THE EFFECTS OF FOREST FRAGMENTATION ON PRIMATES IN THE BRAZILIAN AMAZON

by

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ABSTRACT

Forest fragmentation, arising from deforestation, is a primary threat to primate conservation; however, species do not respond to fragmentation in the same manner. This dissertation examines how forest fragmentation affected 1) the distribution and persistence of six primate species and 2) the behavioral ecology of the northern bearded saki monkey (*Chiropotes sagulatus*). Research was conducted at the Biological Dynamics of Forest Fragments Project, located approximately 80 km north of Manaus, Amazonas, Brazil. Nine forest fragments and two areas of continuous forest were surveyed for primates from July-August 2003 and January 2005-June 2006. Fragment attributes (e.g., size, isolation, matrix attributes) were determined using satellite images. Although some species (e.g., red howler monkey, *Alouatta seniculus*) were common in the forest patches, other species (e.g., black spider monkey, *Ateles paniscus*) were rarely present. Primate species richness was predicted by fragment size, distance to closest forest patch greater than 0.5 ha, and proportion of secondary growth in the matrix, but primate characteristics (e.g., body size, home range, degree of frugivory) did not predict species presence in the fragments. Although the bearded saki monkey is a medium-size, highly frugivorous monkey with a large home range, it was present in forest fragments less than 5% of the species' home range size in continuous forest. Each bearded saki group was followed for three consecutive days during each data cycle. Every five minutes, the location and behavior of the monkeys were recorded. Monkeys in the small forest fragments had smaller group sizes, smaller day ranges, different travel and spatial patterns, and different behavioral activity budgets than monkeys in larger fragments and continuous forest. There was little overlap in diet between bearded saki groups, even when fruiting species were present in several study sites. The lack of successful births in the small forest fragments, discrepancies in diet between groups, avoidance of low-growth matrix, and avoidance of particular habitats raise concern for the population’s future. Forest fragment size and habitat type, as well as the presence and configuration of forest patches and secondary forest growth in the matrix, are important considerations when managing arboreal primate species in a fragmented landscape.

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CHAPTER 1

FOREST FRAGMENATION AND PRIMATE POPULATIONS IN THE BRAZILIAN AMAZON

Abstract. Deforestation is a global problem with environmental, social, and economic consequences. One of the centers of deforestation is the Amazon Basin in South America. As forests are cleared, areas that were once contiguous forest have become a landscape littered with forest fragment remnants. This chapter presents an overview of research on the effects of forest fragmentation on resident primate species in the Brazilian Amazon. The consequences of forest fragmentation and theories associated with the dynamics of fragmentation are reviewed, as well as the history of the Biological Dynamics of Forest Fragments Project (BDFFP), an ongoing 28-year-old study located north of Manaus, Amazonas, Brazil. Research at BDFFP has shown forest fragmentation to affect species richness, forest composition, and microclimate, but there have been few studies on the behavioral ecology of the six resident primate species. This chapter outlines each of the five chapters included in this dissertation, and discusses the overall purpose and importance of evaluating the effects of forest fragmentation on primates in the Brazilian Amazon.

INTRODUCTION

The world's forests are disappearing rapidly at a rate of 1.3 x 10^7 ha per year (FAO 2007). One of the major centers of deforestation is the Amazon Basin, an area that encompasses 8.15 x 10^8 ha in Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname, and French Guiana (Fig. 1). The Amazon is the world's largest rain forest, with approximately 50% of its area located in Brazil. Approximately 57.2% (4.77 x 10^8 ha) of Brazil was forested in

2005 (FAO 2007); however, deforestation in the Brazilian Amazon is estimated to be 2.4 x 10^6 ha per year, or 11 football fields per minute (Laurance *et al.* 2004). Intensive deforestation of the Brazilian Amazon began in the 1970s, and 70% of the clearing can be attributed to cattle ranches (Fearnside and Graça 2006). Activity is primarily concentrated in the "arc of deforestation," located in the southern and eastern areas of the Brazilian Amazon (Fearnside and Graça 2006).

One of the consequences of deforestation is forest fragmentation, an ever-increasing global phenomenon affecting the sustainability of ecosystems across our planet (Lovejoy 2006). Forest fragmentation occurs when sections of contiguous forest are cleared, thereby leaving a mosaic of patches surrounded by a non-forested matrix (Fig. 2). As deforestation for agriculture or urban development continues, the remaining forest becomes increasingly patchy, affecting local climate (Bierregaard Jr. *et al.* 1992, Achard *et al.* 2002), species richness and distribution (Bierregaard Jr. *et al.* 1992, Malcolm 1997, Laurance *et al.* 2000a), predator-prey interactions (Asquith *et al.* 1997), seed dispersal (Chapman and Onderdonk 1998, Estrada *et al.* 1999), and habitat suitability (Gascon *et al.* 2000, Laurance *et al.* 2000b).

The purpose of this dissertation research was to examine the effects of forest fragmentation on resident primates, on both the community and species level. The focus at the community level examined whether characteristics of a forest fragment (i.e., size, degree of isolation, condition of the surrounding matrix) and characteristics of the residing primate species (i.e., body weight, home range size, degree of frugivory) are reliable predictors in determining the composition and overall persistence of a primate community in a fragmented landscape. While such overall distribution patterns are important when evaluating how species with different life histories respond to habitat fragmentation, further investigation is critical in order to detect how a species residing in a forest patch copes behaviorally with forest fragmentation. Therefore, the second portion of this dissertation, at the species level, examines the degree of behavioral plasticity exhibited by the northern bearded saki monkey (*Chiropotes sagulatus*) living in forest fragments of varying conditions (e.g., size, degree of isolation, matrix isolation).

In addition to providing data for general models regarding the response of fauna with varying behavioral and ecological characteristics to forest fragmentation, the application of these findings to primate conservation is a key goal. The conservation of primates on a whole is important for tropical ecosystems, as primates serve as prey, predators, seed dispersers, and pollinators (Strier 2003). To illustrate their role in plant-animal interactions, Chapman and Chapman (1996) found that forest fragments in which the primate population had been reduced had lower seedling densities and fewer types of seedlings than patches of forest with intact primate communities. Emmons (1999) suggested that primates are predictors of mammalian community richness in Amazonia.

In the primate literature the majority of the behavioral ecology research in disturbed habitats focuses on solely a handful of species, such howler monkeys in the genus *Alouatta* (Chiarello 1994, Estrada *et al.* 1999, Silver and Marsh 2003). Thus, conclusions regarding how primates are affected by habitat fragmentation may not be applicable to understudied species, such as the northern bearded saki monkey, due to differences in the plasticity of the species' behavioral and social characteristics. Overall, much needs to be learned about the behavioral ecology of many free-ranging primates (Sussman 2007).

History of Fragmentation Research

Humans have impacted the environment for more than 2.5 million years, from the first use of tools and the subsequent use of fire, to the current widespread landscape changes and species extirpations (Chew 2001, Goudie 2001). In the 1950s, scientists first began documenting and analyzing the effects of forest fragmentation in the temperate zones of North America and Europe (Curtis 1956, Darby 1956). Since then fragmentation research has increasingly gained ground in both the temperate and tropical zones. Seminal works by Diamond (1975), Lovejoy and Oren (1981), Janzen (1988), Laurance (1991b), and Gascon and Lovejoy (1998) have contributed to the understanding of the effects of fragmentation on species richness, forest composition, edge effects, and climate. Although such studies have provided insights into the immediate and longer-term consequences of forest fragmentation, they have not yet explained the exact mechanisms and effects of fragmentation (McGarigal and

Cushman 2002). Findings differ both geographically and among taxa (Harrison and Bruna 1999, Debinski and Holt 2000); therefore there is a pressing need for further research in tropical ecology and the processes associated with tropical forest fragmentation.

Theoretical background

Forest fragmentation research is now widespread throughout the world, as human pressures on the environment have resulted in the clearing of forested areas that were previously intact. Since the first documented study of forest fragments in the 1950s, there have been two prominent theories associated with forest fragmentation: island biogeography theory and metapopulation theory.

