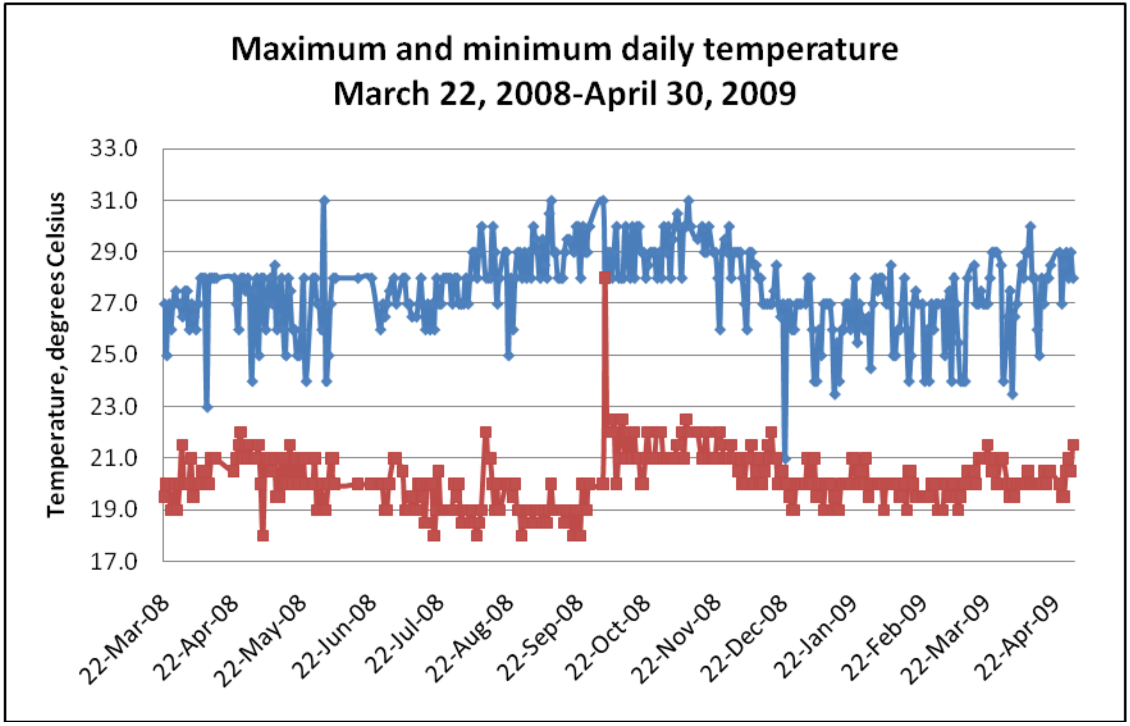
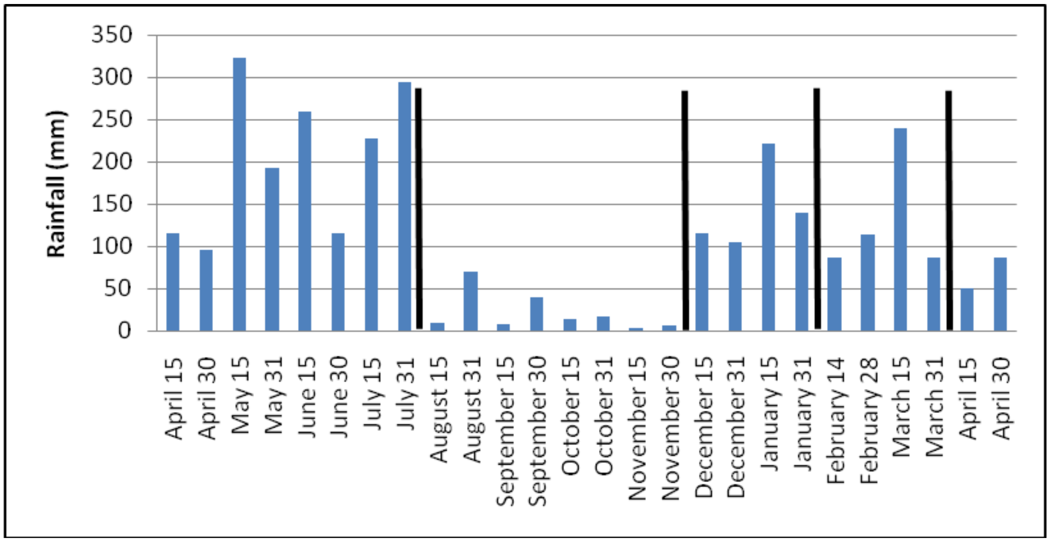


**Figure 2.6.** Cumulative bi-weekly rainfall from March 22, 2008-April 30, 2009. Seasons denoted by black lines in the following order: 1) long wet season, 2) long dry season, 3) short wet season, and 4) short dry season.



# CHAPTER 3

# SOCIAL BEHAVIOR AND GROUPING

## INTRODUCTION

Because males are limited reproductively by their access to females (Trivers 1972), competition for access to females is expected to emerge, particularly in polygynous mating systems (van Hooff and van Schaik 1994; van Schaik 1989; van Schaik 1996). While for many primate species, such competition manifests itself in the formation of one-male units (e.g., *Gorilla* spp., some *Alouatta* spp., most colobine spp.) in which mating occurs primarily between females and the resident male, in multimale groups, females cannot be fully monopolized by a single male, and males compete for access to groups of females. This creates high variance in reproductive success, with some males never gaining access to females. In multimale groups, males solve the problem of access to females by residing in the same group, but behaviors among males are more frequent and proximate. As a result, a variety of competitive and cooperative behaviors have evolved (van Hooff and van Schaik 1994; Wrangham 1980). Competitive behaviors are well known in many taxa, while cooperative strategies are less common.

Bearded sakis (*Chiropotes* spp.) along with uakaris (*Cacajao* spp.), their sister group, present an interesting example of multimale-grouping primates that show low sexual dimorphism, potential female-transfer, egalitarian male-male relationships, and preferential male-male behaviors (e.g., proximity, grooming, body rubbing, tail wagging)

(Ayres 1981; 1986; Peetz 2001; Silva and Ferrari 2009; van Roosmalen et al. 1981; Veiga et al. 2005). Bearded sakis and uakaris range from 3.0 to 3.5 kg and live in large, multimale-multifemale troops that can have as many as 56 members in bearded sakis and more than 100 in uakaris (Aquino 1998; Aquino and Encarnación 1999; Bowler and Bodmer 2009; Defler 2001; Norconk et al. 2003; Pinto 2008).

Virtual parity in the socionomic sex ratio in free-ranging groups and observations that groups fission into smaller units has led some researchers to suggest that bearded sakis and uakaris form subgroups of monogamous pairs (Ayres 1981; Robinson et al. 1987). Mating patterns are entirely unknown for these species, although it is clear that social organization is strikingly different from that seen in the small-group-living or monogamous pitheciine genera (*Pithecia* and *Callicebus*; Norconk 2011). Definitive evidence regarding dispersal patterns is also lacking. Dispersal events have not been observed in bearded sakis, being that such events are difficult to see in primate species in general (Di Fiore et al. 2009), and no molecular analyses have been performed. Studies by Peetz (2001), Veiga and colleagues (2005), and Silva and Ferrari (2009) have shown that adult male bearded sakis are affiliative, spending more time with each other than with females. Like the atelins and *Pan* spp., bearded saki males may live in groups characterized by male philopatry and adult males that engage in predominantly cooperative behavior. Low sexual dimorphism in bearded sakis and uakaris may be another potential indicator of male philopatry and low levels of aggression (Di Fiore and Campbell 2011; Strier 1994; Stumpf 2011),.

Titi monkeys and sakis, the smaller-bodied pitheciines, form cohesive groups, while bearded sakis and uakaris not only form large troops, but also fission into smaller subgroups daily (see Table 3.1; Ayres 1981; Ayres 1986; Bowler and Bodmer 2009; Gregory 2006; Norconk and Kinzey 1994). Bearded sakis may fission into temporary subgroups (Table 3.1), and they also engage in what Norconk and Kinzey (1994:171) described as "local temporary group fragmentation, " i.e., traveling in large groups between feeding areas, and then separating into smaller feeding subgroups upon reaching a feeding area. Subgrouping is thought to offset competition between group members (Norconk and Kinzey 1994), but it is another example of how bearded saki males may minimize direct competition with each other and tolerate living in large multimale groups.

The presence of cooperative social interactions among males does not preclude the possibility that competition is occurring on a more subtle level via sperm competition, as in *Pan* and *Brachyteles* (Harcourt, 1981; Milton, 1985). Long, hooked penile spines in bearded sakis and uakaris (Dixson 1998; Hershkovitz 1993) and relatively large testes suggest that both of these primates engage in sperm competition, i.e., have large reservoirs for sperm that enable them to copulate successfully in quick succession with multiple females (Dixon, pers. comm.). The primitive pitheciine pattern is exhibited by titis and sakis at the base of the pitheciine radiation. Males in these species have small testes and inconspicuous scrota that blend in with the body pelage and small-to-undetectable penile spines (Hershkovitz 1993). In contrast bearded sakis, have relatively large testes and colorful scrota (white to bright pink) contrasting with dark body pelage (see Figure 1.5, pers. obs.; uakaris do not have conspicuously colored scrota; Defler 2004; Hershkovitz 1993), and males engage in genital displays by waving and lifting the tail over the back when standing. Bearded sakis also frequently retract the testes, one at a time or simultaneously (pers. obs. and L. Veiga, S. Boyle, and T. Gleason pers. comm.). Other primates engage in testes retraction (e.g., rhesus macaques, Altmann 1962; muriquis, K. Strier, pers. comm; mantled howlers, S. van Belle, pers. comm.; vervets, Henzi 1981), but only Henzi (1981; 1985) and Wickler (1967) analyzed its context. They regarded it as either a fear response (Wickler, 1967) or a submissive act of “homage” performed by a subordinate male in the presence of a dominant male (Henzi 1985) . In bearded sakis, this behavior has been observed in contexts that include both feeding and resting (pers. obs. and L. Veiga, S. Boyle, and T. Gleason pers. comm.), but its role as a sociosexual signal has not been investigated. Sexual signals in bearded sakis may be relevant to both other males and females, but their context has not been studied.

## Comparative Social Behavior: Bearded Sakis and Other Male-Affiliative Species

Multimale social groups may consist of related or unrelated males, and dispersal patterns play a central role as indicators of male-male tolerance. When group males are not related, within-group mating competition is expected to be high. Males often exhibit characteristics that will help them win competitive interactions, including larger canine and body size, and aggressive behaviors (Darwin 1871). When group males are related, overt competition is expected to be low, reflected in low levels of sexual dimorphism and high levels of affiliative behavior (and would benefit via inclusive fitness: Hamilton 1964; Trivers 1972), even though inter-group competition (defense of territories) may be high (e.g., in chimpanzees and spider monkeys). If male-male cooperation is reinforced by inclusive fitness, aggressive behavior among males is expected to be relatively low if the degree of relatedness is high.

However, Vigilant et al. (2001) and Inoue et al. (2008) showed that the degree of relatedness among chimpanzee males in a group was much lower than expected, given their near exclusive philopatry, and supported the views that within-group male-male competition among chimpanzees is sometimes very high (e.g., Goodall 1986). Lower than expected relatedness may be due to relatively low male survival to adulthood. Hill et al. (2001) found that only 11% of male chimpanzees survived to adulthood thus the likelihood of adult brothers being present in a community is also relatively low. Amongst the atelines, higher male-male versus female-female relatedness has only been tested in woolly and spider monkeys and shown in some (not all) groups (Di Fiore and Fleischer 2005; Di Fiore et al. 2009). Therefore, male bonds may be instilled not only through relatedness (i.e., inclusive fitness), but also through familiarity as co-group members. (Futhermore, as demonstrated by Di Fiore et al. (2009) in woolly monkeys, dispersal patterns may not be entirely "strict," and males may also disperse, albeit with lower frequency.)

To compare patterns of affiliation and competition in primate “brotherhoods,” Strier (1994) looked three male-philopatric atelin genera (*Ateles*, *Brachyteles*, and *Lagothrix*), with two *Pan* spp. added to her analysis (Figure 3.1 and Table 3.2; Stumpf 2011). Strier suggested that males living in multimale groups could experience inter-group competition of two types (high or low) and intra-group competition of two times (scramble or contest). For example, chimpanzees engage in high levels of inter-group competition (territorial defense) and also contest (face-to-face or direct) competition within communities resulting in a strong social hierarchy.

When inter-troop competition is high, coalitionary alliances form among males in a troop (*Ateles*, *Pan troglodytes*, and *Brachyteles*, Figure 3.1). Males in these species consistently react agonistically towards extra-troop males, and to ward off extra-group males, they maintain alliances between each other through affiliative interactions. However, when between-troop competition is lower, alliances between males in a troop are weaker or more variable because coalitionary bonds are less necessary (*Lagothrix* and *Pan paniscus*). For example, although males are related in *P. paniscus*, they show the weakest relationships among adults (i.e., female-female and male-female relationships are stronger than male-male relationships: Furuichi and Ihobe 1994).

Intra-troop contest competition occurs in situations in which access to females “depend[s] on the asymmetries in the potential to exclude others” (van Hooff and van Schaik 1994). For example, social rank or body size differences may exist, and the dispersion of females or food is sufficiently clumped so that males can defend access to them. Scramble competition occurs when “resources [i.e., groups of females] are small and dispersed, or occur in patches far greater than group size” (van Hooff and van Schaik 1994). That is, resources are not monopolizable or defensible; thus inter-individual competition, if it exists, is expected to be less energetically expensive and more subtle. Intra-group competition among males leads to hierarchical relationships as males compete for mating opportunities (*Ateles*, *P. troglodytes*, and *Lagothrix*: Di Fiore and Campbell 2011; Fedigan and Baxter 1984; Furuichi and Ihobe 1994; Strier 1994). While there may be evidence of female choice in the form of copulation solicitations, males are generally considered to be dominant over females in these species (Di Fiore and Campbell 2011; Fedigan and Baxter 1984; Stumpf 2011).

In contrast, within-group scramble competition can lead to egalitarian/less-competitive male-male relationships, since the creation of a hierarchy would not increase a male’s chances of mating (*Brachyteles* and *P. paniscus*). In *P. paniscus* groups, adult males have been shown to be dominant over adolescents, but otherwise, the complex, bonded, and hierarchical relationships characteristic of *P. troglodytes* males seem to be absent (Ihobe 1992). Relationships between males and females in *Brachyteles* and *P. paniscus* are typically egalitarian because females cannot be monopolized. For example, Furuichi and Ihobe (1994) suggest that male-male relationships in *P. paniscus* are weaker than in *P. troglodytes* because there is less competition over females in *P. paniscus*. They explain that competition is reduced because there are more mating opportunities (i.e., “patches” of females are larger): the estrous period is longer, and there are typically more sexually receptive females in mixed-sex parties (Furuichi and Ihobe 1994).

Differences in the frequency and duration of group fission events, party size, and membership may also play a role in group social dynamics (Table 3.2). For example, chimpanzees and spider monkeys are characterized by frequent fissioning into relatively small sex-specific groups or into consortships, containing a single adult male and female (Symington 1990). Bonobos also demonstrate fission-fusion behavior, but parties are generally larger than in chimpanzees (Furuichi 1989; Hohmann and Fruth 2002), and higher percentages of parties are mixed-sex (*P. paniscus*: 74% at Wamba versus *P. troglodytes versus*: 52% at Taï: Stumpf 2011). Strier (1989; 1992a) labels *Brachyteles* as “facultatively cohesive” depending on food patch size, while *Lagothrix* spp. troops are the most cohesive of the atelins (Nishimura 1990) (see Table 3.2). Thus grouping patterns may reflect differences in levels of mating competition and may represent different mating strategies. For example, the occurrence of consortships in chimpanzees may be a consequence of contest competition amongst males for females, while the larger subgroup parties in bonobos may be a product of scramble competition.

This study of bearded sakis will examine relationships of males (and females) within groups. Based on previous studies, males are expected to be affiliative, have low hierarchical structure (egalitarian), and engage in rare inter-troop encounters. In addition, that bearded saki males fit the profile of sperm competition suggests that competition among males is of the scramble (subtle) type. Similarly, relatively large subgroup parties may reflect scramble competition for mates.

**Table 3.1.** Group size and notes on subgrouping in other studies of bearded saki spp. **Green bold type** indicates comments on a relationship between feeding and subgrouping, and **blue bold type** indicates comments on a relationship between season and subgouping.

| Species | Length of study (mon.) | Type of forest (size, ha) | Group size: mean, range | Notes on subgrouping | Reference |
|---|---|---|---|---|---|
| *C. albinasus* | 17 | Continuous | 22.5±3.5<br>19-30 | "…os grupos, quando perseguidos, dividiam-se muitas vezes em 2 ou 3 subgroupos. Também, durante as atividades de **alimentação** havia subdivisão dos grupos e algumas vezes os subgrupos eran vistos separados por 200-300 metros, alimentando-se de ávores de espécies diferentes." [1] "Group splitting is not infrequent, but the separation of individuals never exceeds a few hundred meters." (contrasted with *Cacajao*) | (Ayres 1981; Ayres 1989) |
|  | 11 | Continuous | 56 | "…the groups generally divided into two or more subgroups containing 7-25 […] members [and] subgroup membership varied continuously [although] fusion of the whole social group was rare. […]group members that came together at the end of the afternoon would sleep together, but disperse again in the morning…"[2] | (Pinto 2008; Veiga et al. 2006) |
|  | ? | Continuous | 15-20 | Groups not followed | (Miller in Allen 1916) |
| *C. chiropotes* | 15 | Island (180) | 22 | "During bouts of traveling longest distances, all members of the group used the same route, including arboreal pathways […]. Group dispersion was most evident when the group staying in one area for at least a day […although groups] remained within calling proximity." | (Peetz 2001) |
| *C. sagulatus* | **13** | **Continuous** | **17.5±12.8**<br>**2-45** | **See text** | **Present study** |
|  | 3 | Continuous | 20<br>2-40 | "subgrouping occurred frequently[…], and their grouping behavior was classified as predominantly well dispersed (i.e., group members were within auditory range but regularly beyond visual range) with periods of cohesiveness (group members within visual and auditory | (Gregory and Norconk 2011; Gregory 2006) |

| | | | | | |
|---|---|---|---|---|---|
| | | | | range) on all but one of the contact days.” | |
| | 3 | Fragment (10) | 2-19 | “O menor grupo (de 2 membros) […] pode ter sido desmembrado de um grupo original maior.”[1] | (Ayres 1981) |
| | 28 | Continuous | 8-27 | “Groups may occasionally merge and larger groups sometimes break into subgroups during the course of a day’s **foraging** activities.” | (van Roosmalen et al. 1981) |
| | 6 | Continuous | 16 | “…troops moved from one **feeding** area to the next, fragmenting ‘locally’ when they entered an area with more than one feeding tree.” | (Norconk and Kinzey 1994) |
| | 12 | Fragment (1,100) | 30+ | “The group[s] in the area divide in subgroup[s] in the **feeding** bouts. The size of the subgroup[s] varied [from] 1 to 21 individuals and is positively correlate[ed] with the size of the group…” | (Frazão 1992) |
| | ? | ? | 13.1<br>4-20 | | (Muckenhirn et al. 1975)[3] |
| *C. satanas* | 7 | Fragment (1,300) | 27 | None noted | (Santos 2002) |
| | 6 | Island (16.3) | 7 | None noted | (Silva 2003) |
| | 6 | Peninsula (1,300) | 34 | “[…] agrupamento T4 se dividiu freqüentemente em subagrupamentos menores [e] aconteciam de duas formas: (i) […] subagrupamentos mistos [de] 3, 4, 5 a 10 individuos […] durante períodos de **alimentação** […] ou (ii) dois subagrupamentos mistos maiores [de] 12 até 22 individuos […] quando os animais buscavam outras áreas para realização de suas atividades.” | (Silva 2003) |
| | 12 | Peninsula (1,300) | 39 | “…the groups generally divided into two or more subgroups containing […] 8-22 members [and] subgroup membership varied continuously [although] fusion of the whole social group was rare. […]group fusion was more common during the **wet season**…”[2] | (Veiga 2006; Veiga et al. 2006) |
| | 12 | Island (19.4) | 8 | | (Veiga 2006) |
| | 18 | Continuous | 22.89±5.09 | “…subgroups were forming more frequently in the larger forest class sizes, as the monkeys vocalized more and the proportion of the | (Boyle 2008) |

| | | | | | |
|---|---|---|---|---|---|
| | 18 | Fragment (100) | 12.05±1.44 | actual group size that was present during the behavioral scans throughout the day was greater in the smaller forest fragments.” | (Boyle 2008) |
| | 18 | Fragment (10) | 3.79±0.21 | | (Boyle 2008) |
| | 6 | Fragment (1,200) | 9.2±9.2 | “…fluid social organization (fission-fusion)…” | (Pereira 2002) |
| *C. utahickae* | 8 (6 sit) | Continuous (33,000) | 9.2±3.1 | Groups not followed | (Bobadilla 1998) |
| | 8 (21 sit) | Fragment (7,500) | 6.6±4.1 | Groups not followed | (Bobadilla 1998) |
| | 8 | Island (129) | 24 | “Foram observados subagrupamentos de tamanho e composição variada que permaneceram separados durante todo o período de doa ou por varios días consecutivos.” | (Santos 2002) |
| | 6 | Island (129) | 23 | “…dividiam-se em subgrupos, compostos por sete a 18 indivíduos, que ficavam separados por mais de um dia. A composição sexo-etária destes subgrupos era mista e sofría variações, sendo que os menores eran formados por fêmeas em maior número, machos e jovens.” | (Vieira 2005) |

[1] Both part of the same study by Ayres 1981

[2] Results presented together in Veiga et al. 2006

[3] In van Roosmalen et al. 1981

**Figure 3.1.** A comparison of differences in inter-troop (high vs. low) and intra-troop (contest vs. scramble) male mating competition in five primates that exhibit large, multimale-multifemale troops with male philopatry (modified from Strier, 1994; Strier et al., 2002; *Pan* spp. added). Bold type indicates differences in male-male relationships related to differences in level of **inter**-troop male-male competition, and bold, italicized type indicates differences in male-male/male-female relationships related to differences in ***intra***-troop male-male competition.

♂♂ inter-group competition

♂♂ intra-group competition

| | **High** | **Low** |
|---|---|---|
| ***Contest*** | Group ♂♂ **affiliative**<br>Group ♂♂ ***hierarchical***<br>♂♂ ***dominant*** over ♀♀<br>*Ateles* spp.<br>*Pan troglodytes* | Group ♂♂ **tolerant**<br>Group ♂♂ ***hierarchical***<br>♂♂ ***dominant*** over ♀♀<br>*Lagothrix* spp. |
| ***Scramble*** | Group ♂♂ **affiliative**<br>Group ♂♂ ***egalitarian***<br>♂♂ ♀♀ ***egalitarian***<br>*Brachyteles* spp. | Group ♂♂ **tolerant**<br>Group ♂♂ ***egalitarian***<br>♂♂ ♀♀ ***egalitarian***<br>*Pan paniscus* |

**Table 3.2.** Comparisons of selected life history traits in anthropoid primate genera/species that are characterized by male-philoparty and large groups.

| **Genus/ species** | **Group size, range** | **Adult F:M (No. of stud.)** | **Body size ratio (M:F, kg)** | **Male-male rel.** | **Male-female rel.** | **Female grouping patterns** | **Mating comp. bet/ within troops** | **Sperm comp./ genital sig.** | **Reference** |
|---|---|---|---|---|---|---|---|---|---|
| *Ateles* | 16-42 | 2.29 (15) | 1.08[a] (9.11: 8.44) | Affiliative hierarchical | Male-dominant | Fluid | High/ contest | Lg testes | (Di Fiore and Campbell 2011; Smith 1996; Strier 1994; van Roosmalen 1985b) |
| *Brachyteles* | 7-73 | 1.47 (6) | 1.13[b] (9.4:8.3) | Affiliative egalitarian | Co-dominant | Cohesive/ fluid | High/ scramble | Very lg testes | (Di Fiore and Campbell 2011; Lemos de Sá and Glander 1993; Strier 1992b; 1996) |
| *Lagothrix* | 12-49 | 2.00 (6) | 1.04[c] (7.28: 7.02) | Tolerant hierarchical | Male-dominant | Cohesive | Low/ contest | Lg testes | (Di Fiore and Campbell 2011; Smith and Jungers 1997; Strier 1994) |
| *Chiropotes* | **12-56** | **1.00 (2)[a]** | **1.05[d] (3.10: 2.96)** | **Affiliative egalitarian?** | **Co-dominant?** | **Cohesive/ Fluid** | **???/ scramble** | Lg, pink testes, penile spines | (Hershkovitz 1985; 1993; Peetz 2001; Silva and Ferrari 2009; Smith and Jungers 1997; Veiga et al. 2005) |
| *Cacajao* | **8-100** | **1.00 (1)** | **1.20[e] (3.45:2.88)** | **Affiliative egalitarian?** | **Co-dominant?** | **Cohesive/ Fluid** | **???/ scramble** | Penile spines | (Aquino 1998; Aquino and Encarnación 1999; Ayres 1986; Defler 2001; Hershkovitz 1993) |
| ***Pan troglodytes*** | 22-46.5 | 2.80 (4) | 1.11 (46.3:41.6) | Affiliative hierarchical | Male-dominant | Fluid | High/contest | Very lg testes | (Lehmann and Boesch 2003; Smith and Jungers 1997; Stumpf 2011) |
| ***Pan paniscus*** | 18-32 | 2.10 (2) | 1.36 (45.0:33.2) | Tolerant egalitarian | Co-dominant | Fluid/ cohesive | Low/scramble | Lg testes | (Furuichi et al. 1998; Jungers and Susman 1984; Stumpf 2011) |

[a]*Ateles paniscus*, [b]*Brachyteles arachnoides*, [c]*Lagothrix lagotricha*, [d]*Chiropotes satanas*, [e]*Cacajao calvus*

## Hypotheses and Predictions

The goal of this study was to determine where bearded sakis and, more generally platyrrhines that form relatively large social troops, fit within the framework of the competitive interactions proposed by Figure 3.1.

### Hypothesis 1: Group size fluctuates seasonally with changes in rainfall.

Veiga et al. (2005) documented a seasonal component to bearded saki subgrouping patterns and also supported Boyle's (2008) findings, i.e., increased subgrouping occurred in the wet season when groups were larger; group sizes were smaller in the dry season. It is predicted that fissioning into subgroups for an extended period of time may reduce feeding competition, and when group sizes are smaller and more variable feeding competition is predicted to peak.

### Hypothesis 2: If bearded sakis fit the *Brachyteles* pattern of social interactions, then male-male relationships should be mostly affiliative (non-aggressive), and male-female relationships should be egalitarian. That is, males are not expected to be more aggressive to females than they are to other males. Inter-group competition should be high.

Based on the prediction that bearded sakis exhibit similar strategies as *Brachyteles* males, male-male interactions should be more frequent than male-female interactions. If egalitarian, these relationships should show signs of reciprocity. When all-male groupings occur, they are likely to be opportunities for strengthening bonds between males; therefore, they should be times when males are even more affiliative than usual given a lack of females over which to compete. If contest competition for mates is absent, then there should be evidence for sperm competition, genital displays, and males copulating frequently with multiple females.

## METHODS

### Group Size and Composition

Group sizes were estimated opportunistically using the following methods: actual group counts as the group crossed an open area and two indirect methods of estimating group size (vocalizations and fruit fall). The latter was a necessary method to estimate group sizes because bearded sakis are high canopy feeders and travelers, making accurate group counts from the understory impossible. When opportunities arose to compare counting methods, intra-observer reliability among two or more observers was within five individuals. Because home range overlap seems to be extensive between groups of bearded sakis (pers. obs.), group identity could be determined absolutely only in cases where a group was followed to a sleeping tree and re-encountered the following morning.

Groups frequently separated into subgroups. In many cases, subgroups stayed within auditory range of the human observer, and contact calls between subgroups could be heard. When this type of subgrouping event occurred, group size was not considered to have changed. On other occasions, subgroups diverged far enough from the focal subgroup that contact calls could not be heard from the other subgroups (although, this does not rule out the possibility that the monkeys themselves may have been able to hear and/or see other subgroups). When subgroups were this far removed, group size was considered to have changed, and at the end of the 10-minute sample period, the new group size was noted. Therefore, at times the “group” being counted may have technically been a “subgroup,” i.e., a part of a larger group that had separated from other subgroups. Group size changes were analyzed by season to detect potential ecological strategies related to food availability.

Group composition was estimated using the following categories: adult male, adult female, subadult male, subadult female, juvenile, and infant. As in Peetz (2001), age classes were determined by body size, while sex was identified by body size, beard and coronal tuft size, and genitalia. However, while males are slightly larger with distinctive genitalia, an individual’s sex was often difficult to determine. Juveniles were identified by size and by absence of discernable external genitalia and distinguished from infants by independent locomotion. Infants were included in group counts.

### Social Interactions

A social interaction was defined as any interaction between two or more individuals in close proximity. Social interactions were recorded on an “all occurrence” basis (Altmann 1974), and it was not possible to recognize individual animals. For every interaction, the following data were recorded: sex and age class of all individuals involved; level of proximity (i.e., in contact, within one meter, within two meters, etc.); duration of the observable portion of the interaction; whether the interaction occurred within the context of an all-male, male-juvenile, or bi-sexual group; which behaviors were exhibited during the interaction based on the ethogram (Appendix I); and whether the interaction was followed or preceded by another interaction. During a period of sociality, if the individuals involved changed roles, a new interaction was counted. For example, if Animal A was grooming Animal B, and then B began to groom A, a new interaction was counted. In some cases, it was not possible to identify the sex of the individuals involved in the interactions.

Every interaction was categorized as “affiliative” = positive or neutral interaction assumed to reinforce social bonds or “agonistic” = negative interaction assumed to potentially damage social bonds or reinforce a social hierarchy. Interactions in which two or more animals behaved agonistically in a cooperative manner (e.g., lining up together) where categorized as affiliative/coalitionary. Particular attention was paid to male-male interactions and unique male-male behaviors (e.g., piling up, first described by Norconk, see Appendix I, Figure 1). Female-female and female-juvenile interactions were recorded but very rare (when juveniles or infants were simply riding on their mothers, a social interaction was not counted).

## Mating Behavior

All adult male-adult female interactions were documented, including sitting in contact, grooming, mating, and behaviors involving genital movements and displays. The frequency of male-female interactions was compared to birth periods in order to determine whether male and females interact and/or mate only when females are ovulating or in other times as well.

Qualitative observations were made on variations in the color of the skin of the genitalia to determine whether changes occurred over the course of the day or between seasons. *Ad libitum* observations of changes in genital skin color were also made at the Paramaribo Zoo.

### Data Analysis

For seasonal data analyses, the data sets were split by season as indicated in Chapter 2 (long wet season: April-July 2008; long dry season: August-November 2008; short dry season: December 2008-January 2009; and short wet season February-March 2009). A Kruskal-Wallis test was used to compare average, maximum, and modal group size between the four seasons, and post hoc Tamhane tests were used to identify pairs of seasons between which the differences were statistically significant.

## RESULTS

The study period showed higher than usual rainfall (Figure 2.6), and the seasons occurred as follows: long wet: April-July 2008; long dry August-November 2008; short wet: December 2008-January 2009; and short dry: February-March 2009.

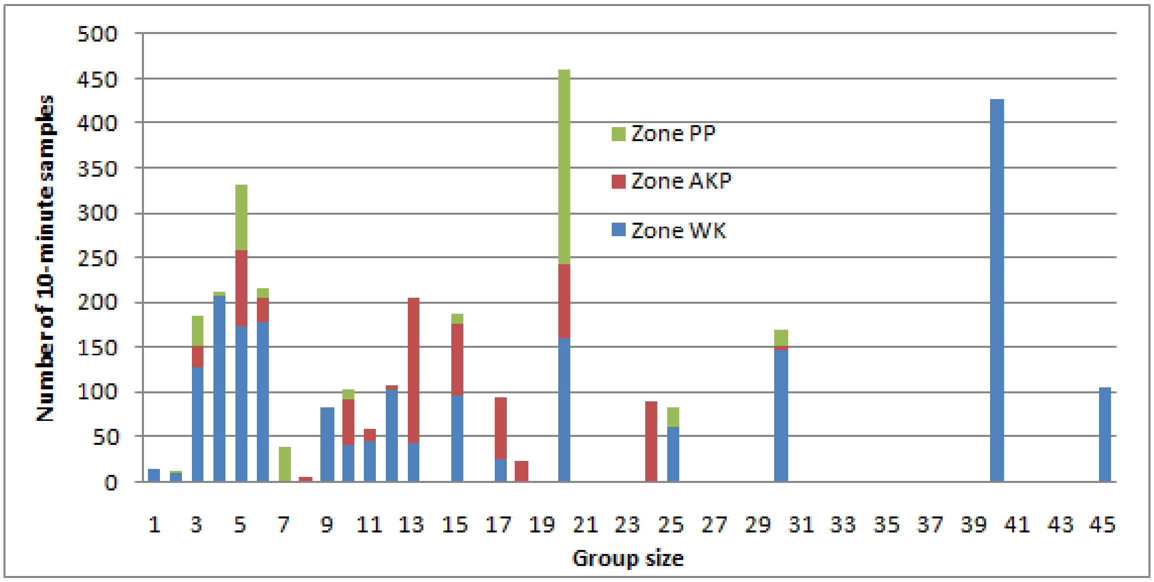
### Variation in Group Size

A minimum of three groups were observed in the study area (Table 3.3). Group size ranged from 1 to 45 individuals (mean=17.48±12.79, mode=20, n=3,207). Group size changed on 27.5% of follow periods that lasted more than three hours (19:69). When group size changed during these periods, it changed an average of 1.58±0.69 times by an average of 8.27±6.85 members. Subgrouping was frequently observed during feeding bouts. The sakis traveled in a large group, and then, upon reaching a feeding area, broke up into smaller feeding parties.

**Table 3.3.** Conservative estimates of the number of groups and subgroup composition in each of the three study zones (see Figure 2.2 for geographic locations of the zones). Mean group size based on 10-minute samples indicated for each zone (with sample size). Mixed group/subgroup composition = adult males and females.

| **Trail zone<br>(number of groups)<br>Mean zone group size** | **Group/subgroup name** | **Group/subgroup size** | **Group/subgroup composition** |
|---|---|---|---|
| Pedreku Pasi Zone (≥ 3)<br>Mean=14.7±8.0 (n=442) | West of OP group | 3-30 | Mixed |
| | KP group | 2-20 | Mixed |
| | SP East of PP group | 10-20 | Mixed |
| Aguago Kununu Pasi Zone (≥ 2)<br>Mean=14.2±6.1 (n=718) | Upper AKP group | 3-20 | Mixed |
| | Lower AKP group | 5-30 | Mixed |
| Witi Kreek Zone (≥ 1)<br>Mean=19.2±14.9 (n=2,047) | Ark subgroup | 3-5 | All male |
| | WK all-male subgroup | 4-5 | All male+juv |
| | WK large group | 3-45 | Mixed |

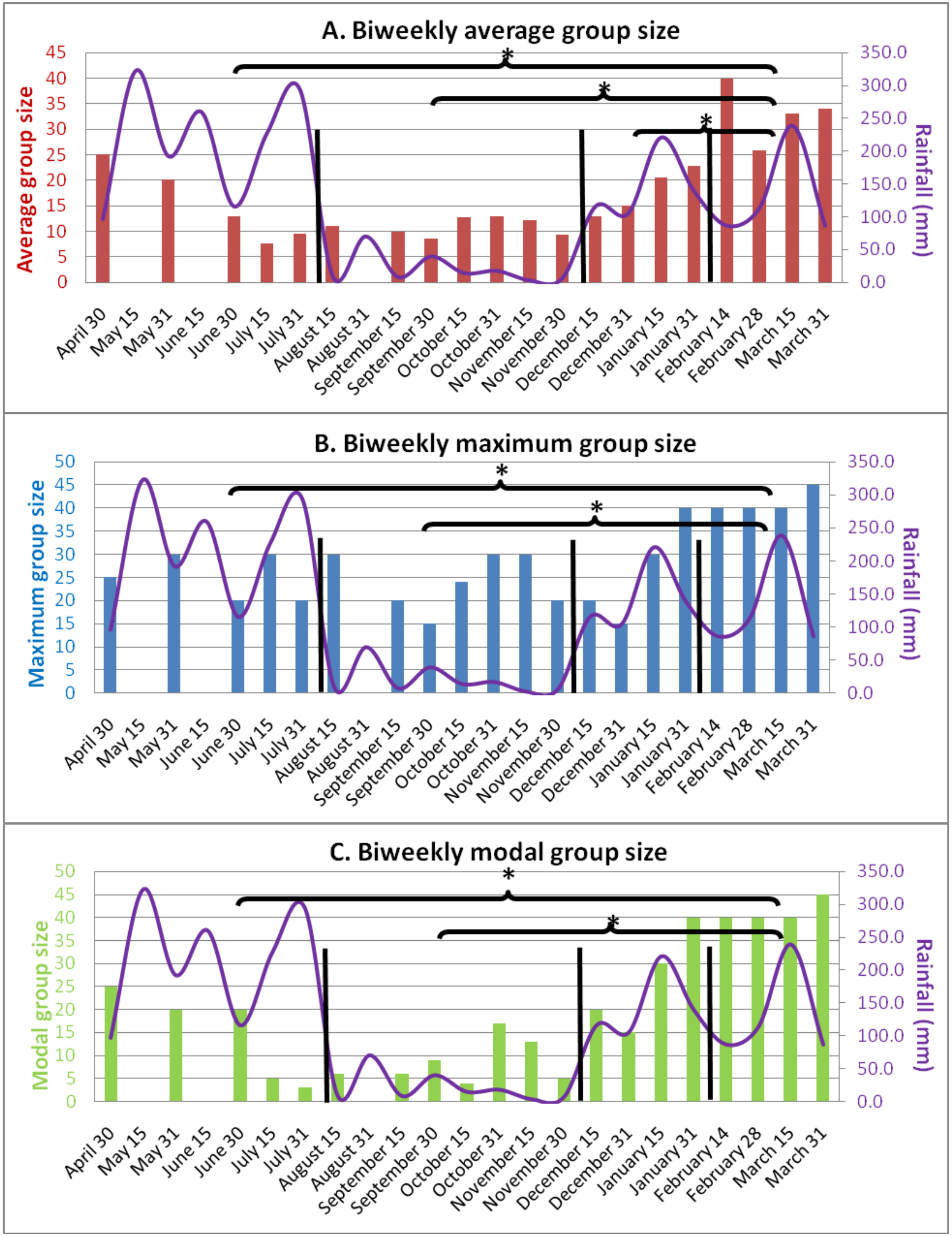
**Figure 3.2.** Bearded saki group size in the three zones assessed via 10-min samples.



## Group Size and Season

Average, maximum, and modal group size varied significantly between seasons (Figures 3.3 A, B, and C and Table 3.4). By all three measures of group size groups were significantly larger in the short dry season than two or all three of the other seasons. After the long dry season, when rainfall is lowest, group size grows into the short wet season they peaks in the short dry season. Group size was also most variable in the long dry season, which showed the highest percent of change in group size (Table 3.5). Conversely in the short dry season, group size only changed during one sample period (from 40 individuals to 3), and in the short wet season group size changed on three occasions but always with the addition or loss of ten members.

**Figure 3.3.** Group size by season. Biweekly A) average, B) maximum, and C) modal group sizes (bars) vary significantly by season (denoted by vertical lines: long wet, long dry, short wet, and short dry). Statistically significant differences between seasons are indicated by brackets and an asterisk. Purple lines indicate rainfall.



A. Biweekly average group size

B. Biweekly maximum group size

C. Biweekly modal group size

**Table 3.4.** Group size by season. Results of the Kruskal-Wallis test of differences among the four seasons and post-hoc Tamhane tests of differences between the seasons for three the group size variables (only statistically significant Tamhane test results are reported, i.e., the short dry season versus two or all three of the other three seasons).

| | **Kruskal-Wallis H** | **Long wet season vs short dry season** | **Long dry season vs short dry season** | **Short wet season vs short dry season** |
|---|---|---|---|---|
| Average group size | H=12.22, p=0.007 | I-J=18.25, p=0.024 | I-J=22.25, p=0.020 | I-J=15.50, p=0.036 |
| Maximum group size | H=8.82, p=0.032 | I-J=16.25, p=0.004 | I-J=17.12, p=0.001 | NS |
| Modal group size | H=12.49, p=0.006 | I-J = 26.65, p=0.017 | I-J=32.68, p<0.000 | NS |

**Table 3.5.** Changes in group size by season during follow periods that were three hours or longer. Number and percent of follow periods in which group size changed and the average number of changes in those periods are illustrated, as is the average absolute value change in group size by number of individual monkeys.

| **Season** | **No. of 3+hr follow periods** | **No. (percent) of periods with a change in group size** | **Avg. no. of changes in group size** | **Avg. change in group size (ind.)** |
|---|---|---|---|---|
| Long wet | 10 | 1 (10%) | 2.0±0.0 | ± 2.5±0.7 |
| Long dry | 26 | 14 (53.8%) | 1.7±0.7 | ± 7.3±4.4 |
| Short wet | 19 | 3 (15.8%) | 1.0±0.0 | ± 10.0±0.0 |
| Short dry | 14 | 1 (7.1%) | 1.0±0.0 | ± 37.0±0.0 |

## Group and Sub-group Composition

At least one male and one female were sighted in every group except for the "Ark" subgroup and the WK all-male subgroup (13.2% of 10-minute samples: Table 3.3 above and Figure 3.4). Group composition on the two days in which the age and sex class of the highest number of group members was determined (both in WK Large Group) was as follows: 1) January 8: estimated group size = 30, sex/age of identified individuals: five adult males, five adult females with infants, five adult females without infants, and five juveniles and 2) January 30: estimated group size = 40, sex/age of identified individuals: three adult males, seven adult females with infants, and seven juveniles. These were very conservative counts. All-male groups or male/juvenile groups were followed on sixteen different days and during all four seasons.

## Social Interactions

Social interactions were most common at the level of dyads (approximately two-thirds of samples) or triplets (26%) (Figure 3.5), and the sex-age composition of the social parties was strongly biased towards males (Figures 3.6). There were relatively few interactions among females and between males and females.

**Figure 3.4.** Percentage of groups that were bisexual, all-male, or of unknown composition based on group scans (n=3,207).

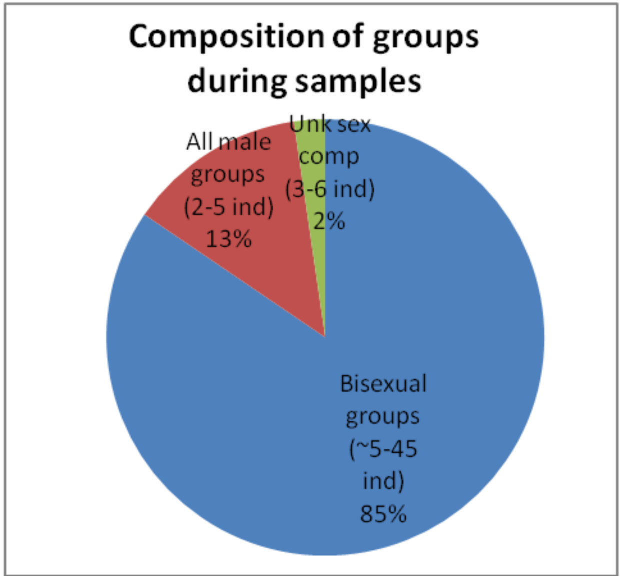


**Figure 3.5.** Number of individuals in social parties. Percentage of cases involving two (n=196), three (n=75), four (n=16), and five individuals (n=2).

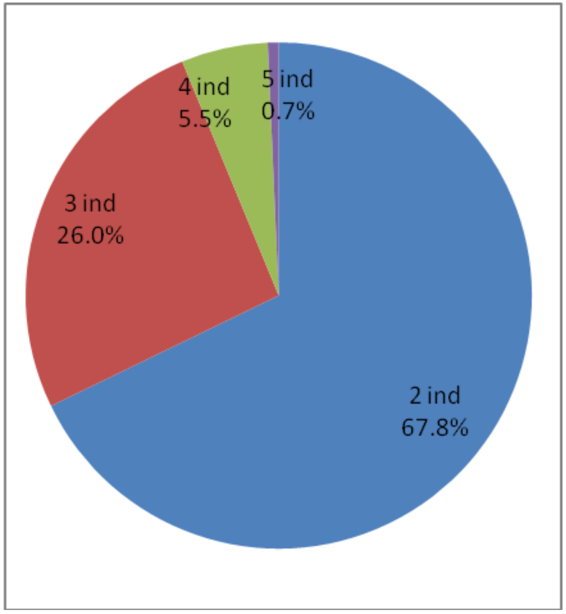
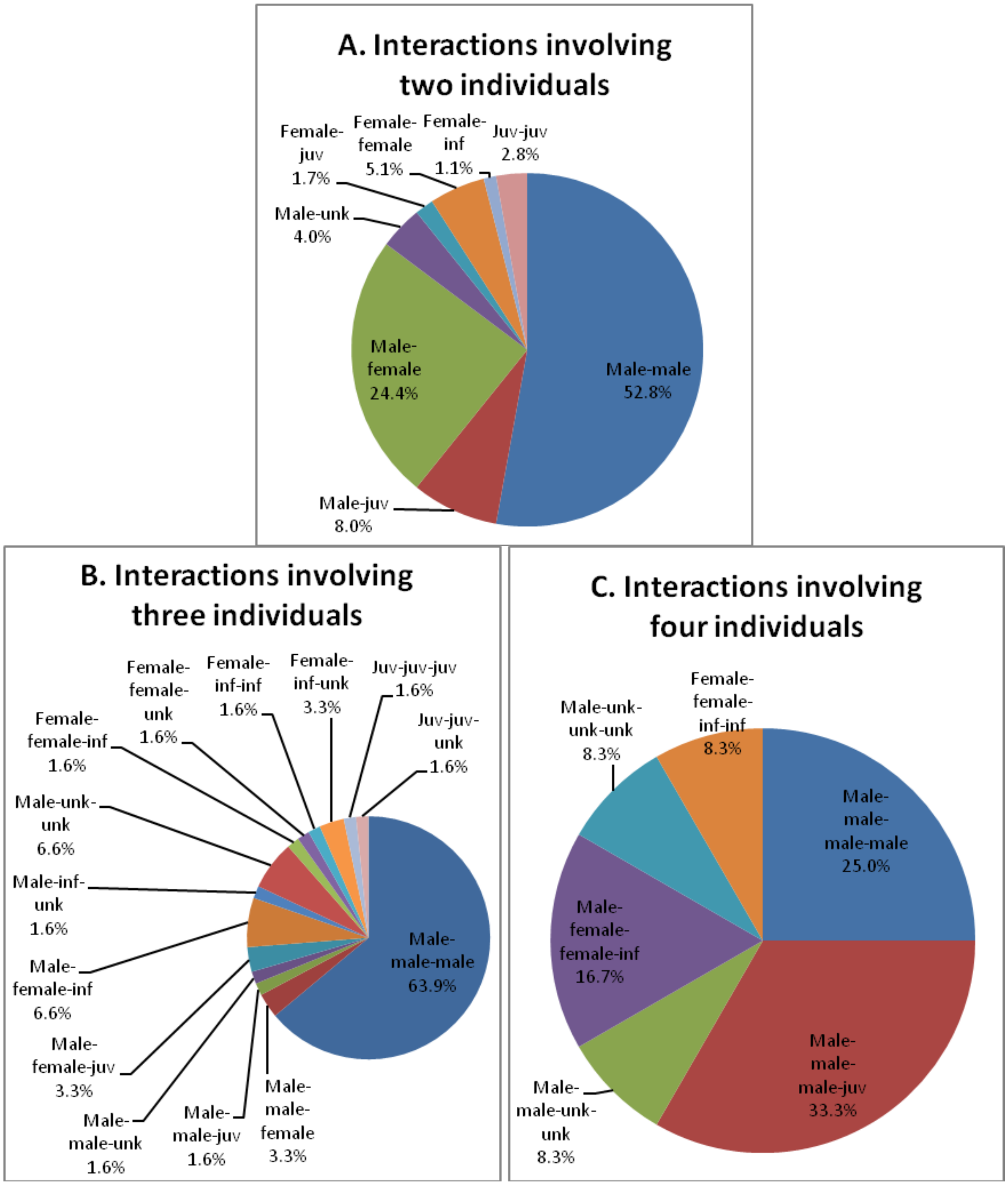


**Figure 3.6.** Sex/age composition of social interactions involving two individuals (n=176), three individuals (n=61), and four individuals (n=12). Samples represent cases in which the sex of at least one individual was known.



## Male-male, Male-juvenile Interactions

Of the 289 social interactions observed, 240 (89.2%) involved at least one male, and 145 (68.7%) involved two or more males. Of the 145 social interactions observed between males, 68.5% involved two males (3.5% of which involved other other age/sex class individuals) and 32.5% involved three or four males (2.5% of which involved other age/sex class individuals). The majority of male-male interactions (60.7%) were observed in the context of an all-male or male-juvenile group. However, all-male groups were typically easier to observe because the monkeys reacted less to the human observers, and they tended to stay lower in the canopy.

All social interactions involving two or more males were affiliative (Figure 3.7). Most of these behaviors (40%) involved sitting in contact with another male, followed by grooming (16%). Grooming was reciprocal in 20 of the 27 cases (74%) (Appendix I, Figure 2, Table 2), albeit reciprocal grooming bouts took place during six extended grooming periods (lasting between 1 and 34 minutes). All of these reciprocal grooming events occurred in the context of all-male or male-juvenile groups (which may have been the same group, with the absence of the juvenile on March 17, 2009).

Highly energetic activities such as play/wresting and “piling up” were observed to occur only in males. When they piled up, they became increasingly animated as more individuals became involved. Males also showed sociosexual interactions, including mounting (n=2; ethogram=“head to genitals”), ano-genital rubbing (n=2), and displaying an erection (n=4). Coalitionary behaviors involving two males engaging in activities together were also observed: lining up (n=19), branch shaking together (n=1), and tail wagging while feeding together (n=1).

Some behaviors observed could have been agonistic, but given their context, they were not interpreted as such. “Chasing” (n=3: male-male, male-juvenile, and male-unknown-unknown) seemed to be in a playful context, i.e., there was no obvious aggression or submissive response. During the single “branch shaking” event the behavior was coalitionary, with the monkeys directing their gaze at the human observer rather than at other members of the group. “Ano-genital rubbing” was mostly seen in lone males (n=7); however, it also occurred, in a social context, with a male in the presence of another male (n=2), a female (n=1), and an individual of unknown sex (n=1). The frequency of “tail wagging” was not estimated as it was seen almost constantly in many social and solitary contexts during feeding, resting, and traveling.

The majority of the 58 interactions between males and juveniles were between a single male and a single juvenile (75.9%), and a small percentage involved more than one male and a juvenile (10.3%) or a male, one or two females, and a juvenile/infant 13.7%). These interactions were affiliative in all cases (Figure 3.8). Furthermore, grooming bouts during male-juvenile dyadic interactions were reciprocal in 92% of cases (23 out of 25). However, all 25 grooming interactions between an adult male and a juvenile occurred on the same day, and therefore may simply indicate a strong relationship between two individuals (see Table 3.6, last row). On November 18, 2008 reciprocal grooming between adult males and between a juvenile and one or more adult male(s) was seen, along with other affiliative behaviors: sitting in contact, lining up, lying down in contact, play chasing, piling up (with the juvenile), play wrestling (with the juvenile), following (by the juvenile), and feeding in contact (n=3 with the juvenile). Testes retraction and erection display were also seen.

**Figure 3.7.** Behaviors exhibited during social interactions involving two or more males (n=169 behaviors). "Other" includes: lie down in contact, display erection, head to genitals, retract testes, ano-genital rub, move into another's place, chase, push/rub, tail wag while feeding together, and branch shake together.

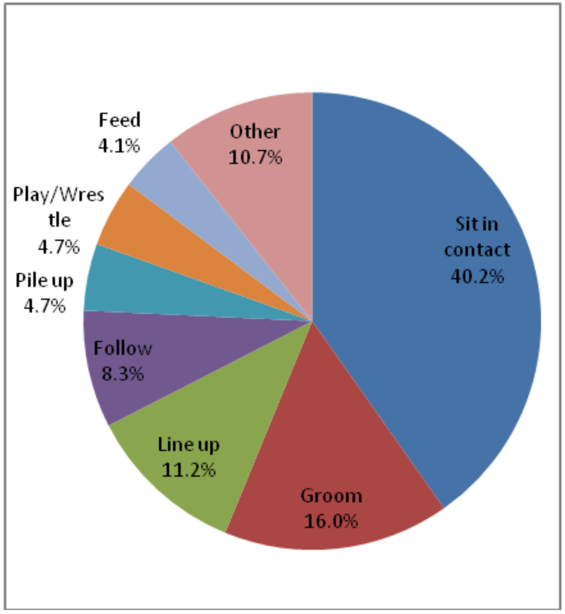
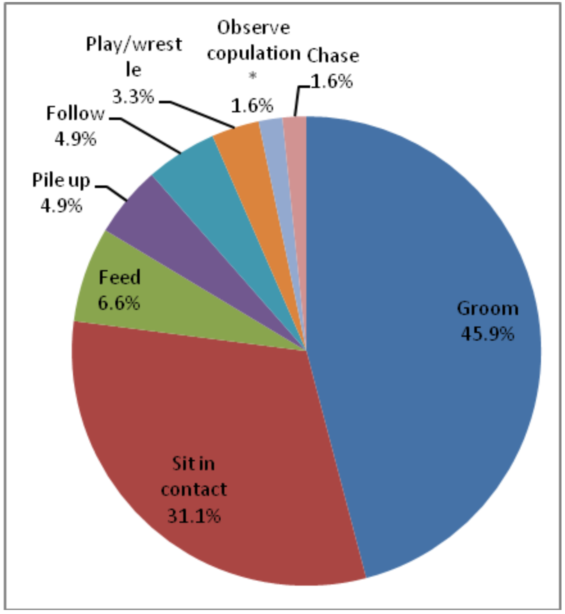


**Figure 3.8.** Behaviors exhibited during social interactions involving males and juveniles (n=60 behaviors). (*One copulation was observed by a juvenile.)



### Female-female, Female-juvenile/infant Interactions

Social interactions involving at least two females were very infrequent (n=9). Grooming (n=4) and following (n=4) were the most common behaviors seen between females followed by sitting in contact (n=3). Of the four grooming interactions observed, two were reciprocal. Females socialized with juveniles and infants somewhat more frequently (n=25) than with other females. The most common behavior observed was sitting in contact (n=11), followed by grooming (n=5), following (n=5), play/wrestling (n=4), feeding in contact (n=1), and allonursing (n=1).

### Male-female Interactions and Mating and Birth Seasons

Twenty four interactions were observed between males and females. Of these interactions, the majority involved a single male and female (83.3%, 25.0% of which were in the presence of a juvenile). There were two interactions involving two males and a female and two involving two females and a male (and juvenile). The most common interactions between males and females were sitting in contact (n=11), copulating (n=9), and feeding in contact (n=3) (Figure 3.9). All other behaviors were observed only once, including grooming, which was not reciprocal, although, in this case a male groomed a female for one minute. Of the nine copulation events (red asterisks in Figure 3.10), during the September 13 event and on one of the September 15 events, the male approached the female.