Island Biogeography Theory.—The most prominent theory throughout the history of fragmentation research has been the theory of island biogeography (Gascon and Lovejoy 1998, Cook *et al.* 2002, Haila 2002). The premises behind the theory are 1) larger islands have greater species richness than smaller islands; 2) islands further from a mainland population have less species richness than closer islands due to fewer net colonization events; and 3) species turnover changes with time (MacArthur and Wilson 1963, 1967). Although MacArthur and Wilson (1967) mentioned forest fragmentation only in the introduction of their work, this theory was subsequently adapted by other researchers to predicting the presence of species in fragmented habitats.

Although island biogeography theory formed a base for early fragmentation research, the usefulness of island biogeography applications to fragmentation has been widely debated. The size and isolation of a forest fragment are often factors in determining a species' recolonization potential, mortality, and dispersion (Diamond 1975, Sierra 2000); however, the theory does not take into account the presence or absence of species in a fragment due to conditions of the surrounding matrix (Gascon and Lovejoy 1998, Cook *et al.* 2002), habitat degradation by edge effects (Laurance 1991b), or succession (Lovejoy and Oren 1981). Therefore, a contemporary view of forest fragments is that they exist as "elements in a heterogeneous landscape" instead of islands surrounded by an "inhospitable" sea (Haila 2002).

In the 1970s, Simberloff and Abele (1976) stated that the theory of island biogeography is neutral in regards to a single large area or several small patches that equal the same total area. This touched off the Single Large or Several Small (SLOSS) debate as to whether it was better to have one large reserve, or several smaller reserves that together constitute the same area as the large reserve (Simberloff and Abele 1976, Wilcox and Murphy 1985, Bierregaard Jr. *et al.* 1992, Tscharntke *et al.* 2002). The SLOSS debate was the basis for the development of the Biological Dynamics of Forest Fragments Project (BDFFP) by Thomas Lovejoy (Laurance et al, 2004). BDFFP served as the field site for this dissertation research.

Metapopulation Theory. —A second theory that is often associated with forest fragmentation research is metapopulation theory. Metapopulation theory is relevant to the study of taxa in fragmented habitat, as it concerns the balance between the extinction of isolated populations and re-colonizations of the area following immigration from surviving populations (Levins 1969, Hanski 1998).

The use of metapopulation theory in conservation biology is relevant for examining extinction and survival patterns for a species, and it has been used for predicting the future viability of populations in fragmented habitat (Hanski 1994, Swart and Lawes 1996, Chapman *et al.* 2003, Hanski and Ovaskainen 2003). Such metapopulation models can therefore be applied to the management of populations (Fahrig and Merriam 1994, Hanski 1994, Swart and Lawes 1996).

Findings of fragmentation research

Forest fragmentation research during the past three decades has focused on a variety of taxa and ecological processes. Although such research has identified certain general patterns and processes that occur when an area of forest is isolated, the effects of fragmentation are not identical for all situations, and there are many aspects of this process that are not yet understood (Laurance *et al.* 2006b). Due to the patchy distribution of some species, and the combined effects of forest disturbance, there is no criterion for an accepted minimum forest fragment size (Laurance *et al.* 2002); however, researchers in the Amazon argue that reserves should be large (>10,000 km^2) and numerous (Laurance *et al.* 2002, Peres 2005).

Forest structure. —Forest fragmentation influences the physical properties of the fragment through edge effects, which then in turn affect species composition (Gascon and Lovejoy 1998). When deforestation occurs, leaving behind a patch of forest, the patch experiences increased solar and wind penetration. As a result, the forest fragment has higher temperature and lower relative humidity than it did prior to deforestation (Kapos 1989, Bierregaard Jr. *et al.* 1992). A review of data from 22 years of research found that Amazonian forest fragments experienced a shift in tree species composition (Laurance *et al.* 2006a). Compared to continuous forest, fragments also have more early successional trees (Laurance *et al.* 2006b), more lianas (Laurance *et al.* 2001b), and greater tree mortality and damage (Laurance *et al.* 1998).

Further research in the Amazon found that near fragment edges, litterfall, seedling recruitment, and seedling mortality were affected by sun and wind exposure (Sizer 1992). Within 300 m of the fragment's edge, there were more pioneer and secondary tree species and fewer old-growth trees than in areas of the forest fragment that were more than 300 m from the edge (Laurance *et al.* 1998). Many taxa showed impacts 100-500 m from edge, while others were even affected 1 km from the edge (Gascon *et al.* 2000). Furthermore, within a forest fragment, tree mortality was greatest near the edges, especially among the larger trees (Laurance *et al.* 2000a).

Species richness.—It is often the case that species richness declines once an area of forest is fragmented (Malcolm 1997, Laurance 2002, Ferraz *et al.* 2003). Although less frequently observed, there have been instances where species richness increased upon fragmentation in taxa such as frogs and small mammals (Malcolm 1995, Gascon and Lovejoy 1998), as well as insects

(Tscharntke *et al.* 2002). For some species of Amazonian birds, population density increased immediately following fragmentation, as the forest patches became refuges; however, population density subsequently fell below the size of the pre-fragmentation population (Lovejoy *et al.* 1986).

Declines in species richness have been attributed to loss of habitat heterogeneity (Bierregaard Jr. *et al.* 1992, Gascon and Lovejoy 1998), endemic species with specific habitat requirements (Dale *et al.* 1994, Heydon and Bulloh 1997, Gascon and Lovejoy 1998), decreased fitness in small populations due to Allee effects (Dobson and Lyles 1989, Cheptou and Avendaño V 2006), species with large home ranges (Skorupa 1986, Bierregaard Jr. *et al.* 1992, Dale *et al.* 1994, Gascon and Lovejoy 1998), the species' diet (Skorupa 1986, Johns and Skorupa 1987) and diet flexibility (Estrada and Coates-Estrada 1988, Horwich 1998, Sussman 1999, Clarke *et al.* 2002), the species' ability to cross gaps (Dale *et al.* 1994), and the condition of the matrix (Gascon and Lovejoy 1998, Gascon *et al.* 1999, Tscharntke *et al.* 2002). Although these factors are important in some species, they do not apply to all species, and thus there is still no consensus regarding what the main factors are that determine species richness in a forest fragment. A review of 20 fragmentation studies by Debinski and Holt (2000) found that the results of these studies lack consistency, and that there is a wide range of species-specific responses to forest fragmentation due to differences in species behavior and temporal fluctuations in resource abundance. While some patterns do exist, it is often difficult to make specific predictions based on ecological theories due to the complexities involved with the ecology of fragmented habitat (Bissonette and Storch 2002).

Biological Dynamics of Forest Fragments Project (BDFFP)

The research presented here was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) reserve (2°30'S, 60°W), located approximately 80 km north of Manaus, Brazil (Fig. 3). BDFFP is the site of a long-term project on fragmentation, currently managed by the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil, in collaboration with the Smithsonian Tropical Research Institute in Panama.

History.—The idea for the BDFFP, initially called the Minimal Critical Size of Ecosystems project, started with Thomas E. Lovejoy in 1976 (Bierregaard Jr. and Gascon 2001). The initial purpose of the project was to determine how much forested area was necessary to keep both the species composition and their interactions intact (Bierregaard Jr. and Gascon 2001). At this time, in order to boost the area's economic development, the primary forest in the soon-to-be BDFFP project area was slated for development into large cattle ranches (10,000-50,000 ha) via a program by Superintendência da Zona Franca de Manaus (Superintendency of the Manaus Free Trade Zone — SUFRAMA). Under Brazilian law at that time, 50% of forest properties had to be maintained as primary forest. Thus, the early BDFFP collaborators worked with the ranchers in order to establish isolated 1-ha, 10-ha, and 100-ha forest fragments on their properties in order to assess the effects of fragmentation on Amazonian fauna and flora. Although the size of the forest fragments vary, (e.g., 1-ha fragments range from 1.1 ha to 2.8 ha), the majority of studies compare them in terms of their three size classes.

The fragments were isolated from the surrounding forest by distances of 70-1000 m (Plate 1), and the remaining forest was left as a continuous forest, which served as a control as a control for comparison (Gascon and Lovejoy 1998, Laurance *et al.* 2003). The initial plan was to isolate 24 fragments; however, political and economical problems in the 1980s resulted in only a handful of isolated forest fragments. Furthermore, the ranchers abandoned some of the agricultural areas, which led to a de-isolation of the forest fragments in these areas due to secondary growth in the abandoned pasture. There are four 1-ha fragments, three 10-ha fragments, and two 100-ha fragments located within the cattle ranches of Esteio, Dimona, and Porto Alegre that I used for this study. These fragments vary in size, degree of isolation, and condition of the surrounding matrix (Table 1).