Infants were observed between November and July (blue bars in Figure 3.10). The birth period was estimated to be between mid November and January, with a peak in mid January, based on the size of infants when they were first observed, i.e., if they were riding on the ventrum (< 1 month of age) or the dorsum (> 1 month of age) of the mother (Appendix I, Figure 3) (Hick 1968, in van Roosmalen et al. 1981). The infants seen at the end of May, 2008 spent time off of their mothers.

Given an early January birth peak (Figure 3.10), the “conception peak,” based on an estimated 5-month gestation period (Hick 1968, in van Roosmalen et al. 1981), would be in early August. The fact that the dates of the observed copulations do not coincide with this time frame indicates either that 1) copulations are difficult to observe, and the data set is very small and not necessarily indicative of a pattern and/or 2) there may be a peak in births, but copulation may occur at various other times as well, particularly if it is not necessarily reproductive.

**Figure 3.9.** Behaviors exhibited during interactions involving males and females (n=31 behaviors).

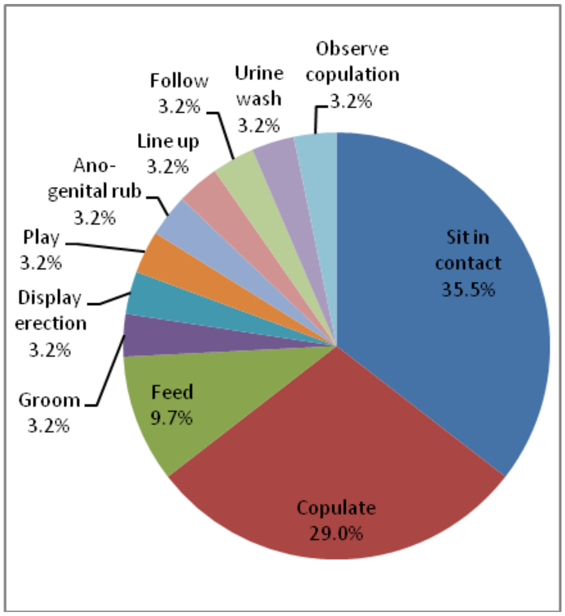
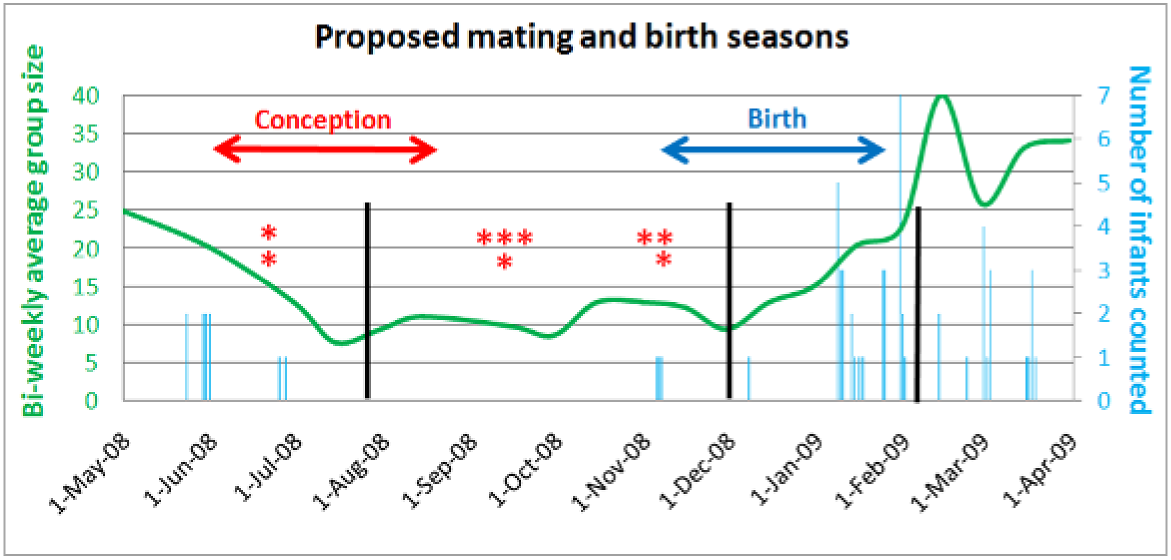


**Figure 3.10.** Proposed mating/conception and birth seasons based on estimated timing of births. The number of infants counted in follow groups (blue columns), bi-weekly average group size (green line), observed copulations (red asterisk), and timing of seasons (vertical black lines: long wet, long dry, short wet, and short dry) also represented. Copulations occurred on June 27 (2); September 13 (2), 15, and 17; and November 4 and 5 (2).



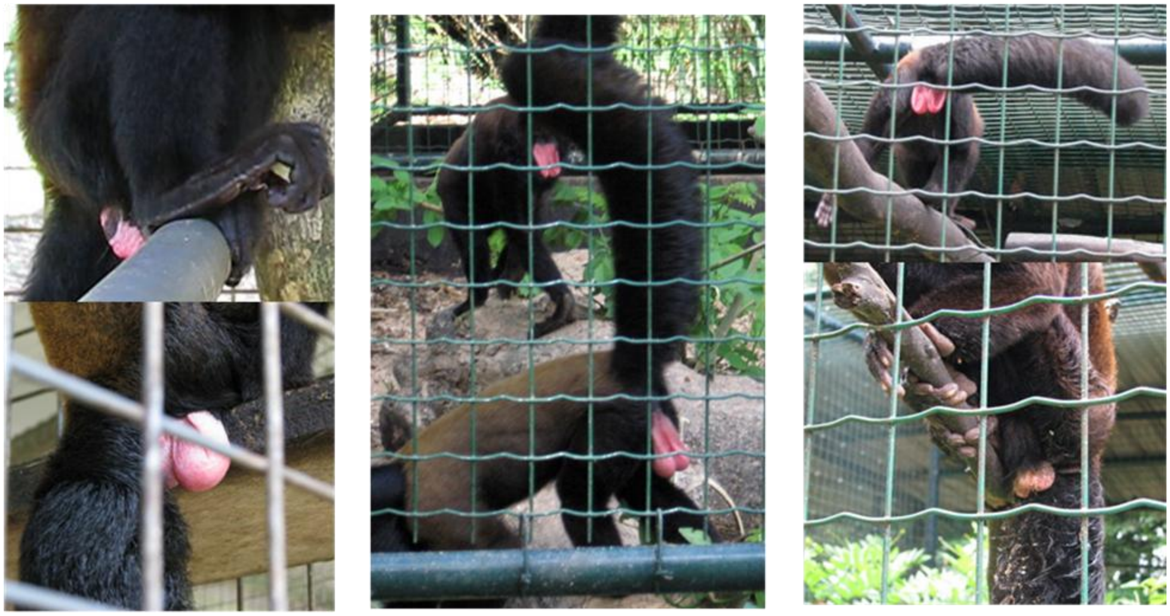
## External Genitalia

Testes retraction was seen during travel, rest, feeding, and grooming, with no distinct pattern indicating that it is either purely involuntary/reflexive or used as a social signaling tool. Testes were retracted together or one at a time, during resting or feeding while neither moving nor in any obvious social context (Figure 3.11). Males displayed erections on eight occasions: following copulation with a female (n=1), with one other male present (n=4), and in solitude (n=3). This behavior occurred more frequently in the context of an all-male group than expected (n=3/4 male-male and n=1/3 solitude cases).

Labia color stayed deep pink over the course of the year at BNP and in the captive individual at the Paramaribo Zoo. However, scrotum color changed in both contexts. Between March and September 2008 all males appeared to have deep pink scrota, but by October and November 2008, color varied from deep to pale pink to white. Scrotum color did not seem to change over the course of the day and could even be used temporarily to identify individuals. Contrary to this pattern the captive male's scrotum was deepest pink in November 2008 (Figure 3.12). Lighting may have contributed to the color difference (the sakis were moved from a roofed to partially un-roofed enclosure from April to September 2008). However, in April 2009, his scrotum was dramatically different in color: pale gray with his testes continuously retracted (pers. obs. and pers. comm., A. Hielkema, zoo curator). This color change is likely related to poor health as he died in May (although, the female died soon afterwards and was not showing any skin color or dramatic activity pattern changes in April).

**Figure 3.11.** Two male sakis, one (left) with both testes retracted and the other (right) with both testes descended.

**Figure 3.12.** Scrotum and labia color in April 2008, November 2008, and April 2009 (testes retracted in the male) at the Paramaribo Zoo, with the female pictured above and the male below.



**April 2008** **November 2008** **April 2009**

## DISCUSSION

### Group Size and Subgrouping

Bearded saki group sizes during this study were similar to those seen at other sites, particularly in studies conducted in continuous forest (Table 3.1). In addition, subgrouping behavior seen in this study was similar to that seen in other studies. As in this study, bearded saki subgrouping is frequently associated with feeding, in that groups stay together, then upon reaching a foraging area, they subgroup into smaller feeding parties (see Table 3.1, blue bold type). In fact, while the groups have been described as “well dispersed […] with periods of cohesiveness” because they spread out over 100-300+ meters (Gregory 2006), Ayres (1989) characterized *Chiropotes* groups as “cohesive” in comparison to *Cacajao* because the latter spread out over 1-2km. Ayres (1989) suggests that *Chiropotes* feeding resources have a more clumped distribution, allowing for increased group cohesion.

As stated above, both Veiga et al. (2006) and Boyle (2008) found subgrouping to have a seasonal component (the former researcher found it to be more common in the wet season, with smaller group sizes in the dry season, and the latter researcher found it to be more common amongst the larger groups studied). These results also coincide with the present study: group size was more variable in the dry season, and groups were significantly larger in the short wet to short dry seasons. In the short wet and dry seasons, the groups consistently spread out into small feeding parties in adjacent trees; whereas, during the long dry season, group size simply changed, and animals spread far from each other for extended periods.

Because of the relationships between group size and season and between subgrouping and feeding, and a potential relationship between season and food availability, it may be concluded that lability in group size may be a strategy to reduce feeding competition. In fact, even within a feeding subgroup, there seems to be feeding competition avoidance. On only seven occasions were animals seen feeding < 3m from each other. During a feeding bout, animals tend to spread out to at least five meters from each other. In fact, feeding bouts tend to be times of best visibility of the group for the observer because the monkeys are sitting still (versus moving around erratically) and making noise (which makes them easier to locate in the trees). However, despite better visibility, very little social contact is seen during feeding periods. Therefore, as originally suggested by Norconk and Kinzey (1994), subgrouping in bearded sakis is likely to serve a similar feeding competition reduction function as does fission-fusion in *Ateles* and *Pan*.

## Social Behavior

Few social studies have been conducted on bearded sakis due to low visibility and difficulty in recognizing individuals. However, similarities arise between the present study and others. In particular, male-male relationships appear to be the most well-maintained in the group, and they seem to be largely affiliative (Peetz 2001; Silva and Ferrari 2009; Veiga et al. 2005). Peetz (2001) observed very low levels of agonism between males and found them to be quite affiliative, exchanging scent through hugging and lining up next to one another. She also found the older male in her study group to be very tolerant of matings by the younger male.

Similarly, Veiga et al. (2005) found that males had other males as nearest neighbors in 63.7% of samples, while in only 15.9% of samples females had other females as nearest neighbors. Furthermore, 54.6% of the time that males were in proximity to each other was spent engaged in social interactions, such as social resting, allogrooming, lining up, playing, and hugging. In contrast, females spent the largest proportion of their same-sex-proximity time traveling (40.5%) or feeding (29.7%) and interacted socially only 16.2% of the time. Agonistic social interactions, i.e., branch shaking, made up only 2% of social interactions amongst males. Another study at the same sites demonstrated a strong bias towards male-male partners during grooming (14 out of 16 events) with evidence of reciprocity (grooming partners swapped positions on average every 1:30±0.42 min during 4:20±1:30 min bouts: Silva and Ferrari 2009).

Contrary to the results of the present study and very likely related to low proportions of males on Danto Manchado Island, Peetz (2001) concluded that females are strongly bonded. She observed female-female grooming pairs on nearly every observation day. Results of the present study and the studies by Veiga et al. (2005) and Silva and Ferrari (2009) are entirely contradictory to the idea that females are bonded. In fact, male-male bondedness and potential relatedness seems to be a more likely scenario given high rates of male affiliation.

Social behavior of the monkeys in these three previous studies may have been altered due to the fact that the animals lived in confined areas. In Peetz's (2001) study on Danto Manchado Island in Venezuela, there were only two males present in the group, and one was not fully adult (and most likely the son of the adult). Although Veiga et al. (2005) gathered a large set of data (n=1,179 social interactions) and results were corroborated by Silva and Ferrari (2009), the animals in these studies occupied a very confined home range of only 80ha. However, the present study provides preliminary data to demonstrate that these patterns of male-male affiliativeness hold true in very large groups in continuous forest as well.

Documentation in this study of novel behaviors such as piling up, reciprocal grooming, and all-male/male-juvenile groups also expands our knowledge of the repertoire of male-biased behaviors in bearded sakis. Interestingly, in this study males were particularly affiliative *in the context* of all-male groups. All-male groups (also called non-breeding groups, NBGs) have been observed in a number of other primate species: *Semnopithecus entellus* (Hrdy 1977; Rajpurohit et al. 1995), *Theropithecus gelada* (Mori 1979), *Macaca mulatta* (Pusey and Packer 1987), *Saimiri sciureus* (Terborgh 1983), *Alouatta seniculus* (Rudran 1979), *Trachypithecus vetulus* (Rudran 1973), *Gorilla beringei* (Fossey 1983; Robbins 1996; Yamagiwa 1987), and *Gorilla gorilla* (Robbins et al. 2004). However, as this list demonstrates, all-male groups are most common in species that form one-male units (Pusey and Packer 1987), and Struhsaker (1969) suggests that it is an antipredation strategy for emigrating individuals. In all-male *Gorilla beringei* groups, higher levels of aggression, but lower incidences of wounding and higher levels of affiliative behaviors such as grooming, play, and socio-sexual behaviors, were found in a comparison with males in heterosexual groups (Robbins 1996). It is believed that the absence of females reduces competitive interactions (Robbins 1996; Yamagiwa 1987).

While small, all-male groups in primates may represent bands of expelled bachelors (e.g., gorillas) seeking membership in bi-sexual groups, the ranging pattern of the all-male group(s) in this study suggests a different scenario. The all-male group(s) in this study used an area almost entirely subsumed by the range of WK Large Group (see Figure 5.2), suggesting that rather than being an aggregation of bachelors, they were instead a subgroup of WK Large Subgroup. In fact, perhaps on the days when WK Large Group was particularly large (~45 members), WK All-male Subgroup made up part of the group.

All-male groups also occurred more frequently in the non-mating season. When it is not mating season, the males, who seem to invest more time socializing with each other than with females (even when females are present), may prefer to aggregate with each other. Subgrouping together may give the males an opportunity to reinforce the bonds between them. The fact that grooming events between males were often reciprocal in this study, suggests a lack of, or certainly a weak, hierarchy. Because male kin are more likely to cooperate rather than compete with each other (and would benefit via inclusive fitness: Hamilton 1964; Trivers 1972), it is possible that affiliative relationship in bearded sakis reflect patrilines and suggest male phylopatry.

Paternal investment in offspring has not been observed in bearded sakis, although has it not been studied extensively. Peetz (2001) observed high levels of tolerance by adult males of food taking by juveniles and social play between adult males and juveniles, potentially indicating indirect paternal investment (Trivers 1972). Silva and Ferrari (2009) observed immature individuals to approach adults and lie on their backs. In this study, at least in one case, reciprocal grooming between a male and a juvenile indicates a more active relationship, particularly in the part of the male. Furthermore, the presence of a juvenile(s) in an otherwise adult male group suggests some level of paternal care, albeit passive. If the juvenile is male, he may learn about and begin to engage in male affiliative behaviors at an early age. On November 18, 2008 during a “piling up” event, the juvenile was very animated as he watched the adult males jumping around the periphery of the “pile.” His behavior suggested that he wanted to be involved, but was still naïve about how to do it.

The most obvious sign of sperm competition during this study was the enlarged, conspicuous testes. Also, preliminary results here showed changes in scrotum color, with a deeper pink color at potential mating times. Testes retraction was seen in various contexts and did not necessarily seem to be a voluntary signal. Erection displays were the most obvious example of genital displays. The fact that males displayed an erection more frequently in the presence of other males rather than females is an indication of potential low grade sexual competition between males, i.e., male-male competition rather than female choice.

## Comparison to Other “Brotherhoods”

In this study, bearded saki males were more social than females; they typically socialized with other males; they showed no signs of hierarchical relationships (e.g., grooming was often reciprocated); they showed no signs of male dominance over females; and they grouped with each other to the exclusion of females and to the inclusion of (a) juvenile(s) (potentially a *male* juvenile). There was no evidence of male dominance over females. There was also no evidence of high inter-group competition for mates because no inter-troop encounters were observed. Therefore, bearded saki females may not be monopolizable “resources,” leading to scramble competition for matings. If contest competition for mates does not occur, hierarchical relationships amongst males would then be unnecessary.

Referring to Figure 3.1 and Table 3.2, bearded sakis indeed were most similar to *Brachyteles*. A clear difference between bearded sakis and muriquis, however is an absence (to date) of documented inter-group aggression. However, shared affiliative, egalitarian male-male and egalitarian male-female relationships between *Brachyteles* and *Chiropotes* may be a sign of high inter-group competition in *Chiropotes* despite lack of documentation. Two scenarios may be considered to explain the absence of documentation of inter-group encounters in bearded sakis. Because bearded sakis generally occupy the top of the canopy and the emergent trees (Gregory and Norconk 2011; Mittermeier and van Roosmalen 1981), they may be able to see other groups that are very far away. Perhaps they do not engage in inter-group encounters because they can see another group and avoid it. Similarly, because groups use very large home ranges, perhaps the chances of running into another group are very low, and therefore, researchers have never observed an inter-group encounter.

Alternatively, inter-group encounters may have been seen but were not easily recognizable because the second group was far away. On a number of occasions during this study and a previous study (Gregory and Norconk 2011) and in a study in Brazil (Silva and Ferrari 2009) entire groups of sakis were observed to engage in long, animated bouts of vocalizing. Because a second group was not seen, it was unclear whether the animals were responding to a predator, another group of sakis, another group of monkeys, or to each other. It is possible that these bouts were inter-group encounters and because the vocalizations are very powerful, they were territorial and may have effectively reached another group despite its being far away.

Another potential explanation for high male affiliativeness in bearded sakis is related to high proportions of males in groups. Perhaps males are highly affiliative to maintain strong bonds between them and high tolerance for each other. In fact, they are at least as affiliative as muriquis, if not more. They demonstrate both strategies that are similar to *Brachyteles* other atelids (e.g., troop fissioning and sperm competition), as well as specific behaviors that are rare or not seen in atelines (e.g., genital signaling and body rubbing). Bearded sakis may in fact be the most male-bonded monkeys known.

# CHAPTER 4

# ECOLOGY

## INTRODUCTION

An organism's lifetime is balanced between energy input (feeding) and energy expenditure (including reproductive and travel activities). While an individual's energetic needs change over the course of its lifetime and in relation to changing reproductive stage, the availability of resources will also change throughout the year (Coelho 1986:199). Although the tropical forests where primates typically live do not experience the extreme temperature fluctuations of temperate forests, there may be considerable variability in rainfall patterns, influencing leafing, flowering, and fruiting cycles (Oates 1987). In consequence, there are seasonal "peaks and troughs in the abundance of particular primate foods" (Oates 1987). When resource availability goes down, animals are expected to either 1) increase time dedicated to feeding and foraging (and therefore increase the energetic costs of finding food) or 2) reduce feeding selectivity at the expense of resource quality while also generally minimizing energy expenditure (Clutton-Brock 1977b; Schoener 1971).

Numerous studies have demonstrated that primate activity patterns change over time in response to seasonality (e.g., Altmann and Muruthi 1988; Defler 1995; Di Fiore and Rodman 2001; Estrada et al. 1999; Isbell and Young 1993; Robinson 1986b; Strier

1987a). For example, following Strategy 2 above, Defler (1995) found in *Lagothrix* that more time was dedicated to (i.e., available to dedicate to) social activity when resources were more abundant. In the same genus, Di Fiore and Rodman (2001) found a slightly different pattern: time spent performing all activities (i.e., eating, foraging, resting, and “other, nonsocial”) except moving and socializing varied significantly by month. Also following strategy two above, their results suggest that rather than increasing time dedicated to foraging or feeding (strategy one above), the monkeys rested more when fruit availability was lower.

In contrast, results of a study of *Cercopithecus* by Isbell and Young (1993) provide support for strategy one. In this study, in all six focal groups, feeding/foraging time (i.e., handling time) increased significantly in the season in which the animals’ diets were limited almost entirely to the seeds of single plant species with presumed high handling time. Finally, a study by Strier (1987a) documented a different pattern in *Brachyteles*. Rather than entirely changing the proportions of time allocated to different activities by season, the monkeys were found to maintain overall time proportions but change activity patterns over the course of a day by season in response to shifts in temperature and rainfall. Strier (1987b) also found that day path length and travel speed varied by season. These studies help develop an understanding of how animals respond to changing resource availability. Here, seasonal patterns in activity budget, travel distance, and feeding habits are analyzed in bearded sakis.

Bearded sakis are large group-dwelling, medium-sized, highly mobile monkeys (see Chapter 3 and Table 4.1). Day paths as long as 6,500m have been documented (Frazão 1992) and home range sizes as large as 1,000ha (Pinto 2008), make these two estimates of range use among the longest and largest for platyrrhines (Tables 4.1 and 4.14). As quadrupedal above branch walkers and runners and generalized leapers (Walker 2005), bearded sakis prefer the upper canopy and emergent trees for their high-speed travel (Fleagle and Mittermeier 1980; Gregory and Norconk 2011; Veiga 2006). Like other members of the pitheciins, bearded sakis are specialized sclerocarpic seed predators (i.e., they remove a hard seed pericarp with their canines and masticate seeds with their flat posterior teeth, Kinzey 1992; Kinzey and Norconk 1990; Norconk et al. 2009). They show a preference for unripe fruit protected by a hard fruit covering, and have numerous associated dental specializations (Kay 1987; Kinzey 1992; Martin et al. 2003; Teaford and Runestad 1992) and minimal dental sexual dimorphism (Ayres 1989; Hershkovitz 1985; Hershkovitz 1987). This high-quality lipid and protein-rich diet (Norconk 1996; Norconk et al. 2009) may provide the energy that allows bearded sakis to be exceedingly mobile (Ayres 1989).

In addition to seeds, bearded sakis also feed on whole fruit or fruit pulp, young leaves, flowers, and insects. In fact, insects appear to be one of the most important seasonal resources for bearded sakis, constituting anywhere from 12.4% of the annual diet (Norconk 1996) to a substantial 21% of their diet (Peetz 2001). Veiga and Ferrari (2006) found that bearded sakis actively seek arthropod prey, although they represented a minor resource during most of the year (~1.5-2.0%). Flowers are another important resource used intermittently throughout the year, and they constituted more than 50% of the diet during a six month study on a land-bridge island in Brazil (Silva 2003).

In her analysis of seasonal patterns in resource use in both *Pithecia* and *Chiropotes*, Norconk (1996:419) suggested that “a diet that is largely seeds instead of fruit pulp may remove sakis from the seasonal effects of low rainfall.” Perhaps because pitheciines are capable of feeding both on an easily accessible resources (ripe fruits and flowers) and resources that are inaccessible to other primates (protected seeds of unripe and ripe fruit) there is not a distinct time of resource shortage for them. However, Norconk (1996) indeed found that the bearded saki diet changes over the course of the year, with adjustments made in the proportions of seeds, mesocarp, and whole fruit and increased diet breadth in dry season. Peetz (2001) also found patterns in feeding habits by season, with bearded sakis spending more time feeding during the periods when they fed on seeds. She hypothesizes that this relationship is a consequence of increased handling time required for seeds versus other resources.

In the present study, bearded saki activity and travel patterns and diet were analyzed from a seasonal perspective. If bearded sakis do not experience times of resources shortage, they may nonetheless adjust diet and travel patterns as the environment changes. Group size was found to change by season (Chapter 3), and this may be a strategy to reduce intragroup feeding competition despite dietary plasticity.

## Hypothesis and Predictions

**Hypothesis: Given that food availability does not remain constant and food availability influences primate ecology, seasonal variation in activity patterns, travel patterns, and feeding ecology are expected in bearded sakis.**

Due to adaptations in the jaws and teeth, bearded sakis are able to exploit a food resource that is highly nutritious and seasonally abundant in space and relatively predictable in time (Norconk 1996; Norconk et al. 1998). As found in other studies (e.g., Ayres 1989; Norconk 1996; Peetz 2001), dietary composition shifts seasonally in bearded sakis. As noted in Chapter 2, the long dry season (August-November, see Figures 2.5 and 2.6) in Brownsberg Nature Park is primarily the flowering season (see Figure 2.4). This is followed by the short wet (December-January) short dry (February-March), and long wet (April-July) seasons which are the heaviest fruiting seasons. Young fruit appears in the short wet season and ripens into the short dry and long wet seasons. Similarly, seeds become available and increasingly abundant in the short wet, short dry, and long wet seasons. The bearded saki diet at BNP are predicted to reflect this pattern, given the fact that they are capable of feeding on flowers and ripe and unripe seeds and fruit.

Animals respond in variable ways to periods of lower food availability. Folivorous primates have been shown to feed and travel longer in times of leaf shortage (e.g., *Trachypithecus leucocephalus*: Huang et al. 2003; *Brachyteles arachnoides*: Strier 1987a) while frugivorous primates have been shown to feed more but travel less (e.g., *Pan troglodytes versus*: Doran 1997; *Eulemur rubiventer* and *Eulemur fulvus rufus*: Overdorf 1996; *Cebus albifrons*: Terborgh 1983). While bearded sakis may not experience periods of resources shortage, *per se*, they may nonetheless experience seasonal changes in resource availability and may make behavioral adjustments accordingly. Peetz (2001) found that the sakis spent a larger proportion of their time feeding not when resources were depleted, but instead when their primary food resource was seeds. Here, the same pattern is predicted: bearded sakis will spend a higher proportion of their daily activity budget feeding during the short wet and dry seasons when they are feeding more on available seeds.

As discussed in Chapter 3, bearded saki group size is variable and groups are not cohesive; fission-fusion is common (Boyle 2008; Gregory 2006; Norconk and Kinzey 1994; Veiga et al. 2006). Since larger groups require more food and use a larger area (i.e., travel further) than smaller groups, it is predicted that day path length will vary by group size (see for a review: Clutton-Brock and Harvey 1977), and as group size increases as will day path length.

Changes in bearded saki group size at BNP (see Chapter 3), and changes in dietary composition, activity, and travel distance predicted here are likely to influence other dietary parameters. In Venezuela, Norconk (1996) found that bearded sakis decreased diet breadth during the wet season when their most preferred resource became available. Numerous studies have found that preferred plant families for bearded sakis include Sapotaceae and Lecythidaceae (see Table 4.15). If the same families are preferred by bearded sakis in BNP, as feeding upon species in these two families increases, diet breadth is expected to decrease. Furthermore, when food patches are larger, bearded sakis should spend more time in each patch and, therefore, use fewer patches in a day.