The BDFFP study area is divided by the BR-174, a highway that stretches from Manaus to Venezuela. In addition to the cattle ranches that are found in the study area, there is further clearing of forest radiating from the BR-174 (Fig. 4). Although the BDFFP study area is technically a reserve, it is currently threatened by agricultural development and forest burning, logging, and hunting, as well as a SUFRAMA colonization program that would bring in 180 families to the study area’s periphery (Laurance and Luizão 2007).

Forest characteristics.—The study site is classified as tropical moist *terra firme* (not subject to flooding) forest (Gascon and Bierregaard Jr. 2001). It receives 1900-3500 mm of rain annually, and there is a dry season between June and October where there is less than 200 mm of rain per month (Laurance 2001). Mean annual temperature for Manaus is 26.7°C (with monthly mean fluctuations of 2°C), maximum temperature ranges from 35-39°C, and minimum temperature ranges from 19-21°C (de Oliveira and Mori 1999). Rainfall during this study (January 2005 – June 2006) averaged 249 mm of rain monthly. Total rainfall for 2005 was 2652 mm, with a 2005 dry season average of 96 mm of rain per month (Fig. 5).

The most common tree species in the primary forest are of the families Leguminosae, Lechthidaceae, Sapotaceae, and Burseraceae (Gascon and Bierregaard Jr. 2001). The forest canopy reaches 30-37 m high (Laurance *et al.* 2003). Species richness of trees ≥10 cm diameter at breast height (DBH) can be greater than 285 species per ha (de Oliveira and Mori 1999).

The matrices surrounding the fragments differ in their management history and current state. These differences are due to the fact that the felled forest surrounding some of the fragments was also burned for the creation of pasture, while other areas were solely felled. Furthermore, some areas have been maintained as pasture, while others have not (Plate 2). In areas that have not experienced burning, *Cecropia sciadophyela* (Cecropiaceae), a pioneer tree species, dominates the landscape. In the abandoned pasture areas, pioneer trees in the genera *Vismia* (Clusiaceae) and *Bellucia* (Melastomataceae) dominate (Bierregaard Jr. and Stouffer 1997).

Studies prior to and after fragmentation have provided a catalogue of changes in species distribution and loss (Lovejoy *et al.* 1986, Rylands and Keuroghlian 1988, Ferraz *et al.* 2003), forest composition and structure (Ferreira and Laurance 1997, Laurance *et al.* 1997, Nascimento *et al.* 2006), and microclimate (Kapos 1989, Murcia 1995).

BDFFP as a study site.—The BDFFP site was conducive to this research project in several ways. First, BDFFP is the longest-running study on tropical forest fragmentation, and thus forest fragments of various size classes are available and the flora within them are well documented. Due to the history of the BDFFP fragmentation, scientists have collected data both prior to and post fragmentation of the area, enabling analyses of the effects of deforestation (Lovejoy *et al.* 1986). In addition, more than 1,000 plant species have been tagged and identified in the fragments during the past several decades (Laurance *et al.* 1997). Furthermore, there is a documented history of the forest fragments during the past three decades, which allows for comparisons and identification of trends. Lastly, due to the presence of researchers in the forest fragments during the last three decades, the resident primate species were habituated to human presence.

History of primate research at BDFFP

Although research at BDFFP has been ongoing since 1979, primate research in the forest fragments has been sporadic. In depth behavioral and ecological research has been done only on red howler monkeys (Neves 1985, Neves and Rylands 1991, Gilbert 1994, 1997, Santamaría and Rylands 2003, Gómez 2004) and white-faced saki monkeys (Setz 1993, 1994, Setz *et al.* 1999) in BDFFP forest fragments (Table 2).

Prior to the isolation of the BDFFP fragments, primate censuses in the demarcated areas were conducted as a means to compare the species composition and densities pre- and post-fragmentation (Rylands and Keuroghlian 1988). That study evaluated one 100-ha fragment (#3304), four 10-ha fragments (#1202, #1207, #2206, and #3209), and continuous forest. There were no surveys of the 1-ha fragments. A study of the 10-ha fragments (#1202, #1207, #2206, #3209, and a linear, rectangular fragment near #1202) followed from October 1985 to March 1986 (Schwarzkopf and Rylands 1989). Later Gilbert (2003) conducted censuses intermittently from 1991 until 2001 in the four 1-ha fragments (#1104, #2107, #2108, and #3114), three 10-ha fragments (#1202, #2206, and #3209), two 100-ha fragments (#2303 and #3304), and continuous forest. The sample size differs in these studies because there was only one 100-ha fragment isolated at the time of the Rylands and Keuroghlian (1988) study, and the 10-ha fragment #1207 was never re-isolated after its initial isolation in

1983. The nine forest fragments from Gilbert’s study were used in this dissertation research.

The six primate species did not respond in the same manner upon initial isolation of the BDFFP forest fragments (Rylands and Keuroghlian 1988). Furthermore, since the 1980s, some primate species have re-colonized various forest fragments, while other species have remained extinct in the majority of the forest fragments.

Red howler monkey (Alouatta seniculus).—The red howler monkey is the second-largest primate species at BDFFP, with an average weight of 6.77 kg (Ford and Davis 1992). Group size averages 8.2 individuals in continuous forest, and average diet composition is 40% fruit and 48% leaves (Gaulin and Gaulin 1982, Sekulic 1982, Julliot 1996, Palacios and Rodriguez 2001). The species’ average home range size varies from 4-166 ha (Gaulin and Gaulin 1982, Sekulic 1982, Julliot 1996, Palacios and Rodriguez 2001), which is smaller than other Neotropical primates of similar body size (Crockett 1998). *Alouatta* is the most widespread Neotropical primate genus (Crockett and Eisenberg 1987), and overall it appears to withstand habitat fragmentation and habitat disturbance better than most other Neotropical primates (Crockett 1998, Ferrari *et al.* 2003, Gilbert 2003).

In the BDFFP reserves, red howler monkeys inhabit fragments in all three size classes (1 ha, 10 ha and 100 ha), and are found in the fragments more frequently than any other primate species (Gilbert and Setz 2001, Gilbert 2003).

Past research at BDFFP found that red howler monkeys living in 10-ha fragments have higher parasite loads than their continuous forest counterparts (Gilbert 1994), and that they contribute to seed dispersal in the forest fragments (Gómez 2004). Red howler monkeys remained in all of the original four 10-ha BDFFP fragments immediately upon the isolation of the forest fragments, and they have been continuously present in one of the 10-ha fragments (#1202) and both 100-ha fragments (#2306 and #3304) in 100% of the censuses conducted since the initial isolation of the forest fragments. This species was the most abundant primate species in terms of groups and individuals per square kilometer in the BDFFP continuous forest during the 1980s (Rylands and Keuroghlian 1988).

Black spider monkey (Ateles paniscus).—Black spider monkeys are the largest of the six primate species at BDFFP, with an average weight of 7.80 kg (Ford and Davis 1992). The species is highly frugivorous, as fruit comprises 89% of its diet (Mittermeier and van Roosmalen 1981, van Roosmalen 1985, Kinzey and Norconk 1990, Guillotin and Dubost 1994). Home range size averages 224 ha (van Roosmalen 1985, Symington 1988, Simmen 1992). Group size averages 14.3 individuals, although the groups do exhibit fission-fusion behavior throughout the day (van Roosmalen 1985, Norconk and Kinzey 1994, Simmen and Sabatier 1996).

There have been no behavioral studies of black spider monkeys in the BDFFP fragments during the past three decades, which is likely due to the species' rarity in the BDFFP forest fragments. Rylands and Keuroghlian (1988) documented the loss of black spider monkeys upon the isolation of 100-ha fragment #3304 in 1983, and the species was absent from all 10-ha fragments during the studies of Rylands and Keuroghlian (1988) and Schwarzkopf and Rylands (1989). Censuses in the early 1990s by Gilbert (2003) also noted the absence of black spider monkeys from all 10-ha fragments; however, in 1995 the species appeared in one of the four 10-ha fragments (#1202) for several censuses. Gilbert (2003) never recorded the presence of black spider monkeys in the two 100-ha fragments. Rylands and Keuroghlian (1988) found the density of black spider monkeys in the continuous forest at BDFFP to be low in comparison with other sites.

Brown capuchin monkey (Cebus apella).—The brown capuchin monkey is a medium-size neotropical primate, with an average body weight of 2.65 kg (Ford and Davis 1992). Group size averages 14.3 individuals (Peres 1993, Zhang 1995, Simmen and Sabatier 1996, Spironello 2001, Norconk *et al.* 2003). Its diet is highly omnivorous, with fruit comprising 65% of the total diet (Mittermeier and van Roosmalen 1981, Guillotin and Dubost 1994, Simmen and Sabatier 1996). Average home range size is 429 ha (Izawa 1980, Peres 1993, Zhang 1995, Spironello 2001), with Spironello (2001) calculating home range sizes of 852 ha in the continuous forest reserve of BDFFP.

Spironello (2001) studied brown capuchin monkeys in the BDFFP continuous forest; however, there have been no behavioral studies of the species in the forest fragments perhaps because brown capuchins did not persist in

BDFFP forest fragments smaller than 100 ha. Prior to my study, the species had never been spotted in either the 1-ha or the 10-ha fragments (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989, Gilbert 2003). Upon isolation of the Porto Alegre 100-ha fragment (#2303), a group of brown capuchin monkeys (11-12 individuals) remained in the fragment. The animals were seen regularly throughout 1983, but then they began leaving and re-entering the fragment during the early months of 1984, and disappeared from the surveys in late-June 1984 (Rylands and Keuroghlian 1988). Gilbert (2003) spotted brown capuchin monkeys intermittently in this same 100-ha forest fragment from 1991 until 2001, but they were never spotted during censuses in the Dimona 100-ha (#2303) fragment from 1991 until 2001. Rylands and Keuroghlian (1988) found the species' density to be lower in BDFFP continuous forest than in other areas of South America, even though the group size was similar between study sites.

*Northern bearded saki monkey (*Chiropotes sagulatus).—The northern bearded saki monkey is a medium-size monkey that weighs an average of 2.81 kg (Ford and Davis 1992). This species obtains approximately 88% of its diet from fruit, a majority of which is seed material (Ayres 1981, van Roosmalen *et al.* 1981, Kinzey and Norconk 1990). Average group size is 21.8 individuals (van Roosmalen *et al.* 1981, Kinzey and Norconk 1990, Norconk *et al.* 2003, Boyle *et al.* In press), and home range size averages 336 ha (Ayres 1981, van Roosmalen *et al.* 1981, Boyle *et al.* In press).

These data for *C. sagulatus* were based on data for *C. satanas chiropotes*, the previous taxonomic classification for the species. Taxonomic revisions and discrepancies continue, but these data are based on what some taxonomists consider the same species, and what other taxonomists consider the same subspecies.

Past research on the behavioral ecology of northern bearded saki monkeys at BDFFP has been limited to a yearlong study of a group in the continuous forest (Frazão 1991, 1992). The presence of bearded saki monkeys in the BDFFP fragments has been variable since the reserves were first isolated. The species left the forest fragments upon their isolation (Rylands and Keuroghlian 1988). Further censuses found bearded saki monkeys absent from the fragments until the mid-1990s when an adult male spent five months in one of the 10-ha fragments (#2206), and in 1995 when an adult male, adult female, and infant were spotted in another 10-ha fragment (#1202) during a period of two weeks (Gilbert and Setz 2001, Gilbert 2003). An adult male was present in one of the 10-ha BDFFP fragments (#1202) in 1997, and then later was joined by an adult female by 2001. Bearded saki monkeys have never been spotted in the third 10-ha fragment (#3206). The presence of the species in the two 100-ha BDFFP forest fragments (#2303 and #3303) was not noted until a census in 2000 (Gilbert 2003), and prior to 2003, bearded saki monkeys had never been spotted in any of the four 1-ha BDFFP fragments. Rylands and Keuroghlian (1988) found the overall density of northern bearded saki monkeys to be lower than most other studies of the species, but greater than that calculated by Ayres (1981).

White-faced saki monkey (Pithecia pithecia).—The white-faced saki monkey is the second-smallest primate species at BDFFP, with an average body weight of 1.68 kg (Ford and Davis 1992). Fruit comprises 86% of the species' diet, most of which is seed material (Kinzey and Norconk 1993, Norconk 1996, Hombug 1997). Group size averages 3.4 individuals (Oliveira *et al.* 1985, Lehman *et al.* 2001, Vié *et al.* 2001, Norconk *et al.* 2003). Home range size varies from 10 ha to 287 ha in continuous forest, though these estimates are from the only two existing publications of the species' home range size in non-island and non-fragmented habitats (Vié *et al.* 2001, Norconk *et al.* 2003). Both group size and home range size are smaller than those of northern bearded saki monkeys, another pitheciine seed predator living in the BDFFP study area.

Rylands and Keuroghlian (1988) found white-faced saki monkey densities in BDFFP continuous forest areas to be low in comparison with other sites in the Amazon, while Schwarzkopf and Rylands (1989) found a correlation between the presence of white-faced saki monkeys and structurally complex forested areas (e.g., abundant lianas and small trees, low numbers of trees with DBH greater than 10cm, and streams). Setz (1993) studied the feeding ecology of the species in a 10-ha fragment at BDFFP and noted seasonal differences in the species' diet. Although Schwarzkopf and Rylands (1989) found white-faced saki monkeys in only one of the 10-ha forest fragments (#2206) from October 1985-March

1986, Gilbert (2003) noticed their presence in each of the three 10-ha fragments and both 100-ha fragments during censuses from 1991-2001; however, the species was not consistently present in each of the 10-ha fragments.

Golden-handed tamarin monkey (Saguinus midas).—Golden-handed tamarin monkeys are the smallest of the six primate species at BDFFP, with an average body weight of 0.52 kg (Ford and Davis 1992). Fruit comprises 66% of its diet, while insects and plant exudates comprise a total of 31% of its diet (Mittermeier and van Roosmalen 1981, Oliveira and Ferrari 2000). Average group size is 5.7 individuals (Kessler 1995, Day and Elwood 1999, Oliveira and Ferrari 2000, Norconk *et al.* 2003), and average home range size is 33 ha (Kessler 1995, Day and Elwood 1999, Oliveira and Ferrari 2000).

There have been no behavioral studies of golden-handed tamarin monkeys in the BDFFP fragments. Past censuses found the species in fragments of 10 ha and 100 ha (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989, Gilbert 2003). The species has never been documented as residents of any of the four 1-ha fragments. Gilbert (2003) noted their presence on the periphery and adjacent secondary growth of the 1-ha fragment of Colosso (#1104), but was unable to determine whether the animals were residents of the forest fragment. Upon isolation of the Porto Alegre 100 ha fragment (#3304), there were four groups of golden-handed tamarin monkeys present; however, there were frequent disputes between two of the groups, and after August 1983 only three groups remained in the forest fragment (Rylands and Keuroghlian 1988).

Rylands and Keuroghlian (1988) found densities of golden-handed tamarin monkeys in BDFFP continuous forest to be lower than densities of the species in Guyana and Suriname.

DISCUSSION

Importance of forest fragmentation research in Brazil

The study of tropical forest fragmentation is important for several reasons. First, tropical forests are home to an estimated 50-90% of the Earth's plant and animal species (WRI 1990). Second, it is estimated that scientists have identified only 10% of the Tropic's extant species. Discoveries of new species continue. For instance, since 1990, ten new species of monkey have been recognized in the Brazilian Amazon (Peres 2005). Third, tropical forest fragmentation (moreover tropical ecology overall) is underrepresented in the scientific literature in comparison to temperate zone research. Therefore, more research on tropical forest fragmentation is required if we are to understand its ecological effects.

Brazil is the fifth largest country worldwide, and the largest tropical country (Brandon *et al.* 2005). Its total biota is estimated to be at 1.8 million species (Lewinsohn and Prado 2005); however, there are still many areas of Brazil that have not been adequately sampled (Peres 2005).