**Table 4.1.** Comparison of day path length, body size, and group size between a variety of primate taxa that are sympatric with *Chiropotes sagulatus*[1], share common heritage[2], share similar habitat (i.e., Guianan Shield or Amazon Basin)[3], have a similar day/home range[4], have a similar group size[5], are of similar body size[6], or have a common diet[7].

| Species | Activity budget T/F/R/O | Day path length | Home Range | Body size M/F | Group size | Reference |
|---|---|---|---|---|---|---|
| ***Chiropotes sagulatus*** | **31.1/20.3/48.5** | **2,362±821** | **742** | 2.88/2.66 | **17.48±12.79** | (**Present study**; Ayres 1981; Boyle 2008; Pinto 2008) |
| *C. albinasus*[2,3,4,5,6,7] | 36.3/23.8/27.5/8.8 | 3,667±1,687 | 1,000+ | 3.18/2.52 | 56 | |
| *C. satanas*[2,3,4,5,6,7] | 21.3/25.0/46.6/7.1 | 2,990±200 | 429±129.5 | | 22.89±5.09 | |
| *Cacajao calvus*[2,3,4,5,6,7] | 58/20/22[a] | 2,500-5,000 | 500-550 | 3.45/2.88 | 43.5±24.1 | (Ayres 1986; Boubli 1997; Bowler and Bodmer 2009) |
| *Pithecia pithecia*[1,2,3,7] | 17.7/31/51.3 | 981±264 | 18.9-40.6 | 1.73/1.52 | 3.7 | (Ford 1994; Norconk et al. 2003; Thompson in prep; unpub. data) |
| *Ateles paniscus*[1,3,4] | | 2,300 | 255 | 9.11/8.44 | 12/18 | (Norconk and Kinzey 1994; Smith and Jungers 1997; Suarez 2006; van Roosmalen 1985b) |
| *At. b. belzebuth*[3,4] | 24.9/16.7/58.2/0.1 | 3,311 | 300 | 8.29/7.85 | 12-16 | |
| *Brachyteles hypoxanthus*[3,5] | 29.4/18.8/49.3/2.5 | 1,283 | 168 | 9.42/8.33 | 26 | (Lemos de Sá and Glander 1993; Strier 1987b) |
| *Lagothrix lagotricha*[3,4,5] | 38.8/25.8/29.9/5.5 | 2,880 | 760 | 9.00/5.75 | 24 (4m11f) | (Defler 1995; Defler 1996; Ford and Davis 1992) |
| *Alouatta seniculus*[1,3] | 6.2/12.7/78.5/2.5 | 379[a] | 5.6 [b] | 7.2/5.6 | 10.3 [b] | (Ford and Davis 1992; Gaulin and Gaulin 1982; Sekulic 1982) |
| *Saimiri sciureus*[1,5] | 27/61/11 | 2,100 | 250-300 | 0.74/0.64 | 23 | (Boinski 1999; Boinski et al. 2003; Boinski et al. 2002; Terborgh 1983; Wright 1986) |
| *Cebus apella*[1,3,4,6,7] | 21/66/12 | 2,268±402 (r=1,746-3,469) | 80 | 3.05/2.39 | 18/10 | (Ford and Davis 1992; Fragaszy et al. 2004; Robinson 1986a; Terborgh 1983; Zhang 1995) |
| *C. olivaceus*[1,3,4,6,7] | ~20/50/20/10 | 2,100 | 257 | 2.97/2.40 | 21 | |

[a]*Cacajao melanocephalus* [b]Averages of four different groups at the same site.

## METHODS

For general methods, see Chapter 2.

### Activity Patterns

Beginning in July 2008, during every 10-minute scan sample, the activity of all visible individuals was recorded using the following three categories: traveling, feeding, and resting. All social resting was also classified as "resting." Since it was often difficult to see several bearded sakis at a time, the numbers of individuals engaged in each activity was typically conservatively estimated, as in a previous study (Gregory 2006) and in other bearded sakis studies (e.g., Boyle 2008). Since counts were made of the total number of individuals involved in each activity per time frame, data are reported in monkey minutes (one monkey minute = one monkey engaged in one activity during one 10-minute sample).

### Feeding Ecology

Feeding data were gathered throughout the study, with data collection focused primarily on the long dry, short wet, and short dry seasons (August-November 2008, December 2008-January 2009, and February-March 2009). The following data were gathered during 10-minute scan samples: GPS location of feeding tree, total number of feeders, and plant species being consumed. Photographs of the fruit, leaves, and trunk were taken when possible to aid plant identification. Feeding bouts on leaves, insects, and flowers were also noted. Feeding trees and lianas were identified using Fruits of the

Guianan Flora (van Roosmalen 1985a), The Field Guide to the Flora of Brownsberg (STINASU, unpubl.), feeding species lists compiled by Veiga (2006) and Boyle (2008), and assistance from the National Herbarium of Suriname through the photographs.

For each sample day, the total time (number of 10-minute samples) spent in each feeding tree, the number of feeding trees used per day, and the number of feeding species used per day were calculated. These values were also calculated for each bi-weekly period.

### Travel Patterns

Throughout the study period, when a bearded saki group was being followed, a waypoint was recorded every 10-minutes with a hand-held Garmin MAP60 Cx GPS unit. The waypoints were mapped using Map Source 10 to make the following calculations: group travel speed (the distance traveled per 10-minute sample period); morning (AM: a minimum of five hours, up to and including 11:50AM), afternoon (PM: a minimum of five hours, 12:00PM and after), and all-day travel distance; and AM, PM, and all-day cumulative change in elevation (the sum of the absolute value of the change in elevation between waypoints).

### Data Analysis

The data sets were divided into seasons where: long wet season = April-July 2008; long dry season = August-November 2008; short dry season = December 2008-January 2009; and short wet season = February-March 2009. Mann-Whitney tests were used for data sets that spanned only two seasons, and Kruskal-Wallis tests were performed on the data sets spanning three season with Tamhane post hoc tests used to identify pairs of seasons between which the differences were statistically significant.

Bi-weekly averages were calculated for travel speed, number of feeding trees, number of minutes spent in each feeding tree, and diet breadth (plant species used/sample period). Differences in travel distances (km) and cumulative change in elevation (m) were compared for AM, PM, and full day samples.

An ANCOVA was used to test changes in travel distance by season for half-day periods with group size held constant due to significant changes by season in group size (see Chapter 3). Multiple regressions were used to test the effect of season on travel distance and group size (long dry vs. short wet-short dry and major flowering vs. major fruiting seasons). Elevation change and travel distance are highly correlated ($r=0.711$, $p<0.001$). Therefore, to analyze the relationship between season, group size, and travel parameters (elevation change and travel distance), only travel distance was used in this analysis.

ANCOVAs were also performed on the dietary data (number of trees used, number of minutes spent in each feeding tree, and diet breadth) by season with group size held constant. Because group size changes significantly by season, it was held constant to elucidate the relationship between the dietary parameters and season.

For activity patterns and diet composition (all seeds, all fruit, flowers, insects, and bark), data were pooled by season and $X^2$ tests and 2-sample proportion tests were performed to compare seasonal changes, with a Bonferroni correction for repeated tests. The strength of association was also calculated using Cramer's V.

Dietary overlap between the seasons was calculated as a percentage using the following statistic from Krebs (1989:381):

$$P_{jk} = [\Sigma(\text{minimum } p_{ij}, p_{ik})]100$$

$P_{jk}$ = Percent overlap between species $j$ and $k$
$p_{ij}$, $p_{ik}$ = Proportions resource $i$ is of the total resources used by species $j$ and $k$

Simpson's Index of the evenness of use by season of the ten most used plant families and species was calculated as follows:

$$D = \frac{\Sigma n_i(n_i-1)}{N(N-1)}$$

$n_i$ = Number of samples of species/family $i$ in the data set
$N$ = Total number of samples in the data set

## RESULTS

### Activity Patterns by Season

In the annual sample, bearded sakis spent about half the sample periods resting (48.5%) and a higher proportion of samples traveling than feeding (31.1% versus 20.3%) (n=24,010 10-minute monkey samples), but significant differences were seen among the long dry, short wet, and short dry seasons ($x^2$=907.84, p<0.001, Cramer's V=0.14; Figure 4.1 and Table 4.2). The long dry season was further divided into two-month-long early and late periods to illustrate the shift from a higher percentage of feeding in the early dry season to a lower percent by the late dry season. This analysis also demonstrated a significant change in activity budget among the four periods ($x^2$=1,007.02, p<0.001, Cramer's V=0.15, Figure 4.1 and Table 4.3). The proportion of time spent traveling remained relatively constant across seasons, and tradeoffs were made between time spent feeding and resting.

**Figure 4.1.** Activity budget for the long dry, short wet, and short dry seasons (above) and a division of the long dry season into a early and late two-month periods. Long dry: n=12,839 (early long dry: n=3,177; late long dry: n=9,662); short wet: n=5,949; short dry: n=4,652.

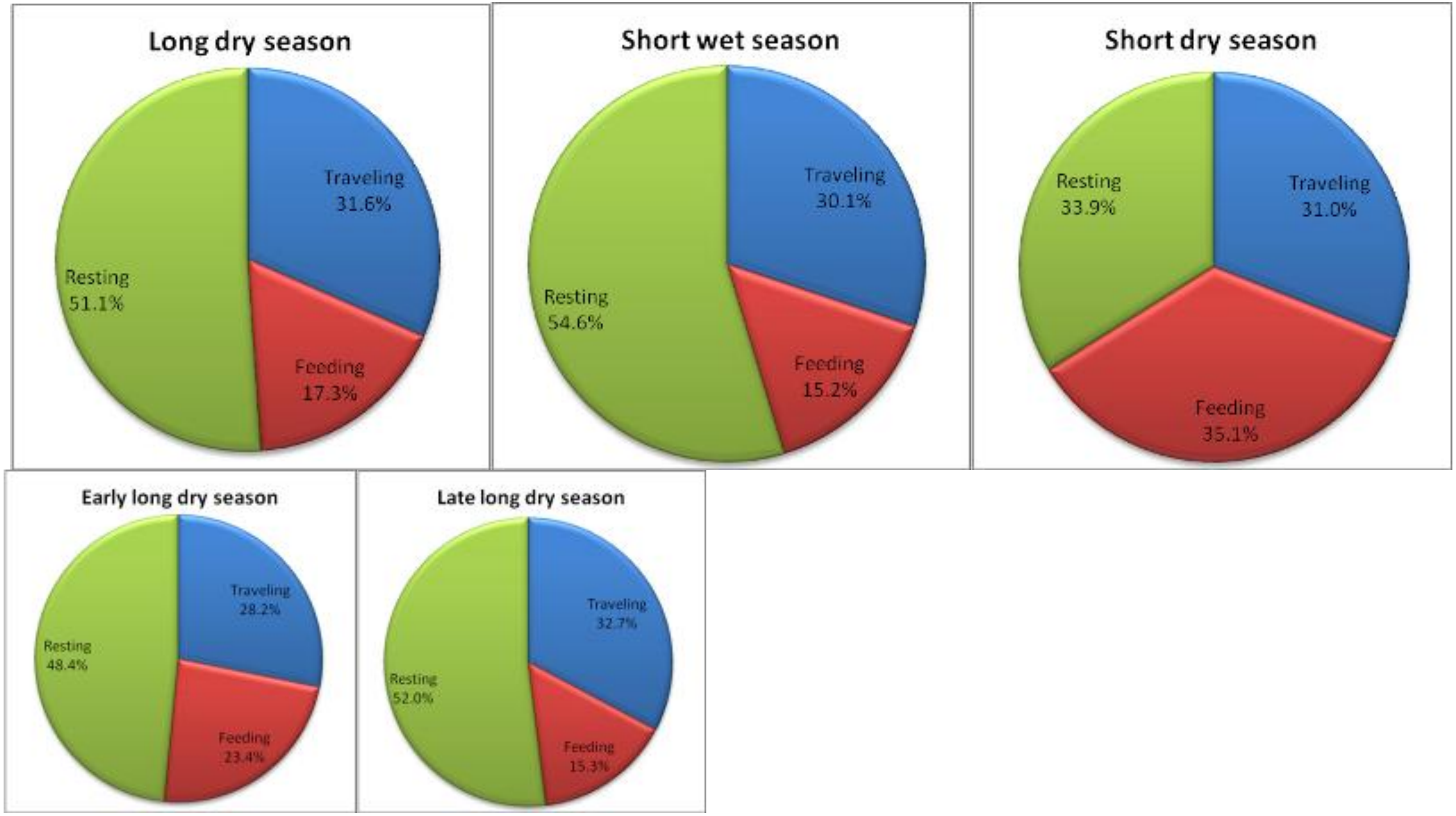


**Table 4.2.** Z scores for two-sample proportion tests comparing the three activities between the three seasons. (* indicates significance at the p=0.01 level with the Bonferroni correction for nine repeated tests (z≥3.26; at the p=0.05 level z≥2.77).)

| | Traveling | Feeding | Resting |
|---|---|---|---|
| Long dry vs short wet season | 2.02 | 3.57* | 4.54* |
| Long dry vs short dry season | 0.77 | 25.13* | 20.22* |
| Short wet vs short dry season | 0.95 | 23.84* | 21.31* |

**Table 4.3.** Z scores for two-sample proportion tests comparing the three activities between the four periods (the long dry season is split into early and late periods). (*=p < 0.05 using the Bonferroni correction for 18 repeated tests (z ≥ 2.99).)

| | Traveling | Feeding | Resting |
|---|---|---|---|
| Early long dry vs late long dry season | 4.80* | 10.46* | 3.45* |
| Early long dry vs short wet season | 1.97 | 9.67* | 5.66* |
| Early long dry vs short dry season | 2.68 | 11.09* | 12.93* |
| Late long dry vs short wet season | 3.39* | 0.14 | 3.26* |
| Late long dry vs short dry season | 2.09 | 26.94* | 20.33* |
| Short wet vs short dry season | 0.95 | 23.84* | 21.31* |

## Feeding Ecology

A total of 4,879 10-minute monkey feeding records were tallied of which 80.3% (3,918) were identified to family, and, if possible, genus and species level. The monkeys fed primarily on the seeds of unripe (61.8%) and ripe (23.6%) fruit (total seeds = 85.39%) and mesocarp and exocarp of unripe (6.2%) and ripe (3.2%) fruit (total fruit = 9.42%), followed by flowers (4.32%), insects (0.46%), and bark (0.41%). They fed on the fruit, seeds, and flowers of a total of 112 plant species (including 15 unidentified fruit species and 3 unidentified flower species) in 32 families (excluding the unidentified species; Appendix II, Table 1). The top ten plant species accounted for 52.1% of the samples (Figure 4.2) and the top ten plant families accounted for 89.5% of feeding samples (Figure 4.3).

**Figure 4.2.** The ten most frequently used plant species. Data collection was heavily biased towards the long dry (August-November), short wet (December-January), and short dry (February-March) seasons). The ten most used species account for 52.1% of samples (n = 2,040).

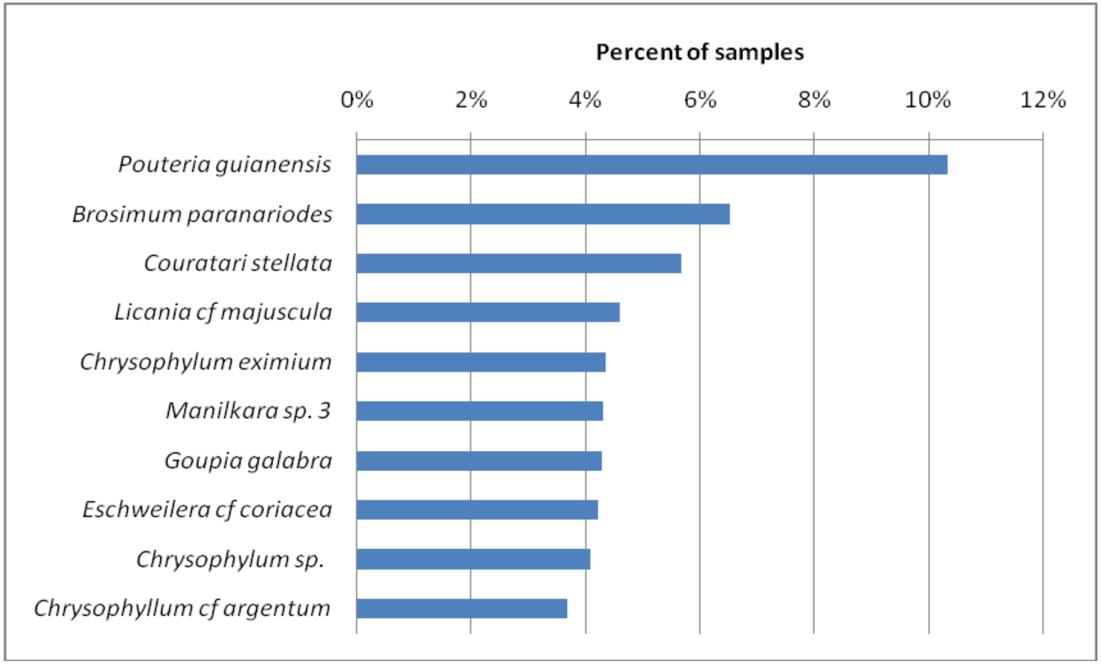
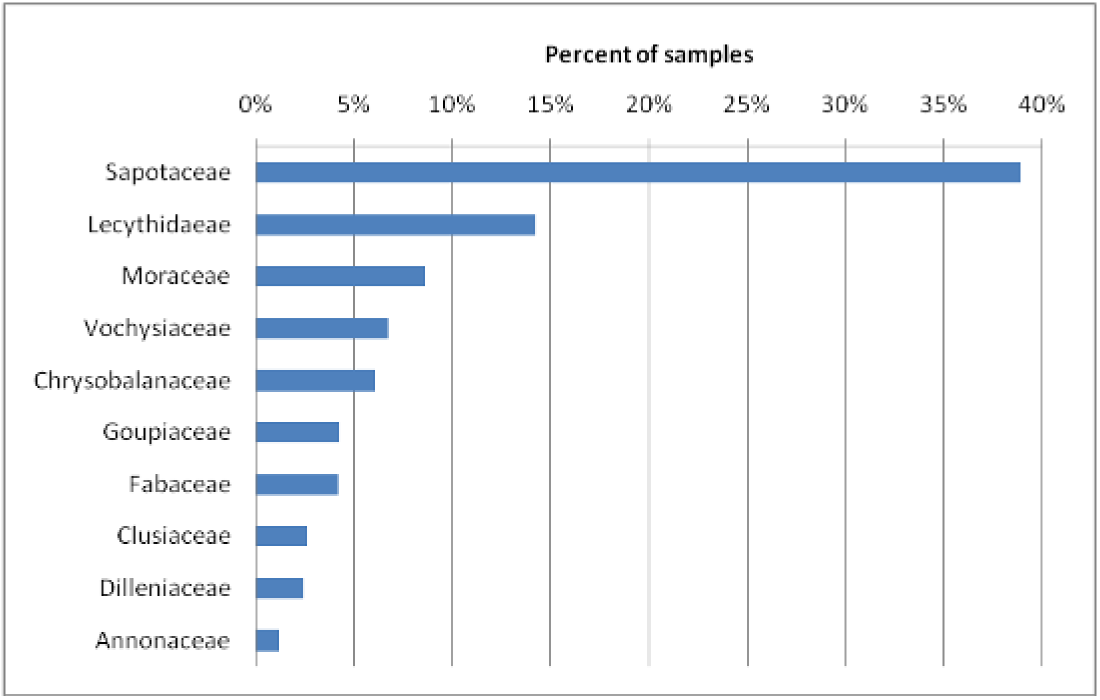


**Figure 4.3.** The ten highest ranked plant families (data collection was heavily biased towards the long dry (August-November), short wet (December-January), and short dry (February-March) seasons). The ten most used plant families account for 89.5% of samples (n = 3,507).



*Pouteria guianensis* (Sapotaceae) was the highest ranked resource, and it was consumed by the bearded sakis during the short dry season and through all stages of ripeness (see Appendix II, Figure 1). During feeding bouts in the early stages of ripeness when monkeys were feeding on the seeds, nearly 100% of the fruit found below the feeding trees was gnarled due to insect damage. As it ripened, *P. guianensis* mesocarp was consumed by five other primate species that inhabit the Mazaroni Plateau:, *Alouatta macconnelli*, *Ateles paniscus*, *Saguinus midas*, *Cebus apella,* and *C. olivaceus* and P. pithecia ingested seeds ( C. Thompson, pers. comm.). While bearded sakis fed on seeds, the other primate species may have been drawn to the exocarp and mesocarp, which would account for the increased "popularity" of the fruit as it ripened.

Unripe and ripe seeds of *Brosimum paranariodes* (Moraceae) were the second ranked resource, and they were consumed for a longer period than *P. guianensis* (long dry thru short wet season, Appendix II, Figure 2). The third ranked resource were young seeds of, *Couratari stellata* (Lecythidaceae), which was also used for a longer period than *P. guianensis* (short dry season in 2008 and short wet to short dry season in 2009, Appendix II, Figure 3), and *Couratari stellata* fruits have little mesocarp and are protected by a hard, tough pixidium. Other primate species were not observed to ingest these fruits.

*Eperua falcata* (Fabaceae) accounted for 2.65% of all feeding samples, and the monkeys consumed not only the seeds (1.00%), but also the flowers (1.17%) and the mesocarp (0.48%) (Appendix II, Figure 4). However, the mesocarp was only consumed on one day (November 5, 2008) and was systematically scraped off of the exocarp with the incisors. The week of November 1, 2008 was nearly the driest week of the study year (rainfall = 0.1mm; the week of September 1, 2008 was the only week that was drier with no rainfall), and this may have influenced ingestion of moist mesocarp at this time.

### Consumption of Flowers, Bark, and Insects

The sakis were observed wadging bark (Goodall 1986:238)[1] from a Lecythidaceae tree (Appendix II, Figure 5) on two different sample days in the early dry season. The monkeys pulled the bark off the branch with their lips and teeth, chewed on it while manipulating it with their hands, and spat out wadged masses

Among the flower species used, two Lecythidaceae species were ingested frequently (Appendix II, Figure 6). Inspection of yellow Lecythidaceae flowers that were aborted by the tree (i.e., not manipulated by the monkeys) revealed that nearly every flower contained a single small larva (pers. obs. and pers. comm., C. Thompson). Since the flowers that were dropped were dismantled, but no flower parts were missing, it is likely that the larvae, rather than the flower itself was consumed. Perhaps this was the case with the other flower species as well; however, typically flower parts were removed, and no larvae were found during inspections.

On two occasions in the late long dry season and the short dry season (October 17, 2008 and February 20, 2009, respectively), the sakis were clearly consuming arthropods. Although visibility was low, numerous sticks containing beetles, ants, or larvae were being dropped by the monkeys for an extended period of time. Although

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[1] “Wadge” as defined by Goodall (1986) is “a wadge of skin, seeds, and fibers, which the chimpanzee may squeeze and suck…” In this case, the bark was peeled, sucked, and spat, for which reason the term “wadge” is used.

these extended feeding events on arthropods were very rare, it is highly probable that the sakis feed opportunistically on arthropods more often than documented. For example, on one occasion, an animal seen at a distance of approximately 100m appeared to be consuming a wasp's nest, but the event was too rapid to document.

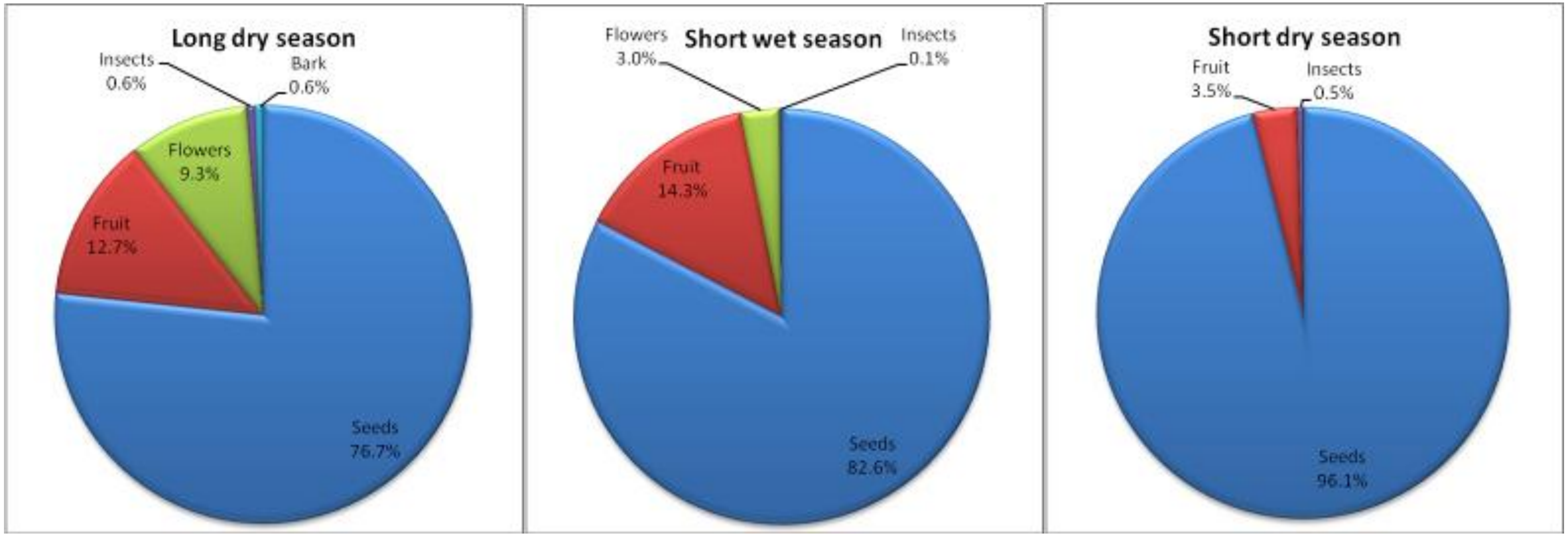
### Seasonal Feeding Patterns

Data from August 2008 to March 2009 (n=4,741, 97.2% of total feeding samples and n=3,710, 94.7% of identified feeding samples) demonstrated a significant difference in the composition of the diets during the three seasons ($x^2$=288.76, p<0.000), with a higher percent intake of flowers in the long dry season, and a higher percent intake of seeds in the short dry season (see Table 4.4, Figure 4.4, and Appendix II, Table 2 for a list of all species consumed by season).

**Table 4.4.** Summary of feeding data by season

| Season | Number of feeding samples | Number of plant species | Number of plant families |
|---|---|---|---|
| Long dry | 1,547 | 42 (5 unk fruit spp., 2 unk flower spp.) | 16 |
| Short wet | 730 | 33 (3 unk fruit spp.) | 14 |
| Short dry | 1,433 | 42 (8 unk fruit spp.) | 16 |

**Figure 4.4.** Foods consumed by percent during the long dry (August-November, 2008), short wet (December, 2008-January 2009), and short dry (February-March, 2009) seasons.



Long dry season

Short wet season

Short dry season

There was considerable overlap in plant species used between the long dry and short wet and between the short wet and short dry seasons, although there was little overlap between the long and short dry seasons (Table 4.5). Amongst the ten most used species there were only two species in common in all three seasons (only *Licania cf majuscula* (Chrysobalanaceae) and *Manilkara* sp.3 (Sapotaceae), Figure 4.5). *Qualea rosea* (Vochysiaceae) was used during all three seasons but was considerably more important in the short dry season (rank 5) than in the long dry or short wet seasons (rank 25 and 17, respectively). Conversely, *Clusia grandifolia* (Clusicaceae) was used in all three seasons but was more important in the short wet (rank 3) than in the long or short dry seasons (rank 18 and 20, respectively). Simpson's Index of the evenness of use of the ten most used species was relatively similar for the three seasons; however, the short dry season showed the most skewed distribution of use (Table 4.6 and Figure 4.5).

Among the ten most used plant families, only four of them were shared between the three seasons (Sapotaceae, Lecythidaceae, Chrysobalanaceae, and Fabaceae, see Figure 4.6). Not surprisingly, Sapotaceae was the most important family during all three seasons, although it was much more important in the short dry season than in the other two seasons. The short dry season also had the most uneven distribution of use of the ten most used plant families, and Sapotaceae was fed upon nearly four times more often than the next most used family (Lecythidaceae) (Table 4.6 and Figure 4.6).

**Table 4.5.** Overlap of plant feeding species by percent and number of species between the three seasons (unidentified species were excluded).

| | Long dry | Short wet | Short dry |
|---|---|---|---|
| Long dry | x | 12 spp | 4 spp |
| Short wet | 34.3% | x | 13 spp |
| Short dry | 11.4% | 38.2% | x |

**Table 4.6.** Simpson's Index of evenness for each season by feeding species and family.

| | Simpson's Index for preferred plant spp. | Simpson's Index for preferred plant families |
|---|---|---|
| Long dry | D=0.125 | D=0.133 |
| Short wet | D=0.109 | D=0.222 |
| Short dry | D=0.169 | D=0.464 |

**Figure 4.5.** Ten most used long dry, short wet, and short dry season feeding species. These species account for 1,091 (n =70.5%) long dry, 547 (74.93%) short wet, and 1,236 (86.25%) short dry season samples.

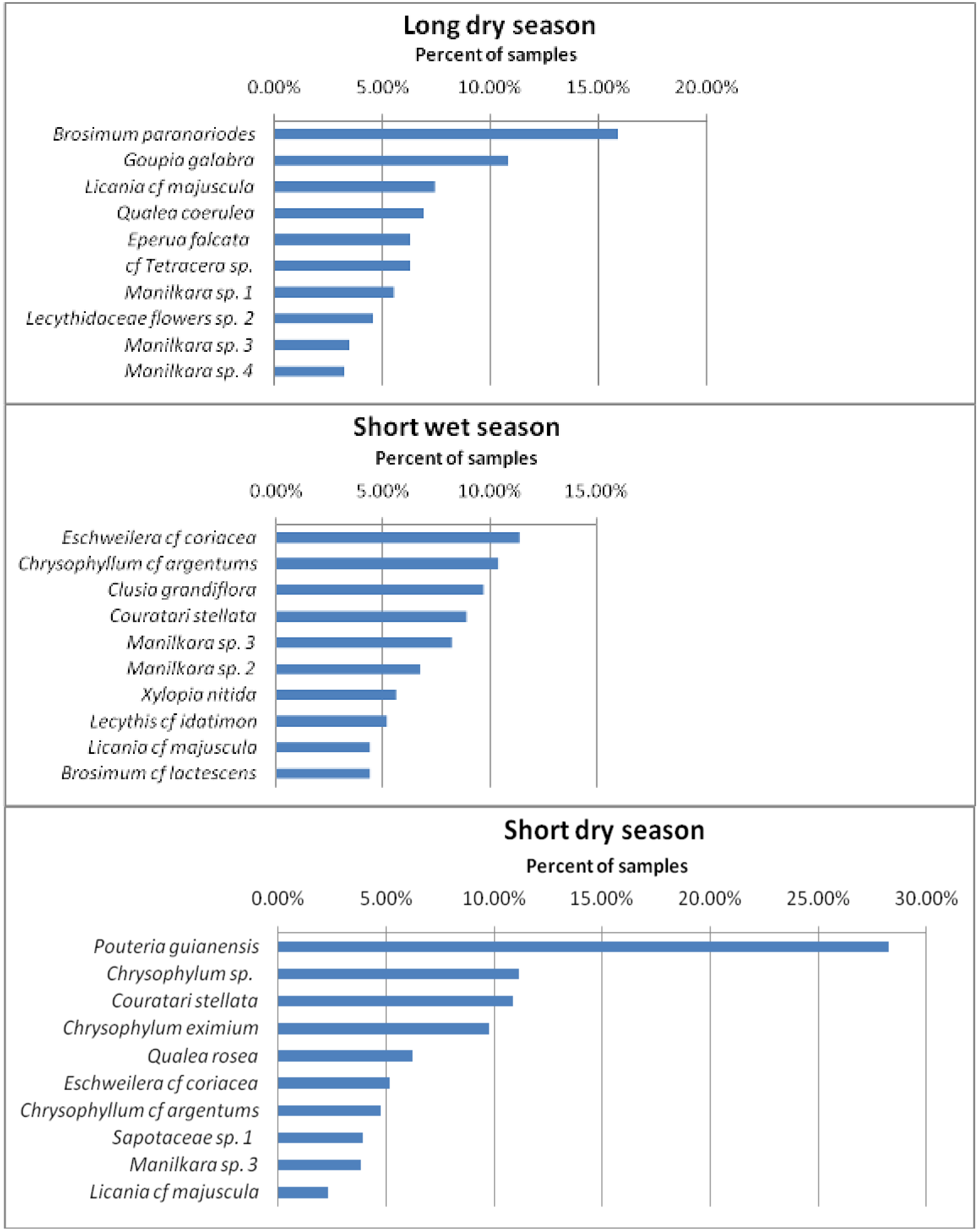
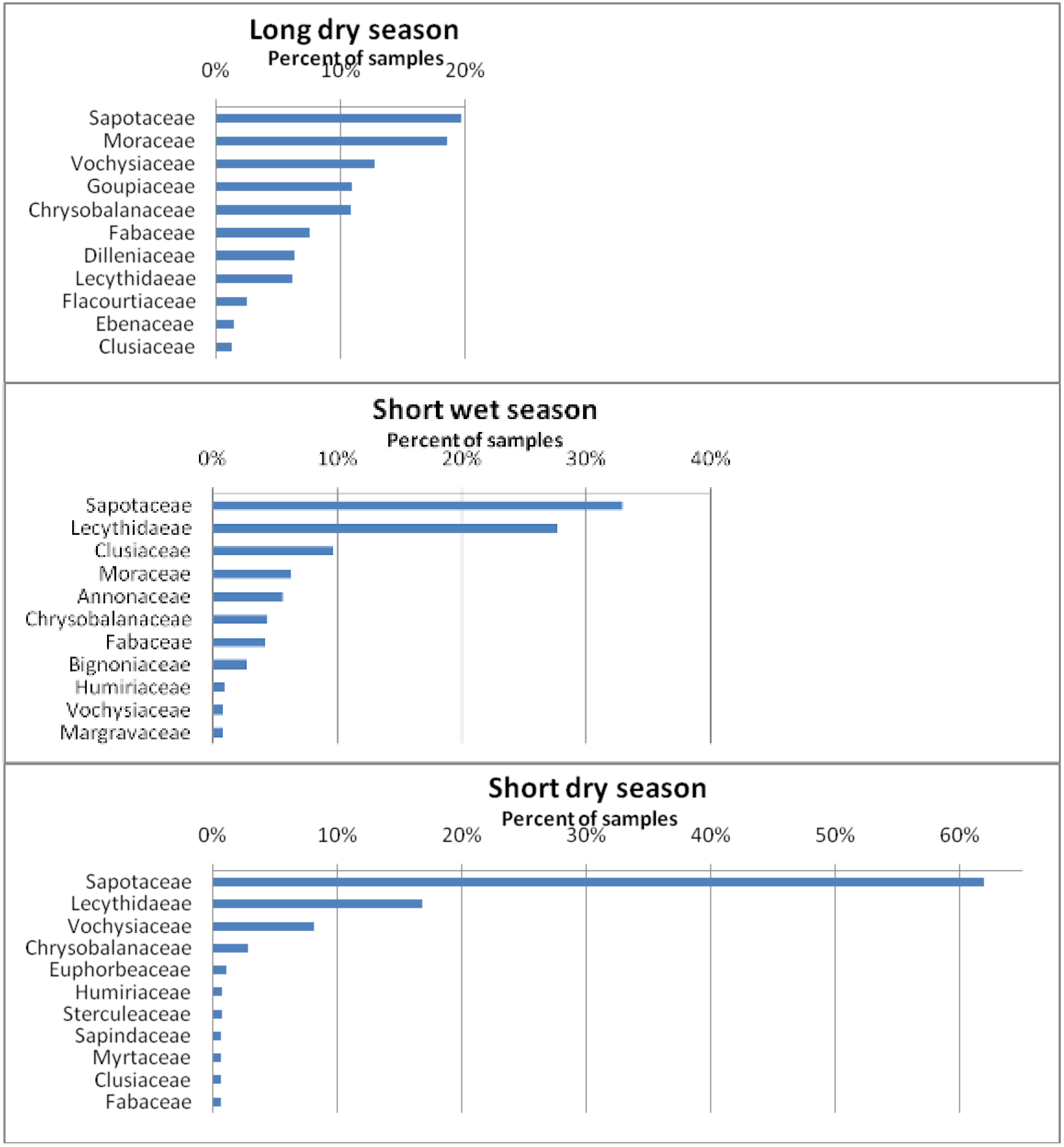


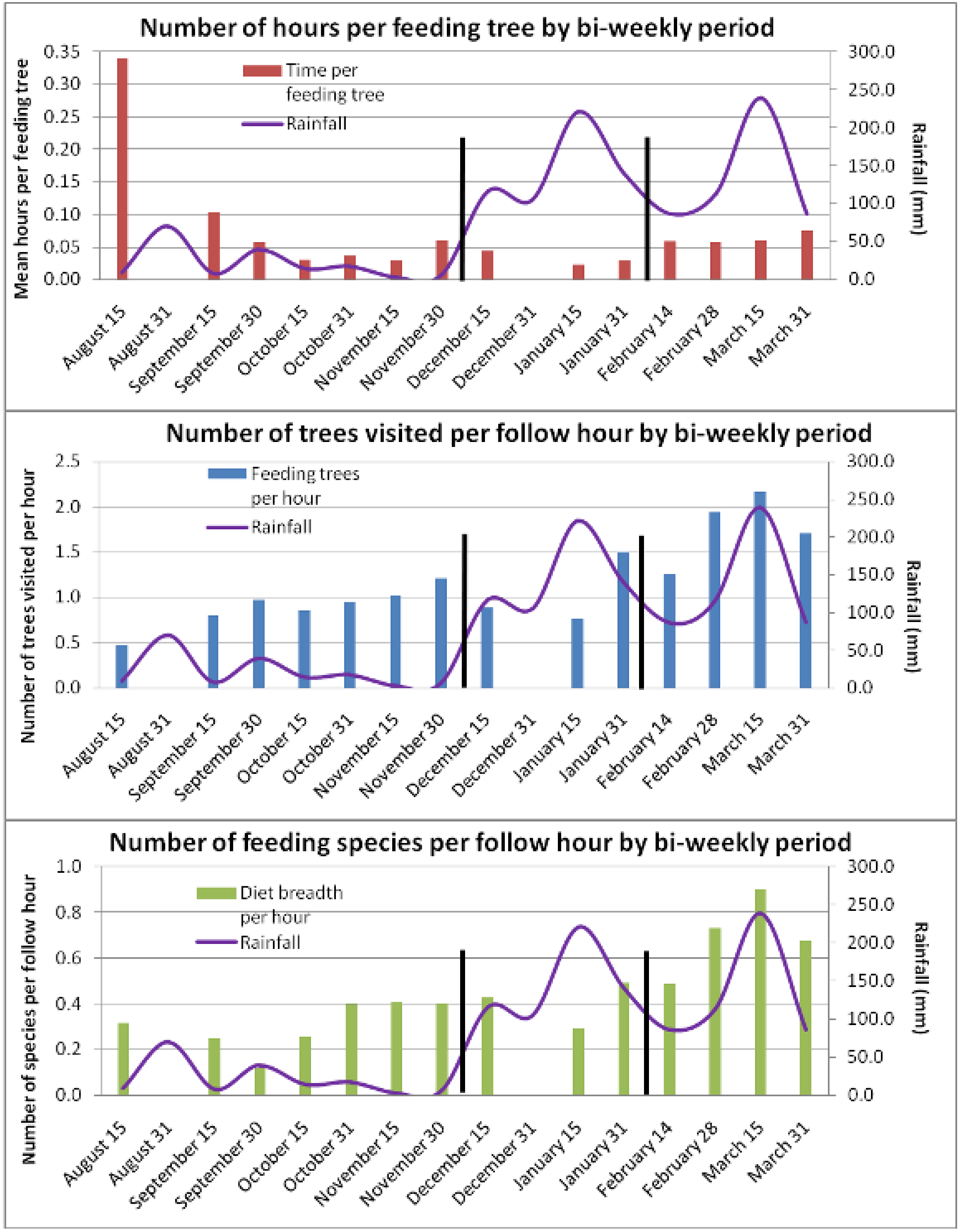
**Figure 4.6.** The eleven most used long dry, short wet, and short dry season families. These families account for 1,511 (97.7%) long dry, 702 (96.2%) short wet, and 1,361 (95.0%) short dry season samples.



Other diet parameters demonstrate a significant difference between seasons in the number of trees fed in and diet breadth but not the amount of time spent in each tree (Figure 4.7). The results of the Kruskal-Wallace tests demonstrated a (Table 4.7). The post-hoc Tamhane tests demonstrated that the source of the variation in the number of feeding trees and diet breadth was between the long and short dry seasons and also demonstrated a nearly statistically significant difference between the short wet and dry seasons in time spent in each feeding tree (Table 4.7).

Because group size changed significantly by season (see Chapter 3), ANCOVAs were performed on the data sets for these three variables in order to hold group size constant. However, with group size as a co-variate, there is, in fact, no significant relationship between season and any of the three dietary variables (Table 4.8).

**Figure 4.7.** Rainfall and feeding parameters. Biweekly cumulative rainfall compared to A) time spent in each feeding tree, B) number of feeding trees used, and C) diet breadth per hour. The vertical black lines indicate the separation between the long dry, short wet, and short dry seasons.



Number of hours per feeding tree by bi-weekly period

Number of trees visited per follow hour by bi-weekly period

Number of feeding species per follow hour by bi-weekly period

**Table 4.7.** Results of Kruskal-Wallace and post-hoc Tamhane tests of the difference between the three seasons in dietary variables.

| | Kruskal-Wallace H | Long dry vs short wet | Long dry vs short dry | Short wet vs short dry |
|---|---|---|---|---|
| Number of feeding trees | H=7.259, p=0.027 | I-J=0.154, p=0.926 | I-J=0.873, p=0.040* | I-J=0.719, p=0.193 |
| Time spent in each feeding tree | H=4.056, p=0.132 | I-J=0.062, p=0.477 | I-J=0.031, p=0.866 | I-J=0.031, p=0.057* |
| Number of feeding species | H=8.63, p=0.013 | I-J=0.096, p=0.578 | I-J=0.390, p=0.035* | I-J=0.295, p=0.106 |

**Table 4.8.** Results of ANCOVA tests of the three dietary variables by season with group size as the covariate and including the interaction variable.

| **Dietary variable** | **Source** | **Degrees of Freedom** | **F-value** | **Significance** | **$R^2$ value** |
|---|---|---|---|---|---|
| Number of feeding trees | Covariate: Group size | 1 | 0.107 | 0.752 | 0.762 |
| | Fixed factor: Season | 2 | 2.953 | 0.110 | |
| | Interaction | 2 | 1.641 | 0.253 | |
| Time spent in each feeding tree | Covariate: Group size | 1 | 0.278 | 0.612 | 0.143 |
| | Fixed factor: Season | 2 | 0.162 | 0.853 | |
| | Interaction | 2 | 0.162 | 0.853 | |
| Number of feeding species | Covariate: Group size | 1 | 0.084 | 0.780 | 0.771 |
| | Fixed factor: Season | 2 | 2.689 | 0.128 | |
| | Interaction | 2 | 1.147 | 0.365 | |

**Table 4.9.** Results of ANCOVA tests of the three dietary variables by season with group size as the covariate and without the interaction variable.

| **Dietary variable** | **Source** | **Degrees of Freedom** | **F-value** | **Significance** | **$R^2$ value** |
|---|---|---|---|---|---|
| Number of feeding trees | Covariate: Group size | 1 | 0.071 | 0.795 | 0.108 |
| | Fixed factor: Season | 2 | 0.424 | 0.666 | |
| Time spent in each feeding tree | Covariate: Group size | 1 | 0.451 | 0.517 | 0.665 |
| | Fixed factor: Season | 2 | 2.267 | 0.154 | |
| Number of feeding species | Covariate: Group size | 1 | 0.427 | 0.528 | 0.706 |
| | Fixed factor: Season | 2 | 2.428 | 0.138 | |

## Travel Patterns

There was no significant difference in total distance traveled in the morning versus the afternoon (AM: n=24, mean=1,279, SD=461.41; PM: n=36, mean=1,238, SD=513.55; t(58)=0.32, p=0.751, equal variances assumed (Levene's test for equality of variances: F=0.24, p=0.628)). For the seasonal analysis, no significant difference in travel rate was detected between seasons (K=3.851, n=20 biweekly periods, p=0.278, Figure 4.8); nor was significant relationship found between season and AM, PM, AM/PM pooled, and full-day distance traveled and elevation change (see Table 4.10).

**Figure 4.8.** Rainfall and travel rate (average distance traveled in meters per 10-minute sample). The vertical black lines indicate the separations between the long wet, long dry, short wet, and short dry seasons, respectively.

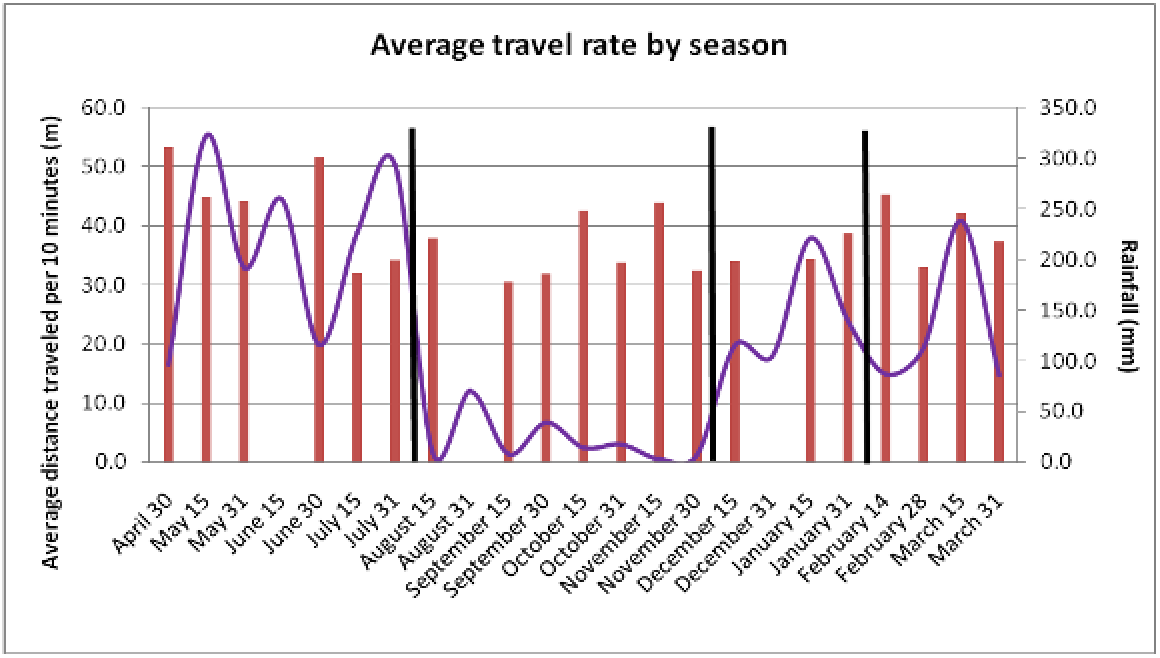


**Table 4.10.** Results of the Kruskal-Wallace test of differences between the four seasons for total distance traveled and total change in elevation during full-day and half-day follow periods.

| | Sample size | Mean (in meters) | Range (in meters) | Kruskal-Wallis H between seasons |
|---|---|---|---|---|
| Full day travel distance | 22 | x=2,362±821 | r=809-3,886 | H=2.042, p=0.564 |
| Full day elevation change | 22 | x=544.4±198 | r=274-925 | H=0.188, p=0.980 |
| AM travel distance | 24 | x=1,279±461 | r=398-2,259 | H=1.115, p=0.773 |
| AM elevation change | 24 | x=273.3±108 | r=67-444 | H=3.379, p=0.337 |
| PM travel distance | 36 | x=1,238±514 | r=300-2,312 | H=4.207, p=0.240 |
| PM elevation change | 36 | x=313.1±141 | r=117-621 | H=0.881, p=0.830 |
| Half day travel distance | 60 | x=1,254±490 | r=300-2,312 | H=4.247, p=0.236 |
| Half day elevation change | 60 | x=297.2±129 | r=67-621 | H=1.449, p=0.694 |

Half day travel distance (mean=1,254.00m, SD=489.8) and the corresponding half day average group size (mean=17.12monkeys, SD=12.62) were correlated (Peason's r=0.30, p=0.022), and monkey groups traveled farther when they contained more members. The regression analysis of travel distance on group size between the two-seasons (flowering: long dry versus heavy fruiting: short wet/dry) demonstrated a highly significant relationship between the two variables (interaction: p<0.01, see Table 4.11). When the seasons were analyzed separately, there was a significant relationship between group size and half-day travel distance in the long dry season but not in the short wet/dry season (Figure 4.9, including regression results).

An analysis of covariance for all four of the seasons demonstrated a statistically significant relationship between travel distance and season, with group size as a covariate (interaction: p<0.01, see Table 4.12). A regression analysis of group size and half day travel distance in all four seasons demonstrated again that the long dry season was the only season in which there is a significant relationship between group size and half day travel distance (Figure 4.10, including regression results). In other words, particularly in the dry season, adding another member to the group translates directly into longer travel distance.

**Table 4.11.** Regression analysis of the relationship between travel distance and group size between the flowering (long dry) and heavy fruiting (combined short wet/dry) seasons.

| | **Source** | **t** | **Significance** | **$R^2$ value** |
|---|---|---|---|---|
| Half day travel distance | Season (0, 1)* | -0.861 | 0.394 | 0.309 |
| | Group size | 2.217 | 0.031 | |
| | Interaction | 2.787 | 0.008 | |

*1=Long dry season; 0=Short wet/dry season

**Figure 4.9.** Regression of half day travel distance on group size for the flowering season (long dry) and the heavy fruiting season (combined short wet and dry).

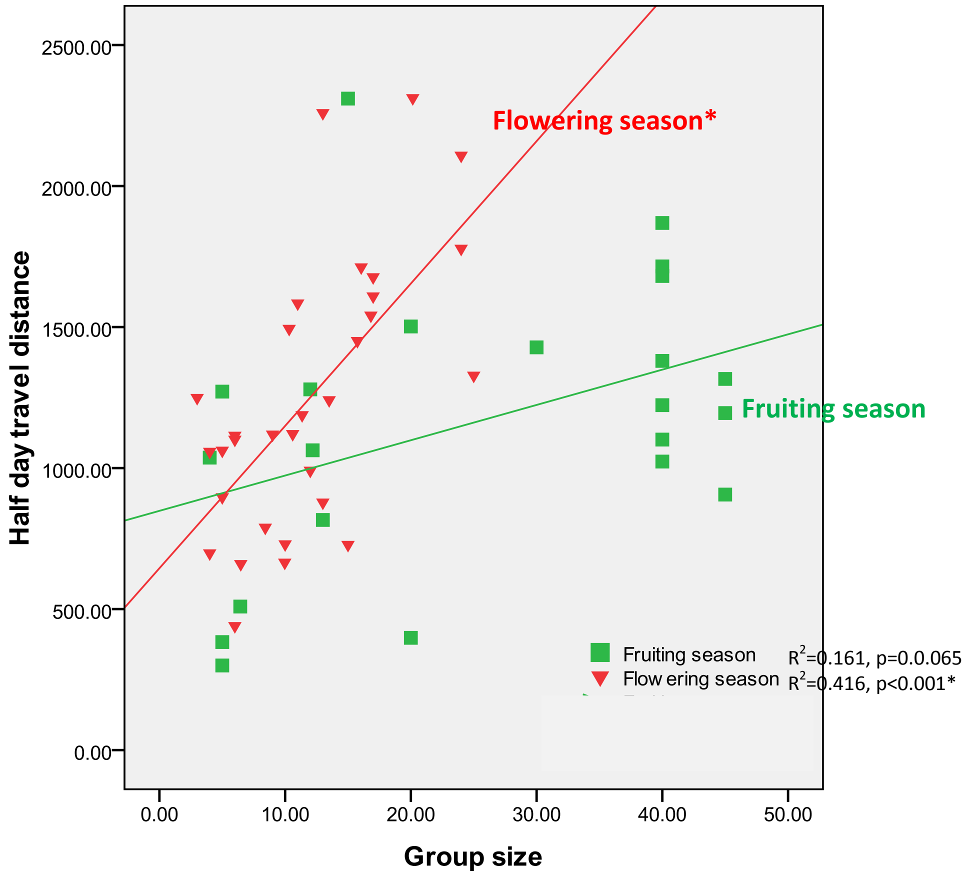
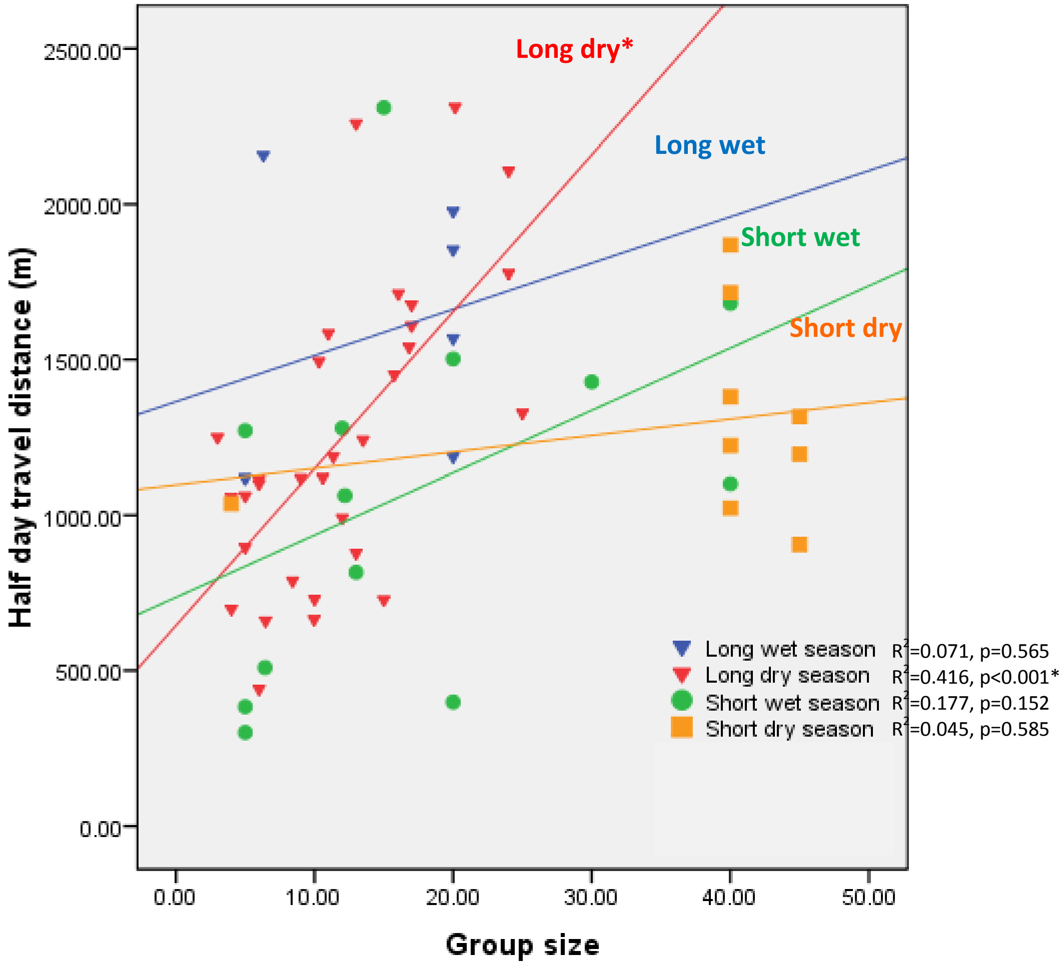


**Table 4.12.** ANCOVA analysis of the relationship between travel distance by season with group size held constant for the four seasons.

|  | Source | Degrees of Freedom | F-value | Significance | $R^2$ value |
|---|---|---|---|---|---|
| Half day travel distance | Covariate: Group size | 1 | 9.303 | 0.004 | 0.341 |
|  | Fixed factor: Season | 3 | 1.346 | 0.269 |  |
|  | Interaction | 3 | 2.421 | 0.076 |  |

**Figure 4.10.** Regression of half day travel distance on group size for all four seasons.



## DISCUSSION

Many previous studies have analyzed bearded saki activity patterns (Table 4.13), diets (Table 4.14), and travel patterns (Table 4.15). In this study, these variables were used to identify bearded saki seasonal strategies. Indeed, bearded sakis showed a change in some behaviors by season. As shown in Chapter 3, group size changed, and as shown in this chapter, diet composition, activity patterns, and travel patterns changed. In the short dry season, when group sizes were at a peak, sakis fed more, and they fed more on seeds. Furthermore, there was a relationship between group size and travel distance, and particularly in the long dry season, larger groups traveled further.