Purpose and outline of this study

This study evaluates the effects of forest fragmentation on a primate community by examining the distribution and persistence of six primate species across a fragmented landscape, and the effects of forest fragmentation on the behavioral ecology of one of those six primate species, the northern bearded saki monkey, *Chiropotes sagulatus*. The purpose for examining the primates on both community and species levels is twofold. First, the community study allowed me to examine how forest fragmentation affects primates on a large scale, which allowed me to make comparisons between different primates species' responses to disturbance, and identify general trends in primate distribution. Second, it allowed me to examine the effects of forest fragmentation in greater detail by quantifying differences in bearded saki monkey behavior and social structure in continuous versus fragmented forest.

This dissertation consists of five chapters. This first chapter, "Forest Fragmentation and Primate Populations in the Brazilian Amazon," presents a review of the forest fragmentation literature and the associated theories that accompany such research. Furthermore, it provides the history and basic findings of the Biological Dynamics of Forest Fragments Project (BDFFP), the area in which this research was conducted.

The second chapter, "Distribution and Persistence of Six Primate Species Across a Fragmented Landscape in the Brazilian Amazon," presents the results from the primate community study. I investigated patterns of presence and persistence of the six primate species located in the BDFFP study area. The responses of the six species to fragmentation varied greatly; however, neither body weight, nor home range size, nor degree of frugivory were predictors of a species' presence in the forest fragments. Results also suggested that forest fragment size and the distance of the forest fragment to the nearest forested area greater than 0.5 ha affected primate species richness. Furthermore, the proportion of old secondary growth in the matrix may have played some role in primate species richness. Overall, there was a decrease in old growth forest and an increase in secondary growth forest from 1984 to 2006, and there has been recent colonization of some of the forest fragments by species that had never been present previously.

The third chapter, “Effects of Forest Fragmentation on the Social and Feeding Ecology of the Northern Bearded Saki Monkey (*Chiroptoes sagulatus*),” examines how forest fragmentation affects the social groupings, foraging behavior, and diet of the northern bearded saki monkey. Differences in group size existed between bearded saki monkeys living in continuous forest and fragments. There was no difference among the bearded saki groups in the proportion of time spent eating and the proportion of fruit in the diet, but there was little overlap in dietary species composition among the monkey groups. Although the bearded saki diet in forest fragments was limited to plant species present in the fragment, the monkeys did not consume all species of available fruit, and they chose certain preferred taxa.

The fourth chapter, “Spatial Use of Forest Fragments by Northern Bearded Saki Monkeys (*Chiropotes sagulatus*) in the Brazilian Amazon,” investigates how forest fragmentation affects the spatial movement and spatial use patterns of the northern bearded saki monkey. Results indicated that in forest fragments this species occupies smaller home ranges, travels shorter daily distances, and travels in more circular and repetitive routes than those animals living in continuous forest. Furthermore, bearded saki monkeys did not use all areas of available habitat within the forest fragments; therefore, a 100-ha fragment may not provide 100 ha of suitable habitat for the species.

The fifth chapter, “Implications for Primate Conservation in Central Amazonia” provides a review of the current state of conservation in the Brazilian Amazon, and details how a federal colonization plan would have ecological, economical, and sociological effects. This concluding chapter ends with suggestions for future management of the Amazon Basin, while stressing the need for continued research in the tropics.

Conclusions

Therefore, this dissertation research not only contributes to the fragmentation literature, but it was the first study at BDFFP to examine the behavioral ecology of the northern bearded saki monkeys living in forest fragments. Furthermore, the compilation of this study’s primate community data with those of Rylands and Keuroghlian (1988), Schwarzkopf and Rylands (1989) and Gilbert (2003) provides nearly three decades of primate census data. I used these data to summarize the current status of the resident primate populations, to document any patterns of primate immigrations and extinctions that had arisen during this period, and to relate the presence or absence of the species to predictive variables such as fragment size and degree of isolation. The use of satellite imagery also allowed me to compare fluctuations in land cover status of the BDFFP study area with primate presence in these forest fragments.

This study also provides important information on the northern bearded saki monkey, as there are few studies of this species (as well as other species of *Chiropotes*) in either continuous forest or fragmented forest elsewhere in the tropics. Additional knowledge about *Chiropotes*' responses to forest fragmentation is important, as it is unusual in its behavioral ecology as a seed predator with large home ranges and large social groups. Prior publications have remarked that bearded sakis (*Chiropotes* spp.) are not able to withstand forest fragmentation (Rylands and Keuroghlian 1988, Gilbert and Setz 2001); however, northern bearded saki monkeys were permanent residents of two 10-ha BDFFP forest fragments for the duration of my 18-month study, and they frequently entered and left both 100-ha forest fragments. Therefore, this was a unique opportunity to document the means by which this species altered its behavioral ecology in forest fragments. Increased knowledge of the northern bearded saki monkey's response to forest fragmentation can be compared with other primate species' behavioral responses to determine on a wide taxonomic level whether certain morphological and behavioral characteristics increase a species' vulnerability to forest fragmentation.

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TABLE 1. Forest fragment history at the Biological Dynamics of Forest Fragments Project (BDFFP).

ID	Ranch	Area (ha)	Size class (ha)	Isolation year	Isolation by fire
1104	Esteio	2.8	1	1980	Yes
2107	Dimona	1.8	1	1984	Yes
2108	Dimona	1.1	1	1984	Yes
3114	Porto Alegre	1.6	1	1983	No
1202	Esteio	13.7	10	1980	Yes
2206	Dimona	14.0	10	1984	Yes
3209	Porto Alegre	11	10	1983	No
2303	Dimona	98.1	100	1990	Yes
3304	Porto Alegre	101.2	100	1983	No
3402	Cabo Frio	Continuous	Continuous	n/a	n/a
1501	KM 41	Continuous	Continuous	n/a	n/a

Notes: Fire isolation data were provided by Bierregaard and Stouffer (1997).

TABLE 2. Primate behavior and ecology research at BDFFP.

Species	Study area	Publications
Alouatta seniculus	Continuous Forest	Santamaría and Rylands 2003
	Forest Fragments	Neves 1985, Neves and Rylands 1991, Gilbert 1994, 1997, Gómez 2004
Ateles paniscus	Continuous Forest	None
	Forest Fragments	None
Cebus apella	Continuous Forest	Spironello 2001
	Forest Fragments	None
Chiropotes sagulatus	Continuous Forest	Frazão 1991, 1992
	Forest Fragments	Boyle *et al.* In press
Pithecia pithecia	Continuous Forest	None
	Forest Fragments	Setz 1993, 1994, Setz *et al.* 1999
Saguinus midas	Continuous Forest	None
	Forest Fragments	None

Notes: Continuous forest studies were conducted entirely in the continuous forest. Forest fragment studies were conducted either entirely in the forest fragments or in forest fragments and continuous forest.

FIG. 1. Map of the Amazon Basin. The Amazon Basin in South America is 8.15 x 10^8 ha, and is comprised of areas of Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Suriname, and French Guiana. Approximately 50% of the Basin is located in Brazil.


Venezuela
Guyana
Suriname
French Guiana
Colombia
Ecuador
Brazil
Peru
Bolivia

FIG. 2. Forest fragmentation. As forested area is cleared with time, forest patches retain surrounded by a matrix of cleared land. Forest patches vary in size, shape, edge-to-area ratio, and distance to the nearest forested area. Dark areas represent forest, and white areas represent the matrix.

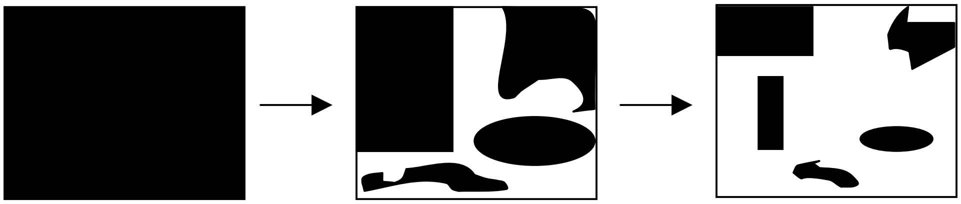

FIG. 3. BDFFP location. The Biological Dynamics of Forest Fragments Project (BDFFP) is located approximately 80 km north of Manaus, the capital of the state of Amazonas. Forest fragments are located throughout three cattle ranches, or *fazendas*, Dimona, Esteio, and Porto Alegre. Cabo Frio and Km 41 were the locations of my continuous forest sites. Fragments are black, clear-cut areas and secondary forest areas are white, and old growth forest is gray.