Slightly contradicting previous data gathered on this population in 2005, the bearded sakis spent more time resting than traveling or feeding (see Table 4.13; Gregory and Norconk 2011). Interestingly, such high rates of resting were not seen in other studies nor in other species of bearded sakis. The difference between the results of the present study and the 2005 study can be explained by the fact that the monkeys were followed for longer periods in the present study. Often bearded sakis at Brownsberg engage in long (up to 2-hour) resting bouts in the afternoon. In the 2005 study, contact was broken at this time in order to allow time to return to the field station by daylight. In contrast, during the present study, contact was maintained until dusk, in order for a follow period to continue the next morning. Also during the 2005 study, during resting bouts, contact was frequently lost because the group could no longer be located by the sound of movement. Increased field experience by the time of the present study allowed for improved contact maintenance, and hence, more contact with the groups during resting bouts.

Discrepancies in percentage of time spent resting between this study and studies at other sites and with other species of bearded sakis may be explained by a number of factors. First of all, in this study “social resting” was included in the category “resting” whereas in other studies these behaviors were counted separately or an “other” category was included (e.g., Boyle 2008; Silva 2003; Veiga 2006). In Boyle’s 2008 study, for example, if the “other” category were combined with the “resting” category, levels of “resting” would in fact, be lower in the present study (48.5% versus 53.7%). Not only were activities categorized differently in other studies, but they were potentially counted differently. For example, rather than scoring each individual’s activity during a scan, in Peetz’s 1991-92 study, the number of individuals engaged in each activity was expressed as a percentage of all individuals recorded in the scan as in Clutton-Brock (1977a).

Another factor influencing differences in activity budgets across studies may be related to the fact that the majority of the other studies were conducted on islands or forest fragments versus continuous forest (as in the present study) (e.g., Peetz 2001; Santos 2002; Silva 2003; Veiga 2006; Vieira 2005). Both Boyle (2008) and Veiga (2006) demonstrated that activity patterns are different in different sized forest classes or forest types. However, rather than showing higher rates of resting in larger forest areas (as the present study might indicate), Boyle’s (2008) comparison of activity in forest fragments versus continuous forest demonstrated higher rates of resting and lower rates of travel in smaller forest size classes. Along with influences of fragmentation on activity, the abbreviated length of some of the other bearded saki studies may have caused differences in activity budget. Studies over short periods of time (Gregory and Norconk 2011; Silva 2003), are unlikely to be as accurate a reflection of annual cycles as longer studies. In the same vein, the fact that the majority of the activity records for the present study were gathered between July 2008 and March 2009 and do not encompass an entire year, may affect the results.

Despite differences in activity budgets between this study of bearded sakis and others, amongst those studies that have analyzed seasonal changes, there were somewhat similar results. Similar to Peetz (2001), in the present study bearded sakis showed higher levels of feeding during the season when the primary feeding resource was seeds. However, in Peetz's study high seed consumption occurred during the single dry season (approximately December-April), while in the present study this was the second and shorter of the two dry seasons (February-March). Veiga's (2006) results are similar to those of Peetz (2001) on the island research site, showing higher rates of feeding in the single dry season when feeding rates on seeds were higher. However, somewhat different from findings of Peetz (2001), on Veiga's peninsula site, times of higher feeding rates were in the dry season, but those times co-occurred with times of highest rates of feeding on flowers rather than seeds.

It is interesting to note that while the monkeys in this study tended to rest more than in other bearded saki studies, daily travel distances were about average (see Table 4.14). This indicates either that travel rates were faster or contact was maintained for longer periods, beginning either before the monkeys began to move in the morning or continuing past the point at which they stopped moving in the evening. Interestingly, the percentage of the activity budget dedicated to traveling was nearly equal across seasons, whereas a trade-off seemed to occur between time spent feeding and resting.

A comparison of home range size between this study and others (see Chapter 5 and Table 4.14) shows that the home range of the WK bearded saki group was much larger than in other studies (with the exception of Pinto 2000, although this home range size was a very general estimate).

During the present study, rates of feeding on seeds were also among the highest for bearded sakis. Only Kinzey and Norconk (1990) and Boyle (2008) documented comparable rates of seed-feeding. Although Kinzey and Norconk's study was performed in lowland forest (versus on a berg such as Brownsberg), the close geographic proximity of that site and Brownsberg allows for high overlap in feeding species. Clearly, as with Boyle's study and many others (see italics in Table 4.15), Sapotaceae and Lecythidaceae were very important feeding families for the sakis in the present study. Seed feeding rates tend to be higher when these two families make up a large proportion of the diet (Table 4.15). One potential conclusion is that the seeds of these two families are very important to the bearded saki diet; when they are not as readily available, sakis may resort not only to using other plant families but also other plant parts (such as fleshy fruits and flowers). A census by Norconk and colleagues (2003) demonstrated that bearded saki densities at Brownsberg are the highest recorded. Perhaps high availability of seeds of these two preferred plant families allows for such high occurrence of sakis.

Returning to the predictions outlined at the beginning of this chapter (see Hypothesis and Predictions section), bearded sakis do in fact make seasonal ecological adjustments. Arguably the most salient seasonal adjustment made is in group size. Group sizes are at their largest in the short wet and dry seasons. This is also the time when trees begin to fruit after flowering during the long dry season. Bearded sakis begin to feed more on seeds at this time. They also begin to show higher rates of feeding and lower rates of resting. Seeds likely require more handling time, as suggested by Peetz (2001) but are also more nutritious than fruit pulp or flowers (Norconk et al. 2009). Therefore, feeding on seeds may enable group size to grow because the corresponding increased group caloric needs can be met. Stated differently, perhaps in the long dry season, when seed availability is reduced, groups diffuse and spread out into smaller subgroups.

Although it was predicted that when groups were larger in the short wet and dry seasons diet breadth would decrease this prediction was not fulfilled. However, the monkeys did shift their diet to mainly seeds. In the short dry season, they fed very “unevenly” on Sapotaceae species, particularly *Pouteria guianensis*. Similar to Norconk’s (1996) finding of reduced diet breadth with the increased use of the #1 ranked resource, in the present study the monkeys reduced the evenness of their feeding effort when the #1 ranked resource was fed upon. Interestingly, unlike the #3 ranked resource (*Couratari stellata) P. guianensis* was #1 despite interspecific feeding competition. The top three ranked resources in this study illustrate the flexibility of the bearded saki diet. They are capable of feeding on fruits at every stage of ripeness (e.g., *P. guinanensis* and

#2 ranked resource: *Brosimum paranariodes*), and they exploit both species that are preferred by other primates (e.g., *P. guinanensis*) and fruits that likely cannot be used by other primates (e.g., *Couratari stellata* which have little mesocarp and are protected by a hard, tough pixidium, the impenetrability of which may release the bearded sakis from competition with the other primates).

Although bearded sakis showed relatively high rates of resting in this study, other New World primate species show relatively similar rates of resting (see Table 4.1), particularly *Ateles* and *Brachyteles*. Day path lengths are also comparable to other New World primates, such as *Ateles*, *Lagothrix*, *Cacajao*, and *Cebus*, despite slightly (*Cacajao*, and *Cebus*) to significantly (*Ateles* and *Lagothrix*) smaller body size. Bearded saki groups are labial in size similar to *Cacajao* and *Ateles*, while also being among the largest for New World primates (except *Cacajao*). Bearded saki home ranges are also at the upper end for New World primates. Therefore, for their body size, bearded sakis are highly mobile, living in large groups and using very large areas. Although smaller animals are expected to have smaller home ranges due to allometrically lower individual caloric needs, the larger a group of animals is, the more nutrients are required (Clutton-Brock and Harvey 1977). Bearded sakis seem to typify this rule, and like *Cacajao*, exploiting a seed diet, rich in protein and lipids, may enable bearded sakis to be highly mobile and live in large groups. Finally, flexibility of diet and group size may be primary bearded saki strategies for adjusting to changes in availability of resources.

**Table 4.13.** Activity budgets of the five species of bearded sakis.

| Species | Length of study (mon.) | Type of forest (size, ha) | Traveling | Feeding and foraging | Resting | Other | Reference |
|---|---|---|---|---|---|---|---|
| *C. albinasus* | 11 | Continuous | 36.3 | 23.8 | 27.5 | 8.8 (social) | (Pinto 2008) |
| *C. chiropotes* | 15 | Island (180) | 18.7 | 47.1 | 21.4 | 12.8 (social, other) | (Peetz 2001) |
| *C. sagulatus* | **13** | **Continuous** | **31.1** | **20.3** | **48.5** | | Present study |
| | 3 | Continuous | 58 | 15 | 27 | | (Gregory and Norconk 2011) |
| *C. satanas* | 6 | Island (16.3) | 45.9 | 23.8 | 27.0 | 3.4 (soc) | (Silva 2003) |
| | 6 | Fragment (1,300) | 55.8 | 25.3 | 16.1 | 2.8 (soc) | (Silva 2003) |
| | 12 | Fragment (1,300) | 35.4 | 28.8 | 26.4 | 9.5 (social, other) | (Veiga 2006) |
| | 12 | Island (19.4) | 26.1 | 34.2 | 23.2 | 16.4 | (Veiga 2006) |
| | 18 | Continuous Fragments (10&100) | 21.3 | 25.0 | 46.6 | 7.1 | (Boyle 2008) |
| | 3 | Fragment (1,200) | 30.0 | 70.0 | 0.0 | | (Pereira 2002) (10 records) |
| *C. utahickae* | 8 | Island (129) | 30.8 | 58.8 | 9.5 | 0.9 | (Santos 2002) |
| | 6 | Island (129) | 51 | 37 | 11 | 1 (social) | (Vieira 2005) |

**Table 4.14.** Studies of use of space by the five species of bearded sakis. (Modified from Veiga 2006)

| Species | Study length (mon.) | Type of forest (size, ha) | Home range (ha) | Gp size: mean, range | Day path: mean, range (m) | Reference |
|---|---|---|---|---|---|---|
| *C. albinasus* | 17 | Continuous | 250-350 (est.) | 22.5±3.5 | 2,500-4,500<br>N/A | (Ayres 1981) |
| | 11 | Continuous | 1,000+ | 56 | 3,667±1,687<br>1,840-7,809 | (Pinto 2008) |
| *C. chiropotes* | 5 | Island (180) | 180 (est.) | 14 | 1,050<br>424-1780 | (Kinzey and Norconk 1993) |
| | 15 | Island(180) | 122.3 | 22 | 1,600±550<br>500-2,700 | (Peetz 2001) |
| *C. sagulatus* | **13** | **Continuous** | **742** | **17.5±12.8**<br>**2-45** | **2,362±821**<br>**809-3,886** | **Present study** |
| | 3 | Fragment (10) | 10 | 2-19 | 1,300 | (Ayres 1981) |
| | 28 | Continuous | 200-250 | 8-27 | 2,500 (est.) | (van Roosmalen et al. 1981) |
| | 6 | Continuous | N/A | 16 | 3,200±1,100 | (Norconk and Kinzey 1994) |
| | 12 | Fragment (1,100) | N/A | 30+ | 1,097±590<br>6,500 | (Frazão 1992) |
| *C. satanas* | 7 | Fragment (1,300) | 57 | 27 | N/A | (Santos 2002) |
| | 6 | Island (16.3) | 16.3 | 7 | N/A | (Silva 2003) |
| | 6 | Fragment (1,300) | 69.8 | 34 | N/A | (Silva 2003) |
| | 12 | Fragment (1,300) | 98.6 | 39 | 4,025±994 | (Veiga 2006) |
| | 12 | Island (19.4) | 17.2 | 8 | 1,560-6,270<br>2,807±289 | (Veiga 2006) |
| | 18 | Continuous | 429±129.5<br>(300-559) | 22.89± 5.09 | 1,900-3,680<br>2,990±200 | (Boyle 2008) |
| | 18 | Fragment (100) | N/A | 12.05± 1.44 | 2,970-3,010<br>2,830±220 | (Boyle 2008) |
| | 18 | Fragment (10) | 12.36±0.31<br>(12.05-13.67) | 3.79± 0.21 | 2,610-3,050<br>1,720±90<br>1,710-1,730 | (Boyle 2008) |
| *C. utahickae* | 8 | Continuous | N/A | N/A | N/A | (Bobadilla 1998) |
| | 8 | Island (129) | 100 (est.) | 24 | N /A | (Santos 2002) |
| | 6 | Island (129) | 57.5 | 23 | 2, 530±0.95<br>1,940-4080 | (Vieira 2005) |

**Table 4.15.** Annual diets of the five bearded saki species at different sites. (Adapted from Norconk 2011; Veiga 2006). Sapotaceae and Lecythidaceae are italicized to illustrate their common occurrence saki diets in many studies.

| | | | | % Feeding | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Species** | **Study length** | **Type of forest** | **Spp/ fam** | **Seeds** | **Fleshy Fruit** | **Flowers** | **Leaves** | **Insects** | **Water** | **Oth-er** | **Important Plant Families (%)** | **Reference** |
| *C. albinasus* | 17 | Continuous | 51/20 | 35.9 | 53.9 | 3.0 | | | | 7.2 | Palmaceae, *Sapotaceae*, Fabaceae, Caryocaraceae Moraceae (54) | (Ayres 1981) |
| *C. chiropotes* | 5 | Island (180) | 39 | 74.8 | 21.6 | 0.4 | 0.2 | 0.5 | | | *Sapotaceae*, Loranthaceae, Moraceae, Meliaceae (74.5) | (Kinzey and Norconk 1993; Norconk 1996) |
| | 15 | Island (180) | 112/36 | 50.7 | 41.6 | 0.9 | 2.5 | 3.9 | 0.6 | 0.4 | *Sapotaceae*, Loranthaceae, Moraceae (76) | (Peetz 2001) |
| *C. sagulatus* | **13** | **Continuous** | **112/32** | **85.39** | **9.42** | **4.32** | | **0.46** | | **0.41** | ***Sapotaceae*, Lecythidaceae, Moraceae, Vochysiaceae (68.6)** | **Present study** |
| | 3 | Fragment (10) | 18/11 | 63.3 | 9.3 | 11.4 | 11.3 | | | 4.8 | Moraceae, Fabaceae, *Lecythidaceae*, *Sapotaceae* (62) | (Ayres 1981) |
| | 28 | Continuous | 86/33 | 66.4 | 27.6 | 4.6 | 1.4 | 3.5 | | | Lecythidaceae, Sapotaceae, Burseraceae (46.5) | (van Roosmalen et al. 1981) |
| | 6 | Continuous | 34 | 86.4 | 9.9 | 1.0 | 1.4 | | | 0.5 Bark | | (Kinzey and Norconk 1990) |
| | 12 | Continuous | 148/35 | 72 | 20.8 | 1.1 | 1.0 | | | 1.4 | *Sapotaceae*, *Leythidaceae*, Moraceae, Mimosaceae (62.6) | (Frazão 1992) |
| *C. satanas* | 3 | Fragment (63) | 37/20 | 62.7 | 36.0 | 1.3 | | | | | | (Porto-Carvalho 2002) |
| | 6 | Fragment | 45/ | 49.6 | 9.7 | 40.7 | | | | | | (Santos 2002) |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | (1,300) | 25 | | | | | | | | | |
| | 6 | Fragment (1,300) | 40/24 | 38.4 | 41.9 | 19.7 | | | | | Araceae, Caesalpinaceae, *Lecythidaceae*, Moraceae (75.1) | (Silva 2003) |
| | 12 | Fragment (1,300) | 147/34 | 54.3 | 25.2 | 12.3 | 2.9 | 4.6 | 0.6 | 0.6 | Simaroubaceae, Arecaceae, Fabaceae, Caesalpinaceae, *Lecythidaceae*, Annonaceae (61.2) | (Veiga 2006) |
| | 6 | Island (16) | 21/18 | 28.9 | 11.8 | 55.6 | | 0.5 | | 3.2 | Araceae, Caesalpinaceae, *Lecythidaceae*, Mimosaceae (74.9) | (Silva 2003) |
| | 12 | Island (19) | 119/33 | 60.4 | 13.7 | 17.4 | 3.6 | 3.7 | 0.9 | 0.7 | *Lecythidaceae*, *Sapotaceae*, Burseraceae, Caesalpinaceae, Chrysobalanaceae, Fabaceae (73.3) | (Veiga 2006) |
| | 18 | Continuous Fragments (10 & 100; data comb) | 244/47 | 83.3 | 16.7 | 4.3 | 0.47 | 2.4 | | 2.4 | *Sapotaceae*, *Lecythidacae*, Chrysobalanaceae, Euphorbiaceae, Leguminosae (58) | (Boyle 2008) |
| | 6 | Fragment (1,200) | 34/19 | | | | | | | | *Sapotaceae*, *Lecythidaceae* | (Pereira 2002) |
| *C. utahickae* | 6 | Island (120) | | 75.6 | 5.4 | 18.9 | 0.1 | | | | | (Santos 2002) |
| | 6 | Island (120) | 110/40 | 36.2 | 43.3 | 16.6 | 3.1 | 0.7 | 0.1 | | Mimosaceae, Caesalpinaceae, *Lecythidaceae*, Annonaceae (63.6) | (Vieira 2005) |

# CHAPTER 5

# SPATIAL ECOLOGY

## INTRODUCTION

Geographic Information Systems (GIS) technology has been applied in many ways to studies of primates. Most commonly, GIS is used to understand primate distribution patterns either for pinpointing potential areas in which primate species would likely be found (e.g., *Chiropotes* and *Cacajao*: Boubli and de Lima 2009) or for creating Habitat Suitability Models to identify conservation priority areas (e.g., *Alouatta*: Bonilla-Sánchez et al. 2010; *Oreonax*: Buckingham and Shanee 2009). Other uses of GIS include understanding gene flow (e.g., *Propithecus*: Quéméré et al. 2010) and disease transmission patterns (e.g., multiple African spp.: Nunn 2009), and even mapping dental morphology (e.g., cercopithecoids: Bunn and Ungar 2009). However, use of GIS in studies of primate spatial and movement ecology are extremely rare (e.g., Lagothrix and Ateles: Di Fiore and Suarez 2007), but there is great potential with GIS for understanding how primates navigate the landscape. In particular, GIS allows for detailed understanding of optimization of landscape navigation, a component of optimal foraging theory (MacArthur and Pianka 1966).

Time for feeding and reproduction is limiting for all animals (Pianka 1994). For this reason, natural selection is expected to have favored “individuals that maximized benefits from foraging relative to costs” (Noser and Byrne 2007:257). In the literature, a various strategies have been suggested to be used by animals to navigate the landscape in ways that perhaps reduce the costs of travel. In this study, two of these strategies were analyzed: the repeated use of familiar pathways and the use of topographic features.

In a number of primate species, repeated use of familiar travel paths has been well documented. MacKinnon documented the use of “arboreal ‘highways’” in orangutans (1974:30), while Sigg and Stolba (1981:67) describe repeated use of “street segments” in hamadryas baboons. MacKinnon (in siamangs and gibbons: 1977:764) and Di Fiore and Suarez (in spider and woolly monkeys: 2007) also describe the use of pathways that are shared *between* species. Milton (1980; 2000), who has documented use of such pathways in howler monkeys, suggests that all primate species are likely to repeatedly use “arboreal pathways.” GIS is an invaluable tool for locating these pathways.

GIS also provides the tools to facilitate analyses of how topographic features influence navigation of variable terrain such as mountains. Di Fiore and Suarez (2007) not only demonstrated that woolly and spider monkeys use topographic features as landmarks for creating route-based mental maps (Poucet 1993), but they also suggest that animals may be inclined to use topographic features (namely ridge tops) to increase efficiency while traversing mountainous terrain. Traversing ridge tops, which has also been proposed as a strategy for orangutans (MacKinnon 1974), may not only minimize the cost of travel, but the ridge tops may also serve as useful land marks to guide travel between fruit trees. Assuming that the same travel routes have been used by generations of monkeys, through repeated use of the same routes, the monkeys may also influence the availability of future arboreal travel paths through defecation of seeds (Di Fiore and Suarez 2007).

The use of ridges is very common among large terrestrial mammals. For example, a study of snow leopards demonstrated a high occurrence of scrape marks left by leopards on ridges (Schaller et al. 1988). Other taxa such as elephants, rhinoceros, and Asian tapirs have also been shown to use ridges, and in fact, methodology for studying these animals often includes searching for animals on ridge tops (e.g., in Asian tapirs: Holden et al. 2003; in rhinoceros: Rabinowitz et al. 1995). Indigenous human populations have been documented to prefer ridge tops for travel to increase efficiency, particularly when carrying game (e.g., Waorani people in Ecuador: Milton 2000; Yost and Kelley 1983). Yost and Kelley (1983) suggest that trails exist on ridges because they are easier to traverse, from an energetic stand point.

In the present study, GIS was used to examine how bearded sakis use the topography of the Brownsberg's steeply ridged slopes and whether they make use of ridges as suggested by other studies. As indicated in Chapter 4, bearded sakis are highly mobile primates that consume seeds and live in large groups, or as stated by Ayres (1989), "*Cacajao* and *Chiropotes* have large home ranges, day ranges, and group sizes that are large relative to their body weights, suggesting high metabolic rates and the need for a diet rich in energy" (p. 712). Norconk et al. (2009) found that seeds rank fourth in nutritional value of primate foods after arils, exudates, and insects, and extrapolating to diet, and being seed predators, *Chiropotes* ranked sixth amongst the 16 platyrrhine genera in dietary energy density (*Cacajao* ranked fourth and all higher ranked genera were callitrichines). In the present analysis of repeated path use and terrain use, it is suggested that not only an energy rich diet but also use of less costly paths when navigating the landscape may be a factor that enables bearded sakis to be highly mobile.

Like all ferro-bauxite plateaus (Hammond 2005b), BNP has very complex terrain and numerous habitat types (De Dijn et al. 2007). As a consequence, tree species may show variable distribution because, for example, "soils on the slopes are deeper than the plateau, allowing a forest with very high stature, at times reaching a height of 60m" (ter Steege et al. 2007:80). At the same time, bearded sakis have shown preferences for large trees for traveling and feeding (Gregory 2006). Because the landscape and the forest are variable, and bearded sakis are selective, they may use the forest differentially. During previous studies at BNP, bearded sakis were more frequently encountered on slopes (pers. obs.), and a brief study in 2008 by Nederbiel (2009) demonstrated that sakis prefer the slope to the top of the plateau. While the forest may be higher on the slopes, and therefore preferred for bearded saki feeding and travel, in order to navigate such treacherous terrain, the monkeys are proposed to use features such as ridges.

## Hypothesis and Predictions

**Hypothesis: The landscape is variable and primates are expected to be selective when navigating it.**

Because bearded sakis demonstrate extremely long day paths (see Chapter 4) and large home ranges, they would be expected to use the environment differentially. As noted above, they tend to prefer large trees (Gregory 2006), and large trees tend to occur in the deep soils of the slopes (ter Steege et al. 2007). Therefore, even though sloped areas are expected to be more difficult to navigate, bearded sakis are predicted to prefer the plateau’s slopes to the flatter top of the plateau.

In using the plateau’s slopes, as demonstrated in atelines (Di Fiore and Suarez 2007), the monkeys are expected to use a couple of strategies to reduce the costs of travel: 1) using familiar pathways and/or 2) using ridge tops. Like other animals, bearded sakis are expected to use familiar paths, not only because of the possibility that they form route-based mental maps (Poucet 1993), but also because using familiar pathways involves less energy waste because resources are potentially known. If this indeed is a strategy used by bearded sakis, mapping of travel patterns should show repeated use of some areas, i.e., areas of high use.

As a correlate to strategy number two above, while traversing the plateau’s slopes, sakis may use an area of lesser slope, i.e., they may navigate mountain sides using the path of least slope (typically a ridge). If sakis are navigating steep slopes by using ridges, high-use areas should correspond to ridges, and the monkeys should navigate the environment using the “least cost path,” i.e., the path of least slope and/or the shortest straight-line path over the course of a travel day.

Because resource availability changes with season, navigation strategies are expected to change with season. A study by Boyle et al. (2009b) of travel path linearity in bearded sakis by found a relationship between forest fragment size and travel path linearity, with more tortuous travel paths in smaller forest fragments. It is suggested that paths are more tortuous in smaller fragments because resources are more limited and must be used repeatedly (Boyle et al. 2009b). By the same logic, during the season in which travel paths are more tortuous, resources are expected to be more limited and hence used repeatedly.

## METHODS

Bearded saki travel paths were documented by following groups as long as possible and marking waypoints every 10 minutes with a Garmin hand-held MAP Cx GPS unit. Bearded saki groups were followed in three zones: Witi Kreek, Aguago Kununu Pasi, and Pedreku Pasi (Figure 2.2). Due to low visibility, groups cannot always be counted and individuals cannot be identified. For this reason, at times it is not possible to determine whether the same group is being followed. Therefore, within the three zones, the number of groups followed was estimated (Table 3.3).

When groups were not encountered at dawn or when contact with groups was lost before dusk, follow periods were considered to be partial-day follow periods. Full-day and partial-day follow periods were treated differently in the analysis of the data: when all full-day and partial-day follow periods were pooled they are referred to as "all follow periods," and when they were treated separately, they are referred to as such. The waypoints were mapped using Garmin's Map Source 10 and ESRI's (Environmental Systems Research Institute) ArcMap® 9.3. ESRI's Spatial Analyst toolset and the Hawths toolset were used for calculations.

## Home Range

An analysis by Boyle et al. (2009a) in Brazil of home range estimation tools for bearded sakis demonstrated that a minimum convex polygon (MCP) analysis most accurately estimates home range size in large tracts of forest. Using the 10-minute waypoints, the Hawth's tool extension for ArcMap was used to calculate the size of the total area used by all of the saki groups and the size of the area used in each of the three zones. For the Zone WK, the use area of the all-male groups was mapped in order to determine if they were subsumed within the use area of the large, mixed-sex group (see Table 3.3) and, hence, a subgroup(s) of the large group.

## High-use Areas

Traditional methods of identifying high-use areas (i.e., "highways") in primate studies involve the use of traditional mapping techniques (i.e., primate travel paths are hand or digitally drawn onto research-area maps). Here, GIS ArcMap software was used to perform a spatial interpolation of the area of the study to locate high-use areas. "Interpolation is a procedure used to predict the values of cells at locations that lack sampled points [and] is based on the principal of spatial autocorrelation […] which measures degree of relationship/dependence between near and distant objects" (Childs 2004:32). In other words, interpolation can be used to convert a map containing use-waypoints into a map showing a use-preference gradient over a surface. A review of the literature showed no previous use of this technique in studies of use-areas of primates or any other animal taxa.

To test predictions 2 and 3, preferred use areas were identified using the ArcMap spatial analyst “distance weighted interpolation” function. Data from all follow periods (n=106) were used. Five-by-five-meter cells were created, and to determine the pixel’s score, one count was given to the five-by-five meter pixel for every waypoint that fell within it. High use was defined by repeated use or long duration (i.e., multiple 10-minute waypoints and multiple 10-minute samples at the same waypoint during feeding or resting) at a site. In this analysis, a pixel’s value is calculated through an algorithm that accounts both for the number of waypoints within the pixel and the values of the adjacent cells. In this way, a map demonstrating a gradient of use across the entire use-area is created, and the analysis illustrates high-use areas.

Then, a similar methodology was used for all of the travel *paths* over the course of the study. In this analysis, rather than simply scoring the 10-minute waypoints, all travel segments between the waypoints were converted into “points” using the Hawth’s Animal Movements “convert paths to points” function. In this way, travel segments were converted to strings of points at approximately five meter intervals and were referred to as “travel corridors.” This was an analysis strictly of travel corridors rather than “multi-use” (i.e., feeding and resting) areas. Therefore, points were only scored for a travel event and were not given multiple counts if the monkeys stayed at the point to rest or feed. Travel corridors were then visually compared to the topographic map of the area to see if the corridors lined up with ridges.

For Zone WK, the interpolation analysis was more effective than for the other two zones because sample sizes were largest (WK: n=65; AKP: n=20; and PP: n=17 follow periods).

## Slope Preference

In order to determine whether the sakis show a preference for steeper slopes (Prediction 1) (i.e., the species of feeding trees found on steeper slopes), the slope of areas used by the monkeys was analyzed using a 30x30m Digital Elevation Model (DEM). (Each 30x30 meter box will be called a "cell.") The DEM was acquired from East View Cartographic, and slope is evaluated from satellite images. Therefore, the slope value for each pixel of the DEM represents the slope of the tops of the trees (where the monkeys are) rather than the ground (where the observer is).

The occurrence in percent of 30x30m cells of each of seven slope categories (0-9.9°, 10-19.9°, 20-29.9°, 30-39.9°, 40-49.9°, 50-59.9°, 60-69.9°; slope did not exceed 69.9°) was calculated (N=39,273 cells in the use-area). The proportion of cells used by the monkeys was then compared to this slope map of the study site. A pixel was given a count each time it was used. Comparisons were made using a Chi-square test.

## Least Cost Path

ArcMap cost-weighted analyses have been used to analyze movement patterns in a wide range of taxa from livestock (Ganskopp et al. 2000), large carnivores (Larkin et al. 2004; Singleton et al. 2002), and hedge hogs (Driezen et al. 2007) to birds (Graham

2001), and in various other habitat-use scenarios (Adriaensen et al. 2003; Pinto and Keitt 2009). However, use of this tool was not found in any primate studies.

The ArcMap “cost weighted path” and “least cost path” spatial analyst functions were used to generate “least cost travel paths” for the 22 full days on which the monkeys were followed. Identifying the “cost” as “slope” (because ridges show a more gradual slope), the most direct paths were created for each day from the “start” waypoint to the “end” waypoint (Prediction 4). The “cost weighted” function was used to create a cost raster of the area radiating out from the “start” waypoint, and then the “shortest path” function was used to create a path to the “end” waypoint.

Two types of least-cost routes were created: 1) a route between the first (“start”) and last (“end”) waypoints used in a follow day and 2) a route between feeding trees. To create the least cost path between feeding trees, the “cost weighted” function was used to make a cost raster radiating out from the “start” waypoint, and then the “shortest path” function was used to create a path to the first feeding tree. This methodology was then repeated between the first and second feeding trees, and so on, until the path reached the “end” waypoint. Due to the size of the raster cells (30mx30m), the vertices of the line segments created in the least cost path analysis did not begin or end exactly at the waypoints (but instead in a slightly different location within the 30mx30m “pixel” since accuracy of the GPS unit (apprx.±8m) in creating waypoints is higher than the resolution of the DEM). Therefore, they had to be edited so that the path passed through the waypoints. The least cost paths were compared visually to the actual paths used by the monkeys (i.e., paths that included trees simply used for travel). The paths were also measured in ArcMap using the “ruler” function, and their lengths were compared.

Finally, the linearity of travel paths was evaluated. Linearity, as described by Boyle et al. (2009b), is the length of actual travel path used by the monkeys (the path between all of the waypoints collected at 10-minute intervals) divided by the straight-line path between the first and last waypoints. Values that approach zero indicate a highly circular route, and values that approach one indicate a highly linear, non-tortuous route. Presumably a more direct route is less costly to navigate. The linearity of the travel path was calculated for all of the full-day follow periods and all half-day follow periods. T-tests were used to compare the linearity of the travel routes between full and half-day travel routes, and between morning (AM: a minimum of five hours, up to and including 11:50AM) and afternoon (PM: a minimum of five hours, 12:00PM and after) travel paths. Kruskal-Wallace tests were used to compare the linearity of travel routes during full and half-day samples by season, and post-hoc Tamhane tests were used to detect the sources of significant differences by season.

An analysis of covariance was performed on the half-day travel route linearity data with group size held constant to detect a potential relationship between route linearity by season independent of group size. Multiple regressions were also performed on half-day route linearity data and group size to identify a potential relationship between these variables by season.

## RESULTS

Between three and six (Table 3.3) bearded saki groups were followed for a total of 540 contact hours: 22 full-day follows and 84 partial-day follows. All data were pooled for calculations of use area/home range. For slope preference and interpolation analyses, all of the waypoints were used. For the least cost path analysis, only the full-day travel paths were used, and for the linearity of path analysis, both the full-day travel paths and the half-day travel paths were used.

## Home Range

The MCP (minimum convex polygon) area including all of the waypoints was 3,747ha, and the areas of Zones AKP, WK, and PP were 382ha, 742ha, and 733ha in size respectively (Figure 5.1). In Zone WK the use area of the all-male group(s) was entirely subsumed with the use area of the large, mixed-sex group (Figure 5.2).

**Figure 5.1.** Distribution of points used by the monkeys in the three study zones, and size of each zone calculated as a MCP. The yellow-brown shading indicates the slope of the land (0-70°, there were no areas steeper than 70°) based on the 30x30m digital elevation model (DEM). Topographic lines are at 50m intervals. An absence of waypoints does not indicate an absence of monkey groups.

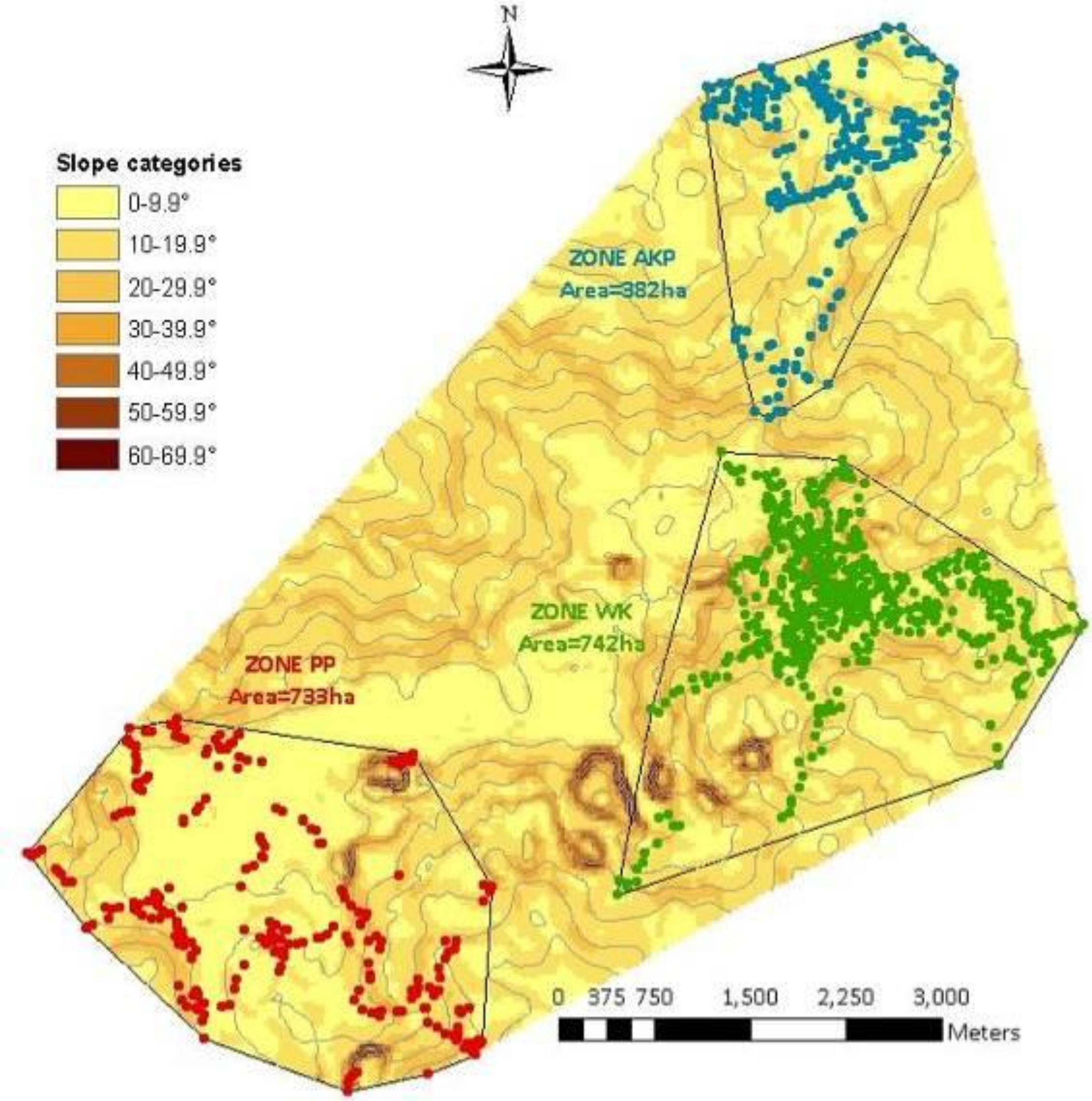
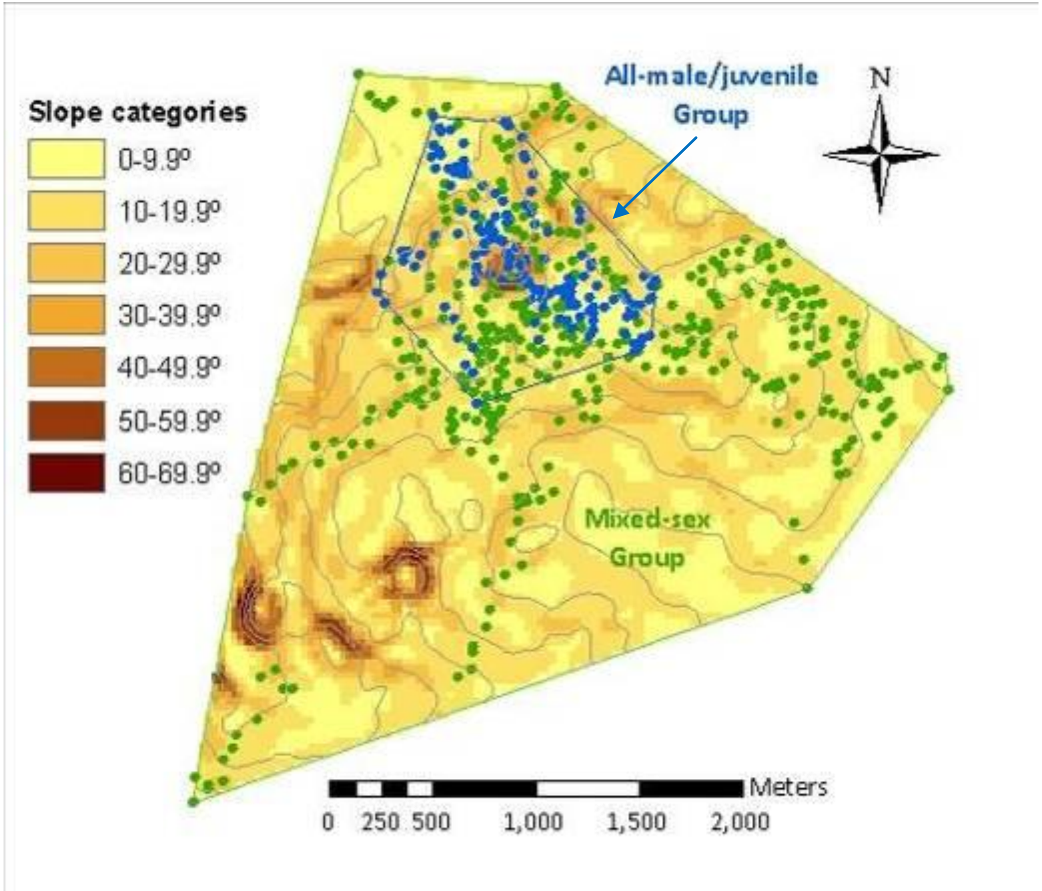


**Figure 5.2.** Use area of the all male/juvenile groups(s) in the WK Zone (total area of use of all-male/juvenile group(s)=116.7ha versus 742ha total).



## High-use Areas

It is clear that bearded sakis use some areas more extensively (preferentially) than others (Predictions 2 and 3). A comparison of the preferred use area of WK Zone (Figure 5.3A) and the main ridges in the Zone (Figure 5.3b red line=main ridge and blue line=secondary ridge) demonstrates that the monkeys use ridges. The monkeys frequently crossed over the main ridge (red line) or followed it down-slope from west to east or up-slope. The upper part of the secondary ridge was also frequently used (Figure 5.3B, blue line). Unexpectedly, the steepest part of the Zone near the junction of the two ridges was also used, perhaps because it is a junction.

In the conversion of paths to points (Figure 5.4), which focuses only on travel corridors (not all use areas like the analysis in the previous paragraph), the interpolation is represented three dimensionally to more clearly illustrate preferred use areas (Figure 5.5). A Google Earth image also illustrates the ridges indicated in Figure 5.4B. Similar to the previous analysis, the monkeys navigated the area using the two main ridges.

**Figure 5.3.** Interpolation analysis. A) Interpolation map of high use areas in the WK Zone. Highest use areas are darkest; unused areas are white. Cells are 5m x 5m. Values are in decimals because the value of each pixel is determined by both the use-score of the pixel itself and also that of the neighboring pixel. B) Primary (red line) and secondary (blue line) ridges in Zone WK, topographic lines at 20m increments. The secondary ridge becomes a stream bed approximately half way along.

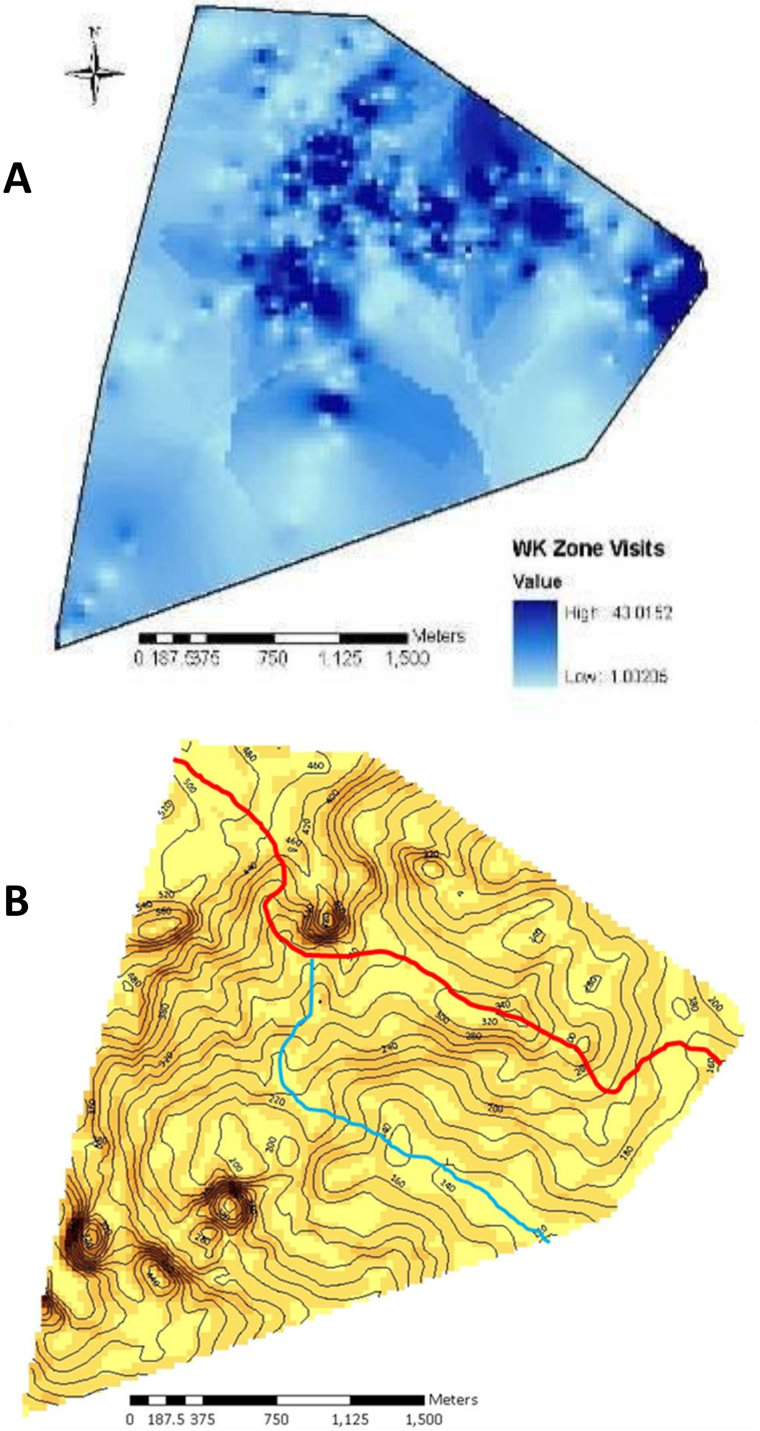


**Figure 5.4.** Conversion of paths in Zone WK to points. A) All travel paths in Zone WK, with blue points indicating 10-minute waypoints. B) Paths from A converted into points; the magnified area in the red box illustrates the conversion. Points are approximately 5.5m apart.

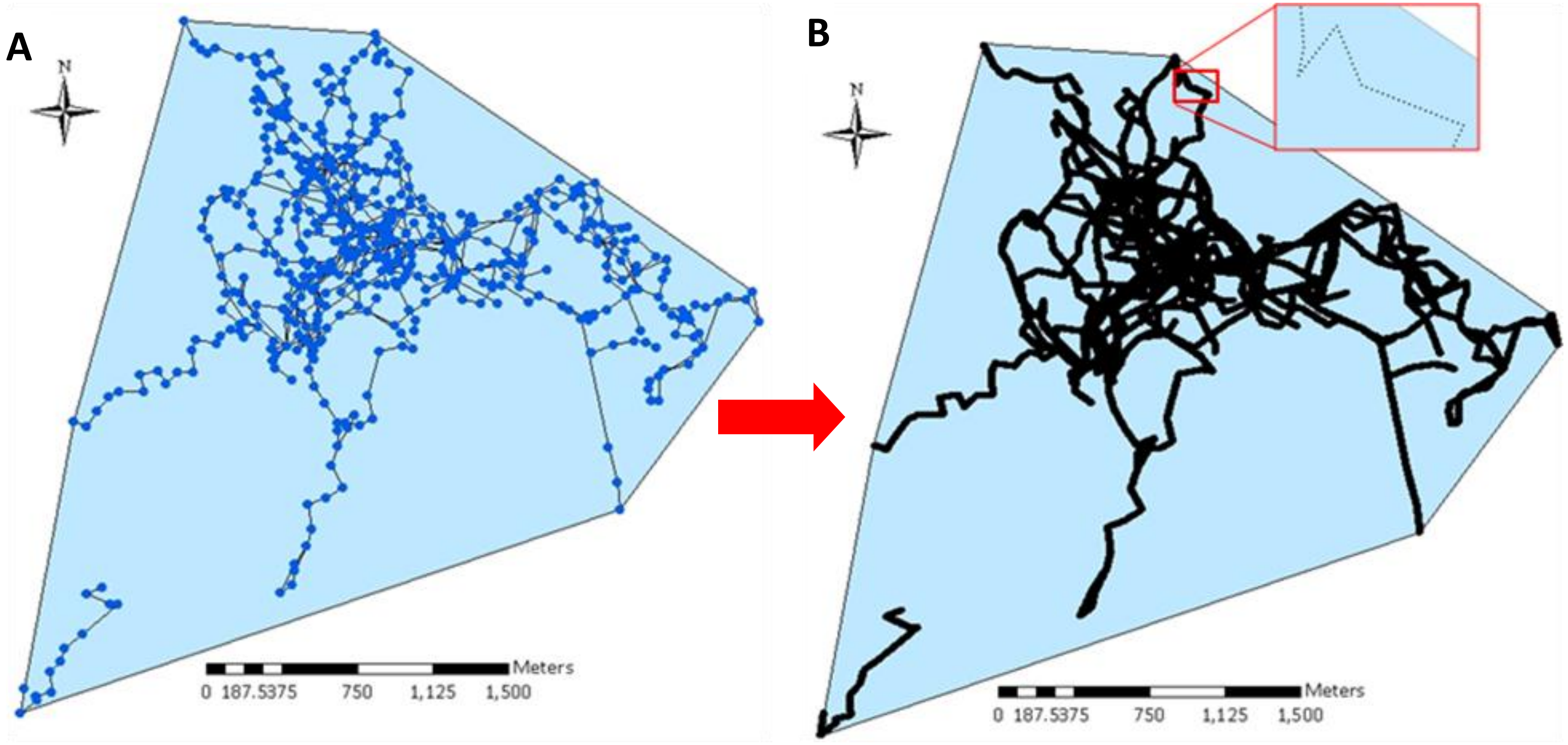
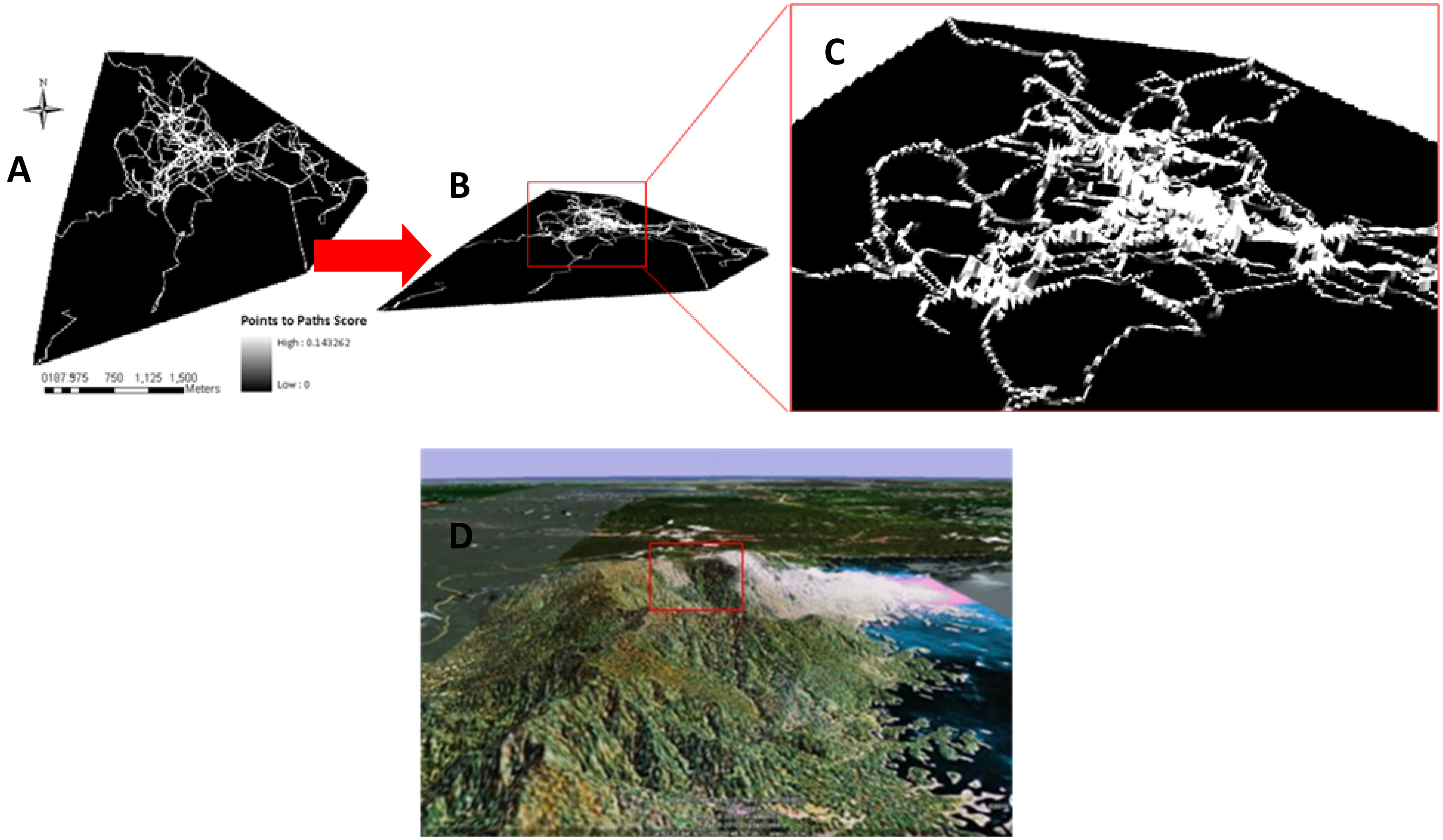


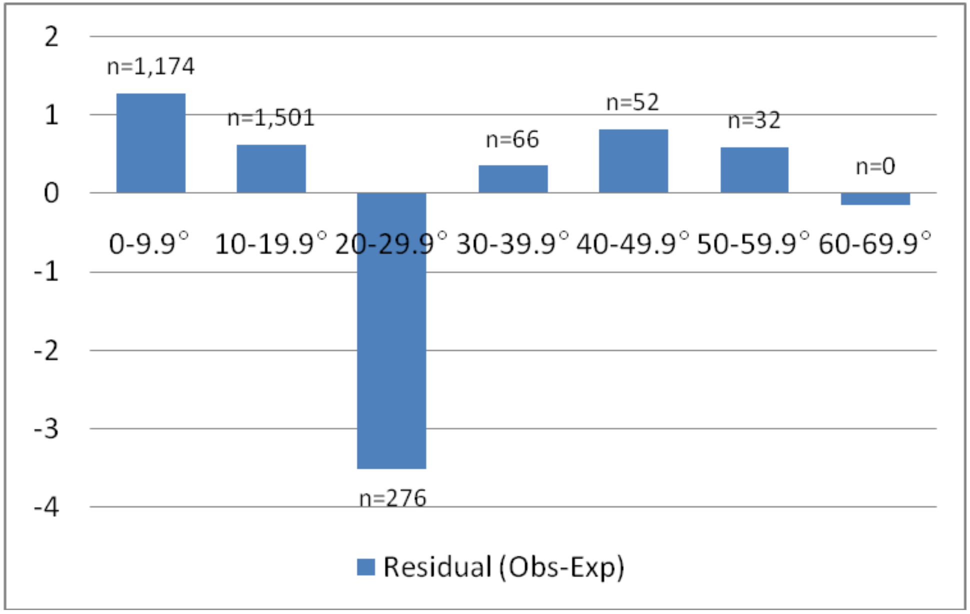
**Figure 5.5.** Travel path interpolation. A) Interpolation of travel paths from Figure 5.4A in Zone WK converted into points. B) Image A is tilted and the interpolation is illustrated in three dimensions for clearer veiwing. C) The area in the red box is enlarged to exaggerate the “topography” created by the three demensional interpretation of the interpolation. D) The tilted Google Earth image from Chapter 2, illustrating the actual topography of the plateau (similar to Figure 5.3B above).



## Slope Preference

In the analysis of slope preference across all three zones, except for one slope category, the monkeys used the slope of the mountain relatively evenly (Prediction 1). Although all of the slope types were used relatively evenly, the monkeys exploited the plateau's slope categories significantly differently than they occurred ($\chi^2$=2.79, $p<0.05$, n=3,101 points in cells, Figures 5.1 above and 5.6). The monkeys used both gradually and steeply sloped areas more than expected based on their occurrence, and they used intermediately sloped areas less than expected (20-29.9$^{o}$).