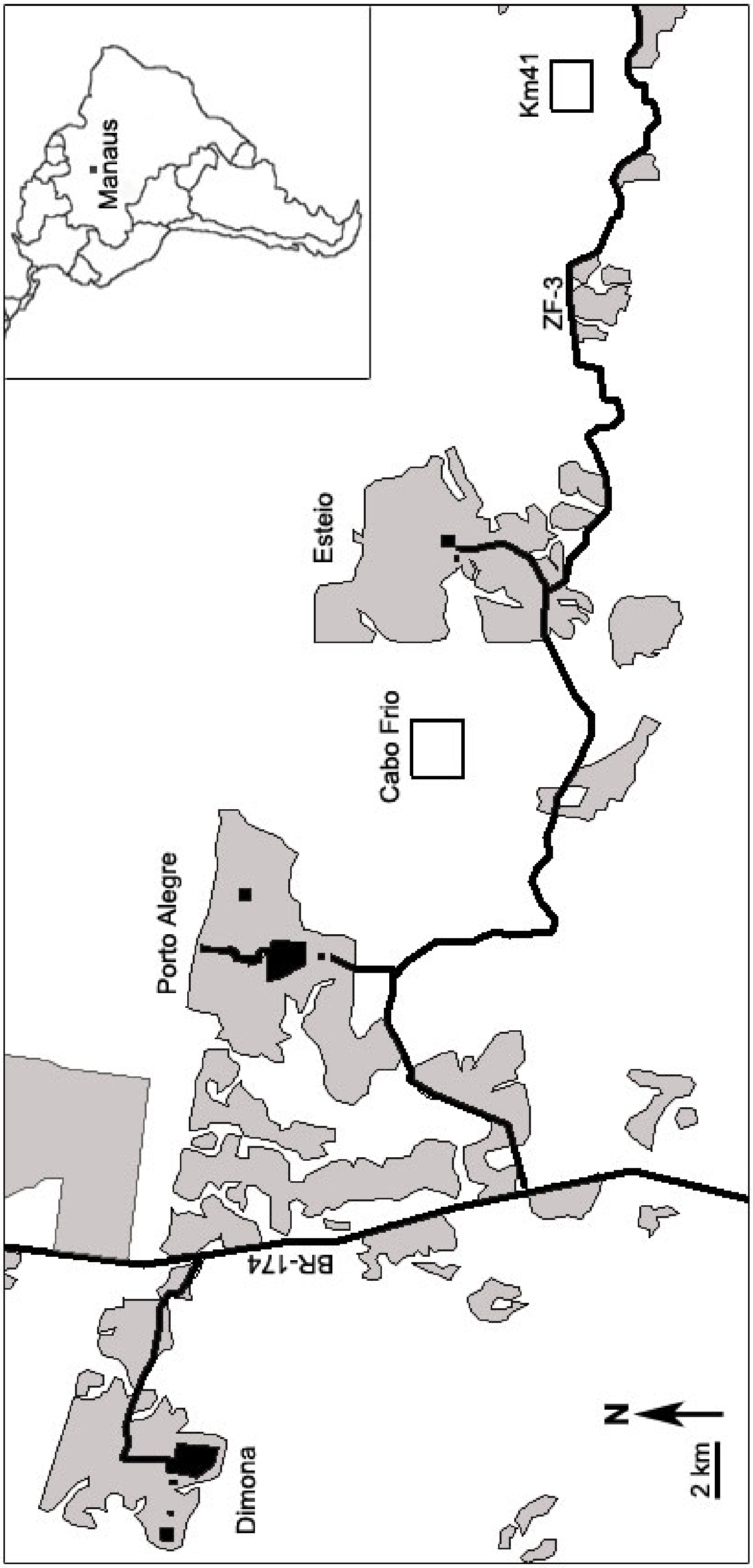
Manaus
Km41
ZF-3
Esteio
Cabo Frio
Porto Alegre
BR-174
Dimona
N
2 km

FIG. 4. Deforestation along the BR-174. Landsat ETM+ satellite imagery from 2006 shows the pattern of deforestation along, and spreading outward from, the BR-174 highway. The BR-174 extends north from Manaus to Venezuela, and passes through the Biological Dynamics of Forest Fragments (BDFFP) study area. The map represents forest (gray), cleared areas (white), and water (black).

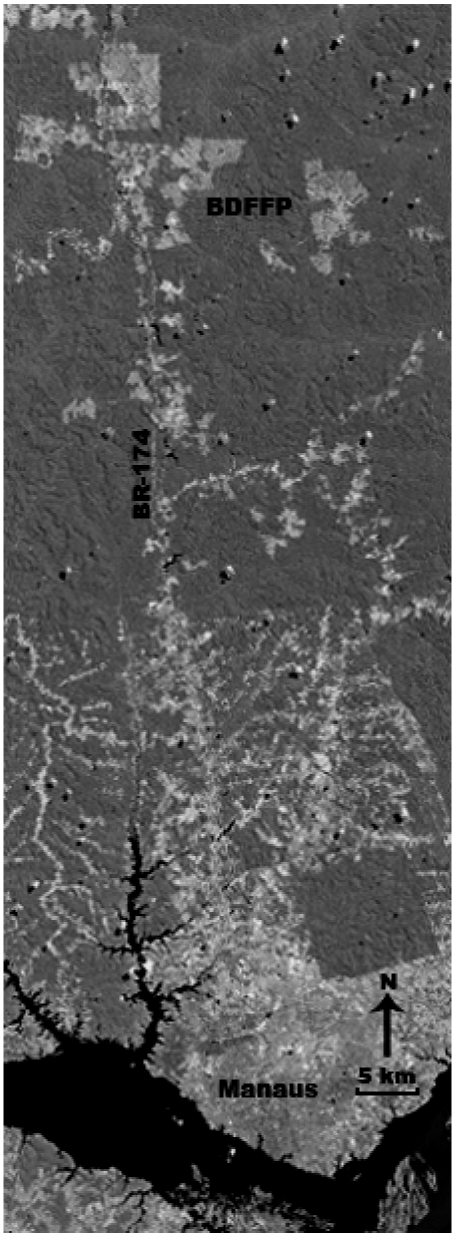
BDFFP
BR-174
N
5 km
Manaus

FIG. 5. Average monthly precipitation (January 2005 – June 2006). Average monthly precipitation was 249 mm, with a pronounced dry season from June until October (determined by averaging precipitation readings at five collection points throughout the BDFFP study area).

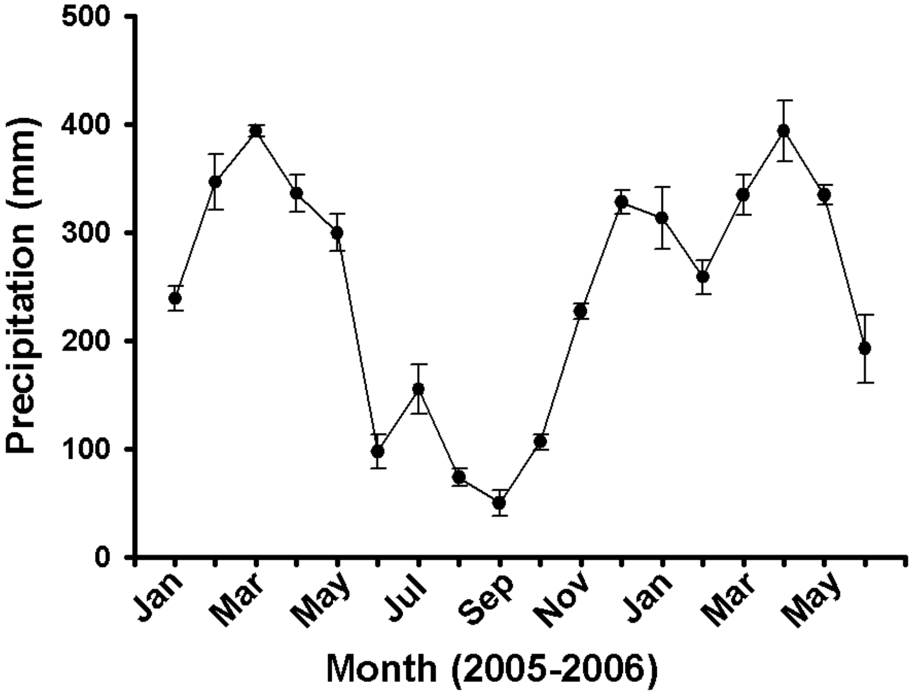
500
400
300
200
100
0
Precipitation (mm)
Jan
Mar
May
Jul
Sep
Nov
Jan
Mar
May
Month (2005-2006)

Plate 1. Isolation of the forest fragments at BDFFP. Isolation of the forest fragments began in 1980. (A) Areas around the demarcated forest fragments were cleared of vegetation (Dimona 1-ha Fragment #2108). (B)The forest clearing resulted in isolated forest fragments (Dimona 1-ha and 10-ha Fragments #2108 and #2206). Photo credits: R. Bierregaard, Jr.

(A)

(B)

PLATE 2. Northwest border of 100-ha fragment #3304. The northwest border of 100-ha fragment #3304 illustrates the edge between the border of the forest fragment and a matrix of high pasture (approximately 30 cm tall). Photo credit: S. Boyle.

CHAPTER 2

DISTRIBUTION AND PERSISTENCE OF SIX PRIMATE SPECIES ACROSS A FRAGMENTED LANDSCAPE IN THE BRAZILIAN AMAZON

Abstract. Forest fragmentation, arising from deforestation, is a worldwide conservation concern; however, species do not respond to habitat fragmentation in the same manner. At the Biological Dynamics of Forest Fragments Project (BDFFP) study area, located 80 km north of Manaus, Amazonas, Brazil, forest fragmentation has affected the distribution and persistence of the six local primate species since the isolation of the study's fragments in the 1980s. Some species, such as the black spider monkey (*Ateles paniscus*), have been extremely sensitive to habitat fragmentation, while other species, such as the red howler monkey (*Alouatta seniculus*), have inhabited forest fragments as small as 1 ha. Northern bearded saki monkeys (*Chiropotes sagulatus*) have colonized several of the fragments since 2001, golden-handed tamarin monkeys (*Saguinus midas*) and white-faced saki monkeys (*Pithecia pithecia*) have regularly used fragments of 10 ha and 100 ha, and brown capuchin monkeys (*Cebus apella*) have been primarily restricted to the 100 ha fragments. Step-wise multiple regression models were ran to test 1) whether characteristics of a fragment and 2) whether characteristics of a primate species could predict the presence of primate species in the BDFFP fragments. The six species did not follow simple patterns in terms of their presence in the fragments; body size, home range size, and degree of frugivory were not found to be predictors of a species' presence in a forest fragment. A forest fragment's size, distance to nearest forested area >0.50 ha, and the proportion of the matrix comprised of old

secondary growth forest predicted primate species richness in the fragments; however, these relationship were not straightforward because two variables (size and distance to nearest forest patch) were strongly correlated. Furthermore, the extent to which the individual primate species traveled in and out of the fragments varied, suggesting that species' tendencies to cross open areas are not identical. It is important to consider the array of species' responses to a fragmented landscape, particularly when predicting the viability of a species with particular behavioral and ecological characteristics. Further studies are needed, especially studies that examine the extent of the primates' use of the secondary growth matrix. Such knowledge would be invaluable with respect to both landscape and species management in central Amazonia.

INTRODUCTION

Forest fragmentation is one of the main threats to the conservation of species worldwide (Gascon *et al.* 2001, Tabarelli and Gascon 2005) including both vertebrate and invertebrate species (Didham *et al.* 1996, Nupp and Swihart 2000, Kurosawa and Askins 2003). However, the responses of taxa to forest fragmentation vary, as some species respond positively while others become locally extinct (Skorupa 1986, Johns and Skorupa 1987, Malcolm 1995, Gascon and Lovejoy 1998, Tscharntke *et al.* 2002, Ferraz *et al.* 2003).

Island biogeography theory (MacArthur and Wilson 1967) was traditionally invoked to explain species richness in forest fragments by examining the relationship between the size of a forest fragment "island" and its distance from “mainland” intact forest (Gascon and Lovejoy 1998, Cook *et al.* 2002, Haila 2002). While these patterns oftentimes hold (Diamond 1975, Sierra 2000), they do not take into account the matrix surrounding the forest fragments (Gascon and Lovejoy 1998, McIntyre and Hobbs 1999, Cook *et al.* 2002, Debinski 2006, Kupfer *et al.* 2006), habitat degradation by edge effects (Laurance 1991b), or succession (Lovejoy and Oren 1981). Furthermore, this theory deals solely with species richness (defined as the number of species present), not with the presence (or loss) of individual species and the interactions between them (Kattan and Murcia 2003).

The following factors have been shown to influence a species’ response to the fragmentation of its habitat: diet (Skorupa 1986, Johns and Skorupa 1987, Sussman 1999), home range size (Skorupa 1986, Bierregaard Jr. *et al.* 1992, Dale *et al.* 1994, Gascon and Lovejoy 1998), degree of behavioral plasticity (Estrada and Coates-Estrada 1988, Horwich 1998, Sussman 1999, Clarke *et al.* 2002), specialized habitat requirements (Dale *et al.* 1994, Heydon and Bulloh 1997, Gascon and Lovejoy 1998), and the ability to cross gaps (Dale *et al.* 1994).

Diet, home range, and behavioral plasticity

Fruit distribution and abundance are major factors in determining the size and complexity of a frugivore community (Dumont 2003), and the resources that support and sustain frugivores during periods of resource scarcity appear to determine the carrying capacity of the community (Terborgh 1986).

Primates vary in diet composition and specialization, and larger-bodied, frugivorous primates typically require large home ranges (Clutton-Brock and Harvey 1977, Harvey and Clutton-Brock 1981, Johns and Skorupa 1987, Onderdonk and Chapman 2000). Skorupa (1986) found that large home ranges and a high proportion of fruit, seeds, and flowers in the diet were associated with poor species survival in African rainforest primates subjected to forest fragmentation. While diet may be a primary factor in a species' survival in *some* studies, a species' degree of frugivory and its presence within forest fragments are not always correlated (Johns and Skorupa 1987, Estrada and Coates-Estrada 1996, Onderdonk and Chapman 2000, Marsh *et al.* 2003). Therefore, further data are necessary to determine whether a more complex pattern exists between diet specialization and survival in fragmented habitats.

The degree of behavioral plasticity that a species exhibits can influence its survival, particularly when resources are scarce. When portions of their home range are deforested, frugivorous-folivorous howler monkeys (*Alouatta* spp.) demonstrate flexibility and adaptability in their feeding strategies (e.g., consume more leaves in forest fragments, consume a variety of plant species), social behavior (e.g., live in smaller social groups), and travel patterns (e.g., occupy smaller home ranges) when portions of their home range are deforested (Estrada and Coates-Estrada 1988, Horwich 1998, Clarke *et al.* 2002, Bicca-Marques 2003). It is thought that this dietary flexibility allows *Alouatta* to exploit a variety of habitats (Sussman 1999).

Specialized habitat and gap-crossing ability

Species that require a specialized habitat for survival are oftentimes more sensitive to forest fragmentation, as the specialized habitat may be destroyed or rendered inaccessible (Dale *et al.* 1994). Such habitat accessibility also relies on the species' ability to cross the matrix surrounding the forest fragments. This matrix is an important factor in the species composition of the fragments (Gascon and Lovejoy 1998, Gascon *et al.* 1999, Tscharntke *et al.* 2002, Brotons *et al.* 2003). Gascon *et al.* (1999) found that the variability among matrix habitats in supporting vertebrate forest species is often related to the history and land-use of the matrix. Thus, if the surrounding matrix consists of pasture, there may be fewer species able to survive in the pasture environment or use it as a corridor to other fragments than if the matrix consisted of secondary forest that provided at least some food resources, shelter, and protection from predators and sun. Matrix attributes such as configuration around the patches, conditions, and connectivity can be a driving force in determining the overall effects of forest fragmentation (Gascon and Lovejoy 1998).