**Figure 5.6.** Use by the monkeys of the seven slope categories (based on 10-minute waypoints) minus their occurrence. Sample sizes indicate the number of times each category was used.



## Least Cost Path

The analysis of least cost paths gleaned mixed results (Prediction 4). On some days, sakis seemed to follow the plateau's contours and ridges, but on other days, no such pattern was found. Data for all 22 full-day follow periods, including the length of the two least cost paths and the length of the actual travel path is presented (Table 5.3). In some cases, the least cost path between the feeding trees was longer than the actual travel path (e.g., September 17, 2008), and in other cases the least cost path between the start and end points approached the length of the actual travel path (e.g., March 2, 2009). However, perhaps more valuable than the lengths of the paths, the maps of the travel paths for each day allow for more detailed visual interpretations of potential reasons that travel paths were used.

As the least cost path maps demonstrate (Appendix III, Figures 1-22), on some days the monkeys appeared to use a path similar to the least cost path. For example, on March 19, 2009 (Appendix III, Figure 22) the actual travel path is very similar to both the least cost path from start to end and the least cost path between the feeding trees. In contrast, a couple of weeks earlier, on March 2, 2009 (Appendix III, Figure 21) the same group took a very long path across a huge valley, going down one slope and up the other. Although the monkeys did not navigate in a "ring" around the valley (the black least cost path from start to finish), they did generally avoid very steep sloped areas (the darker brown cells). They also followed the least cost path between the feeding trees closely, but this is a consequence of the fact that they fed in nearly every tree through which they passed (i.e., the least cost path between the feeding trees was “forced” through nearly every point they used).

There were also days on which the monkeys traveled a moderate amount, but fed very little. For example, on January 13, 2009 (Appendix III, Figure 18), the travel path does not remotely resemble the least cost path between the feeding trees because the monkeys fed in very few trees. They also traveled a relatively tortuous path in spite of low food intake. Similarly, on some days the monkeys took entirely circular paths. For example, there were days when the monkeys circled back on their travel paths a number of times (e.g., November 5 and 18, 2008, Appendix III, Figures 12 and 15), and on other days the path made a large loop (September 17, 2008 and January 31, 2009, Appendix III, Figures 6 and 20). On these days, in some cases few feeding trees were used (e.g., September 17, 2008) while on others many were used (January 31, 2009). In general, there was a wide range of feeding trees used in a day (range=2-28, mean=11.0±6.1).

Perhaps the most revealing result of this analysis was the fact that while on most days the monkeys used areas with relatively few steeply sloped cells (e.g., May 30, July 15, September 14, September 15, September 16, October 13, October 16, October 17, October 31, November 5, November 6, and November 18, 2008 and January 3, January 25, and March 19, 2009), they certainly did not avoid steep slopes altogether. For example, some of the steepest parts of Zone WK were used repeatedly not only for feeding (September 18, November 13, and December 4, 2008), but also for sleeping

(September 17, 2008: the red star indicates the start point for the follow day and hence the sleeping area) and even for travel without feeding (January 13, 2009).

There was not a significant difference in half-day travel route linearity in the morning versus the afternoon (AM: n=24, mean=0.5248, SD=0.1979; PM: n=36, mean=0.4608, SD=0.2114; t(58)=1.180, p=0.243, equal variances assumed (Levene's test for equality of variances: F=0.00, p=0.992)). However, there was a significant difference between the full and half-day travel paths for travel route linearity, and the full-day travel paths were less linear (half day: n=60, mean=0.4864, SD=0.2068; full day: n=22, mean=0.3324, SD=0.1510; t(80)=3.189, p=0.002, equal variances assumed (Levene's test for equality of variances: F=1.771, p=0.187); full-day travel route linearity data are reported in Table 5.1). This difference may be attributed to the fact that the further a group travels, the more likely an area is to be reused.

Significant differences in linearity of travel route by season were not detected for the full or half-day samples (Table 5.1). However, the test by season of the linearity of the full-day travel paths did approach significance. Although sample size was small, the post-hoc Tamhane tests demonstrated that the long wet season routes were significantly more linear than the long dry season routes (long wet: n=2, long dry: n=13; I-J=0.1358, p=0.011), as were the short dry season routes (short dry: n=2, long dry: n=13; I-J=0.3157, p=0.001).

An analysis of covariance was also performed on the half-day travel route linearity data with group size as a covariate to account for potential effects of increased group size on the tortuousness of the travel route. However, no significant relationship between half-day travel route linearity and season was found when group size was held constant (Table 5.2). A regression analysis of group size and half-day travel route linearity in all four seasons demonstrates that the short wet season is the only season in which there is a significant relationship between group size and half day travel route linearity (Figure 5.7). Interestingly, in the short wet season, the larger the group is, the more tortuous (i.e., less linear) the route.

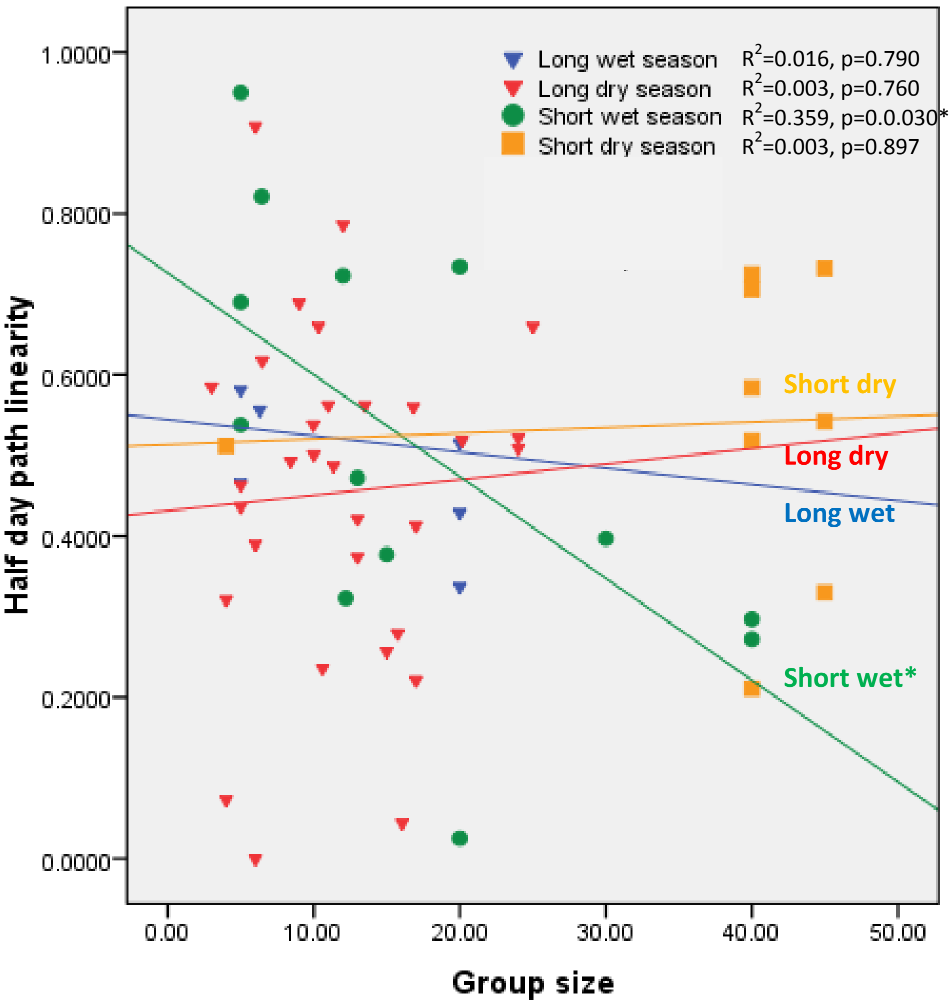
**Table 5.1.** Results of the Kruskal-Wallace test of differences between the four seasons for linearity of travel path during full-day and half-day follow periods.

| | Sample size | Mean (in meters) | Range (in meters) | Kruskal-Wallis H between seasons |
|---|---:|---|---:|---|
| Full day travel path linearity | 22 | x=0.3324±0.1510 | r=0.0500-0.6300 | H=7.268, p=0.064 |
| AM travel path linearity | 24 | x=0.5248±0.1979 | r=0.0-0.8210 | H=0.899, p=0.826 |
| PM travel path linearity | 36 | x=0.4608±0.2114 | r=0.0250-0.9500 | H=1.375, p=0.711 |
| Half day travel path linearity | 60 | x=0.4864±0.2068 | r=0.0-0.9500 | H=1.708, p=0.635 |

**Table 5.2.** ANCOVA analysis of the relationship between half day travel path linearity by season with group size held constant for the four seasons.

| | Source | Degrees of Freedom | F-value | Significance | $R^2$ value |
|---|---|---:|---:|---:|---|
| Linearity of half day travel path | Covariate: Group size | 1 | 0.707 | 0.404 | 0.148 |
| | Fixed factor: Season | 3 | 1.784 | 0.162 | |
| | Interaction | 3 | 1.667 | 0.185 | |

**Figure 5.7.** Regressions of half day travel route linearity on group size for all four seasons.



## DISCUSSION

As indicated in Table 3.3, groups of varying size were followed in each of the three zones. These may have been separate groups, particularly in Zones PP and AKP. However, in Zone WK, it is more likely that these were subgroups, and hence, all part of the same large group. Furthermore, as demonstrated in Figure 5.1, the use area of the small, all-male (juvenile) group(s) was subsumed by the use area of the large, mixed-sex group, and therefore this is likely to be a subgroup.

With a larger data set including full annual cycles of areas of use on all of the groups followed within the study period more accurate home range sizes could be calculated. Nonetheless, the home range area for the WK Group is the largest home range ever calculated for a bearded saki group (Table 4.x), with the exception of Pinto (2008). However, in Pinto's study, the home range (1,000+ha) was estimated and not calculated with mapping software.

As predicted, the slope preference analysis demonstrated that bearded sakis preferred the steeply sloped areas of the park. Because steeply sloped areas are more difficult to navigate, monkeys would be expected to use these areas even less than the degree to which they are available. Instead, the monkeys used relatively steeply sloped areas to a *higher* degree than expected based on availability. As suggested above, such a preference is likely to be related to their inclination to use the largest trees in the forest (Gregory 2006), and the likely high abundance of large trees on the plateau's slopes (ter Steege et al. 2007). Further research may demonstrate that growing conditions on the slopes favor the large-treed families preferred by the sakis, such as Sapotaceae and Lecythidaceae (see feeding species analysis in Chapter 4).

The results of the analysis of high-use areas indeed show a preference by the monkeys for ridges. As predicted, the area used most in Zone WK not only for travel but also for resting and feeding corresponded to the area where the two main ridges occur. The results of the least cost path analyses are somewhat less conclusive with regards to a specific pattern of ridge use. Rather than demonstrating a clear preference for the "easiest path" (with regards to slope and Euclidean distance), differences between the paths selected and least cost paths suggest that path selection is perhaps more complex than the model allows. Further analyses and more data may demonstrate a clearer pattern. Conversely, bearded sakis may not show a clear preference for ridges and more gradual slopes because their path selection may be influenced by myriad other factors. For example, they may deviate from using the ridge because there are preferred resources, i.e., feeding tree species, off to the sides of the ridges.

Additionally, the monkeys may experience the slope differently than it is represented in these models (i.e., monkeys do not use the planar canopy travel paths depicted in the models but rather they frequently change forest levels within the canopy), and therefore, they may be using a strategy that cannot be easily detected. As noted previously, other studies that have used the GIS cost-weighted-path function to predict travel patterns based on topography were used for terrestrial animals such as carnivores, livestock, and hedgehogs (Driezen et al. 2007; Ganskopp et al. 2000; Larkin et al. 2004; Singleton et al. 2002). Data from studies of arboreal animals maybe more difficult to interpret, and future studies may require more complex models.

Yet another explanation for the discrepancies between actual travel paths and least cost travel paths may be that bearded sakis experience different energetic and dietary constraints than larger-bodied, nearly-strictly-frugivorous animals such as atelines (e.g., results from Di Fiore and Suarez 2007). For example, at the same site in Ecuador where Di Fiore and Suarez studied atelines, a study of squirrel monkey travel patterns yielded converse results. The squirrel monkeys used more tortuous paths that were often perpendicular to the slope, i.e., a relatively energetically costly path (Reilly and Suarez 2010). This strategic difference is likely to be attributable to differences in body size, and being smaller bodied, squirrel monkeys are not as energetically constrained in their movement as are large-bodied atelines. Perhaps the same is true for bearded sakis. Furthermore, a highly energy rich diet of seeds in bearded sakis (Ayres 1989; Norconk et al. 2009) may allow for a less constrained use of terrain. Also, being that un-ripe seeds are a more ubiquitous resource, bearded sakis may be able to find feeding resources more easily than atelines can.

The present study illustrates new ways in which GIS technology can be applied to studies of primates. Through refinement of the techniques used here and development of models suitable for arboreal animals, much may be learned about primate movement patters through GIS. While cost-weighted analyses may be somewhat more difficult to apply to an arboreal landscape, interpolation proved here to be very valuable in locating preferred areas used by the monkeys. Identifying areas of preferred use is not only valuable for understanding primate movement ecology, but it is also useful logistically for locating groups of primates and for creating resources (such as localization maps of different primate species) for researchers who may be new to a study site.

**Table 5.3.** Data summary for the 22 full-day follow periods during the study period.

| Date | Season | Zone | Group sizes | Group composition | Travel distance | Euclid-ean distance | Linearity | Least cost path length | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | Start to end | Feeding trees |
| May 30, 2008 | Long wet | PP | 20 | Mixed | 3546 | 1500 | 0.4230 | 1608 | NA |
| July 15, 2008 | Long wet | PP | 5 | Mixed | 2239 | 960 | 0.4288 | 960 | 2026 |
| September 14, 2008 | Long dry | WK | 6, 20 | Mixed | 2303 | 692 | 0.3005 | 766 | 1071 |
| September 15, 2008 | Long dry | WK | 6, 9 | Mixed | 1229 | 389 | 0.3165 | 415 | 1031 |
| September 16, 2008 | Long dry | WK | 6, 9 | Mixed | 1779 | 1000 | 0.5621 | 1099 | 1655 |
| September 17, 2008 | Long dry | WK | 12, 15 | Mixed | 2232 | 265 | 0.1187 | 304 | 2288 |
| October 6, 2008 | Long dry | WK | 4 | All male | 1756 | 258 | 0.1469 | 276 | 1673 |
| October 13, 2008 | Long dry | AKP | 24 | Mixed | 3886 | 1400 | 0.3603 | 1521 | 2555 |
| October 16, 2008 | Long dry | AKP | 5, 13, 24 | Mixed | 1259 | 239 | 0.1898 | 252 | 1027 |
| October 17, 2008 | Long dry | AKP | 17 | Mixed | 3286 | 919 | 0.2797 | 975 | 2225 |
| October 31, 2008 | Long dry | AKP | 10, 15, 20, 30 | Mixed | 2269 | 674 | 0.2970 | 696 | 1621 |
| November 5, 2008 | Long dry | AKP | 7, 13 | Mixed | 2615 | 790 | 0.3021 | 815 | 1989 |
| November 6, 2008 | Long dry | AKP | 13 | Mixed | 3137 | 660 | 0.2104 | 738 | 2586 |
| November 13, 2008 | Long dry | WK | 15, 20, 25 | Mixed | 3640 | 1700 | 0.4670 | 1864 | 2673 |
| November 18, 2008 | Long dry | WK | 5 | Male & juv. | 1959 | 432 | 0.2205 | 443 | 1754 |
| December 4, 2008 | Short wet | WK | 5 | All male | 1654 | 697 | 0.4214 | 733 | 1490 |
| January 3, 2009 | Short wet | AKP | 5, 15 | Mixed | 809 | 196 | 0.2423 | 198 | 818 |
| January 13, 2009 | Short wet | WK | 30 | Mixed | 2369 | 786 | 0.3318 | 861 | 901 |
| January 25, 2009 | Short wet | WK | 12 | Mixed | 1889 | 813 | 0.4304 | 871 | 1855 |
| January 31, 2009 | Short wet | WK | 40 | Mixed | 2782 | 143 | 0.0514 | 171 | 2505 |
| March 2, 2009 | Short dry | WK | 40 | Mixed | 3095 | 1800 | 0.5816 | 2778 | 2795 |
| March 19, 2009 | Short dry | WK | 45 | Mixed | 2222 | 1400 | 0.6301 | 1552 | 2098 |

# CHAPTER 6

# CONCLUSIONS

## General Conclusions

The results of this study provide further support for the existence of affiliative male-male relationships in bearded sakis. Not only are previous results (Peetz 2001; Veiga et al. 2005) of male preference for same-sex social partners and affiliative interactions between males corroborated, but there is also initial documentation of all-male (sub)groups. Higher rates of affiliative behaviors between males when in all-male groups suggest that these times are potential opportunities for bond reinforcement. While genetic data is lacking, and it cannot be confirmed that males are bonded because they are related, male philopatry is a distinct possibility in bearded sakis, given the tendency of these two characteristics to co-occur (e.g., *Brachyteles*, *Ateles*, and *Pan troglodytes*, Di Fiore and Campbell 2011; Hamilton 1964; Stumpf 2011; Trivers 1972). Affiliative relationships between males and low (or no, as seen in this study) aggression may facilitate bearded saki group cohesion, enabling large bearded sakis groups to form.

While bearded saki groups are large, results of the seasonal analyses show that group size *flexibility* is perhaps the most salient adaptation to seasonal fluctuations in resource availability. Bearded sakis also seem to seasonally adjust the balance between time spent feeding and time spent resting (although *not* in time spent traveling), and when they begin to feed more on seeds, they tend to spend more time feeding. At this time, groups are at their largest, with births also occurring. Conversely, when seed feeding is reduced, the monkeys rest more and group size shrinks. Being more nutritionally valuable than fruit pulp or flowers (Norconk et al. 2009), seeds are likely to be a preferred resource despite potential longer handling time (Peetz 2001). When seeds are the main food resource, group size can grow because group caloric needs can be met more effectively. However, when seed feeding rates decrease, perhaps due to reduced availability, the bearded saki ability to shift to other resources, combined with reducing group size and more resting, may diminish the impact of what would otherwise be a season of shortage.

Large group size is likely to be related to the use of large home ranges in bearded sakis (see Schoener 1971 for a discussion of group size and home range size). In this study, group sizes were among the largest documented in bearded sakis (up to 45, a conservative estimate), as were home ranges (742ha being the best estimate). Daily travel distances were relatively long as well. Interestingly, adjusting travel distance appears to be another seasonal strategy for bearded sakis. However, only in the long dry season, the season of lower seed consumption, does a significant relationship between group size and travel distance arise. At this time, travel distance increases with the addition of each group member. Perhaps when the monkeys feed less upon valuable seeds, they must travel more sparingly.

Other ecological strategies investigated in this study include navigation of the landscape via “least cost” paths. Typical of primates and other mammals (see Chapter 5), bearded sakis repeatedly used the same familiar areas. These areas tended to be on ridge tops, which are presumed to be easier for navigation not only energetically, but also perhaps cognitively, serving as landmarks (Di Fiore and Suarez 2007). Although sakis were not found to consistently choose the path of least slope, the GIS model that created these paths may have been too simplistic for use on arboreal animals navigating through tree branches. The analysis of seasonal patterns in the linearity of half day travel paths showed an interesting relationship between the linearity of travel path and group size. Only in the short wet season was the relationship between travel path and travel route linearity significant. Contrary to predictions, adding group members increases the tortuousity of the travel path. Perhaps resources could be reused in this season because they were not fully depleted during earlier visits.

## Future Research

Because it is difficult to identify individual bearded saki monkeys, detailed studies of social behavior have not been possible. For example, while studies such as this one and others have determined that males are affiliative with each other, it has not been possible to determine whether males have preferred social partners (i.e., friends) or whether there is a social hierarchy (although this seems unlikely). Similarly, it is not clear whether animals have preferred mating partners. In fact, because subgroup composition has not been determinable, it is not known if subgroup composition is relatively consistent. Certainly, if this were the case, there would be interesting implications for mating, given increased time spent with the same individuals (e.g., similar to consortships in chimpanzees). In the future, techniques such as radio collaring or marking individual monkeys may make the study of individual relationships possible.

However, given their small body size and high mobility, bearded sakis are not good candidates for these methods.

Genetic research in the future will provide great insight into bearded saki dispersal patterns. While affiliative relationships amongst group males imply male philopatry, there is no definitive genetic evidence to confirm this idea. Furthermore, the evolutionary perspective does not necessarily implicate male philopatry in bearded sakis. Dispersal patterns in the closest living relative of bearded sakis, the uakaris, are unknown, and Pitheciine fossils resemble extant members of the genus *Pithecia*, which shows dispersal of both sexes. Because genetic research on bearded sakis may be non-invasive (e.g., fecal sampling), this area has great potential in the near future.

Broadening our knowledge of the genus *Chiropotes* should also involve comparisons across species of bearded sakis. The relative lack of data on members of this genus has led to a tendency to compare studies as if the genus represented one species. While members of this genus show morphological, genetic, and geographic variability, differences in social behavior and ecology have not been well explored.

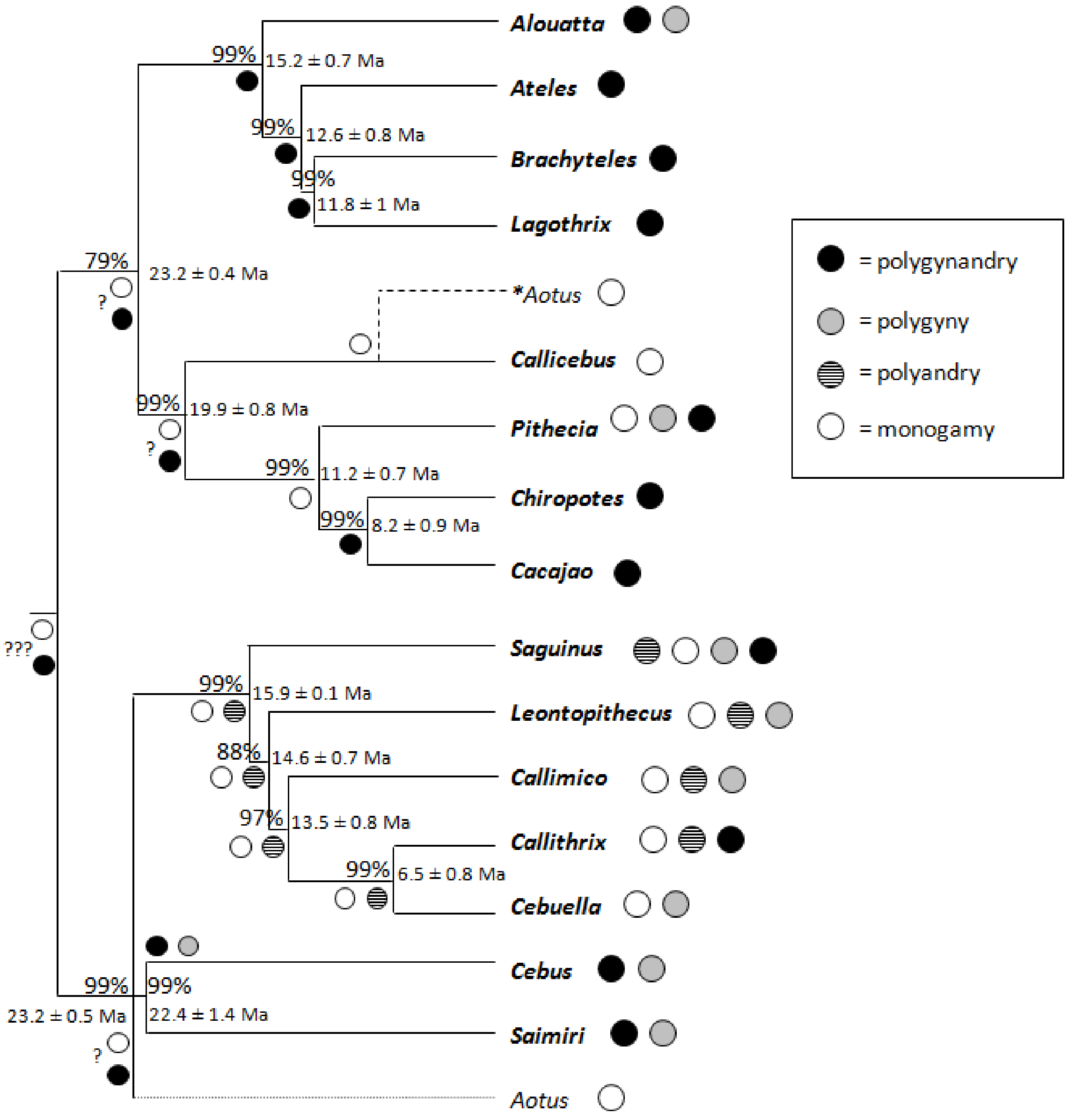
## Bearded Saki and Platyrrhine Evolution

While grouping patterns that include multiple adult females are somewhat common in mammalian taxa, multimale groups are less common. Within the platyrrhine radiation, not only are there many different taxa that exhibit multimale grouping, there are many different ways in which males aggregate and tolerate each other (Strier 1994; 2000). From polyandrous callitrichines, to potentially male-bonded muriquis, bearded sakis, and uakaris, to non-male bonded, age-graded groups in squirrel and capuchin monkeys, the New World monkeys run the gamut of multimale grouping patterns (see Campbell et al. 2011 for reviews on all subfamilies).

Dispersal regimes amongst platyrrhines are also diverse, demonstrating male philopatry (*Ateles*, *Brachyteles*, *Lagothrix*, some *Alouatta* spp., some Callitrichines, some Cebines, and possibly *Chiropotes* and *Cacajao*), male-biased dispersal (some Cebines), and dispersal by both sexes (*Pithecia*, *Aotus*, *Callicebus*, some *Alouatta* spp., and some Callitrichines) (Campbell et al. 2011). Because grouping and dispersal patterns are likely to be phylogenetically conserved (Di Fiore and Rendall 1994), differences between lineages should be attributable to different evolutionary trajectories.

As noted previously, fossil pitheciines bare a closer resemblance to extant *Pithecia* spp., particularly in body size (extinct pitheciine ancestors *Soriacebus ameghinorum* and *Nuciptor rubricae* are thought to have weighed approximately 1,800g and 2,000g, respectively: Fleagle et al. 1987; Meldrum and Kay 1997). Similar morphology may imply similar grouping patterns and dispersal regimes. Unlike multimale *Chiropotes* and *Cacajao* groups, *Pithecia* groups are variably one/two-male and one/two female (Lehman et al. 2001; Thompson 2010) with potential bisexual dispersal, as in *Callicebus*. With bisexual dispersal in the last common ancestor, there would be no phylogenetic support for male philopatry in *Chiropotes* and *Cacajao*. However, given shared ancestry with the atelins, male philopatry and multimale groups may be primitive to all atelids (atelines and pitheciines). If this is the case, it may also be a candidate for the primitive condition for all platyrrhines (Figure 6.1).

**Figure 6.1.** New World primate phylogeny, modified from Schneider (2000). Results combined from 17 sequences of the β2-M, EPSILON, G6PD, and IRBP genes aligned in tandem. Dates represent divergence times estimated using the molecular clock strategy. Branch lengths to scale based on divergence time, and maximum parsimony values based on 1000 replicates indicated at nodes. *Aotus* added in the pitheciin clade to indicate a possible sister relationship between *Callicebus* and *Aotus* as suggested by morphological data from Rosenberger (1981; 1992; 2002). Mating systems indicated by circles based on reviews in Campbell et al. (2011). Reconstruction of ancestral mating systems based on divergence times and fossil evidence indicated at nodes.



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