Purpose of this study

To date there is no consensus as to which factors are primarily responsible for influencing a species' response to forest fragmentation

(Harrison and Bruna 1999, Debinski and Holt 2000, Kattan and Murcia 2003). Therefore, the purposes of this study were to (1) document the distribution and persistence of a primate community in a fragmented landscape and determine which species are a high-priority conservation concern; (2) document changes in the matrix's land cover since the initial isolation of the forest fragments in this study, nearly three decades ago; and (3) determine whether it is possible to categorize a species' vulnerability to forest fragmentation by testing variables related to the landscape (i.e., forest fragment size and isolation, matrix land cover) and the species' life history and behavioral ecology (i.e., body size, home range size, diet, diet flexibility).

I predicted that species with large bodies, large home range sizes, and highly frugivorous diets would be not be present in the forest fragments, while species with small bodies, small home ranges, and highly folivorous or insectivorous diets would be present in the forest fragments to a greater extent. I also predicted that fragments that were larger and closer to continuous forest would have greater species richness than smaller fragments farther from continuous forest. Furthermore, I predicted that the matrix surrounding the forest fragments would not be uniform for all forest fragments, and that forest fragments surrounded by a matrix comprised of tall secondary forest (defined as trees that were tall and sturdy enough to provide arboreal travel routes for the monkeys) would have greater species richness than forests surrounded by pasture.

METHODS

Study site

I conducted this study at the Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km north of Manaus, Brazil (2°30'S, 60°W). BDFFP is the site of a long-term project on fragmentation, facilitated by the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil. The forest fragments, which are categorized into size classes of 1, 10 and 100 ha, were initially isolated from the continuous forest by distances of 70-1000 m (Laurance *et al.* 2006b). Gascon and Bierregaard, Jr. (2001) provide a detailed history of BDFFP.

The study site is classified as tropical moist *terra firme* forest (Gascon and Bierregaard Jr. 2001). It receives 1900-3500 mm of rain annually, and there is a dry season between June and October (Laurance 2001). Mean annual temperature for Manaus is 26.7°C (with monthly mean fluctuations of 2°C), maximum temperature ranges from 35-39°C, and minimum temperature ranges from 19-21°C (de Oliveira and Mori 1999).

I studied four 1-ha fragments, three 10-ha fragments, and two 100-ha fragments located within the *fazendas* (ranches) of Esteio, Dimona, and Porto Alegre. These nine fragments vary in size, distance to continuous forest, and condition of the surrounding matrix.

Six primate species range in the BDFFP study area: red howler monkey (*Alouatta seniculus*), black spider monkey (*Ateles paniscus*), brown capuchin monkey (*Cebus apella*), northern bearded saki monkey (*Chiropotes sagulatus*), white-faced saki monkey (*Pithecia pithecia*), and golden-handed tamarin monkey (*Saguinus midas*). The six species vary in body size, home range size, and diet (Table 3). The appeal of studying these six primate species is that they are diurnal, social vertebrates that have varied histories at BDFFP. Average body size ranges from 0.52 kg in the golden-handed tamarin monkey to 7.8 kg in the black spider monkey (Ford and Davis 1992).

Currently there are uncertainties regarding taxonomy in the genus *Chiropotes*, with the number of species ranging from two to six (Hershkovitz 1985, Silva and Figueiredo 2002, Bonvincino *et al.* 2003). Prior to the recent taxonomic revision, the species found at BDFFP was considered *C. satanas chiropotes*. In this study I follow the taxonomy proposed by Silva and Figueiredo (2002), and use the designation *C. sagulatus* because it is the taxonomy most accepted by researchers who study *Chiropotes*.

Primate community data collection

I collected data from July-August 2003, and from January 2005-April 2006. I surveyed nine forest fragments at the Dimona, Esteio and Porto Alegre ranches—four 1-ha (#1104, #2107, #2108, and #3114), three 10-ha (#1202, #2206, and #3209), and two 100-ha fragments (#2303 and #3304)—and two areas of continuous forest. I conducted census cycles in each of the forest areas once in 2003, four times in 2005 and once in 2006 in order to account for annual and seasonal fluctuations in primate presence and resource abundance.

Each census cycle lasted approximately 2.5 months. The durations of the cycles were as follows: January-March 2005 (Cycle 1), April-June 2005 (Cycle 2), August-October 2005 (Cycle 3), October-December 2005 (Cycle 4), January-March 2005 (Cycle 5). Data collection was conducted in April 2006 for a sixth cycle of the 10-ha fragment #1202, as part of the study on northern bearded saki monkey behavioral ecology. Comparisons were made between the cycles in order to determine seasonal differences in fruit abundance and primate species richness.

On the first day in each study area I conducted a primate census by walking line transects along already established trails, following the methods of Rylands and Keuroghlian (1988) and Gilbert (2003). If northern bearded saki monkeys were present during this census, I spent the next three days following these monkeys as part of a separate behavioral study (see Chapters 3 and 4). Each primate census was conducted by a trained field assistant and myself. Two parallel trails were walked (one person on each trail). The censuses began at approximately 0630 because the monkeys were most active during the morning hours. Therefore, it was easier to visually spot and hear movements by the monkeys during their active time than during the afternoon when there was less activity. Due to the regular presence of BDFFP researchers at the study sites throughout the past three decades, the primates were habituated to humans. All six species were located in the continuous forest. Therefore, differences in observability among primate species were minimized as much as possible. The total census time and distance covered for each full data collection cycle (2003: *n*=1; 2005: *n*=4; 2006: *n*=1) was 45 hr and 33.3 km, for a total of 253 hr and 195.2 km walked.

Upon locating a primate group, I recorded the primate species, its group size and composition by sex and age (adult, juvenile, and infant) when possible, and the group's geographic location using a handheld Global Positioning System (GPS) receiver (Garmin GPS III® Plus in 2003 and Garmin GPS V® in 2005 and 2006). I did not use group size and composition in the data analysis in this chapter because it was not always possible to record all members of the group upon the initial sighting of the monkeys. I also noted the presence of primate species in the forest fragments *ad libitum* while collecting data for the study on northern bearded saki monkeys (see Chapters 3 and 4). This second study provided an additional 1,186 hr in the field, during which time *ad libitum* primate sightings were recorded. These *ad libitum* data were separated from the census data during analyses in order to avoid detection biases.

I plotted the location of each primate sighting on a map in ArcView 3.3 (Environmental Systems Research Initiatives, Inc., Redlands, California, USA). By categorizing each sighting by location, time of sighting, and group size, I was able to determine the spatial distribution of the primate groups temporally.

I also combined my census data from 2003, 2005, and 2006 with previous BDFFP census results (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989, Gilbert 2003) in order to determine overall patterns in the distribution and re-colonization of the primates in the forest fragments during the past three decades.

I classified each of the six species by body size, diet, and home range size using findings from published literature. I only used data from studies of the species in continuous habitat, except in the case of white-faced saki monkeys. Data on this species included studies of translocated groups and animals isolated on islands since the behavioral ecology of white-faced saki monkeys is poorly understood and there were no other published data (Norconk 2006). I averaged data from all studies for each species, and scored the six species based on the variables of body weight, group size, home range size, daily distance traveled, and percent frugivory.

Phenological data collection

During each study cycle in 2005 (*n*=4) and 2006 (*n*=1) I collected phenological data in order to account for seasonal changes in fruit and flower abundance and diversity. I collected these data by identifying and counting the trees, lianas, and hemiepiphytes with fruits and/or flowers along two parallel transects that bisected each of the 1-ha and 10-ha forest fragments. Each transect was approximately 10 m wide. Distance between transects was approximately 70 m in the 10-ha fragments and 10 m in the 1-ha fragments. In the 100-ha fragments. I collected data along one long, linear transect instead of two due to the length (1000 m) of one transect. Phenology censuses were conducted along linear transects in order to account for plant species found both near and far from the forest edge. For comparison with the fragment surveys, I also demarcated 1-ha, 10-ha, and 100-ha study plots in the two continuous forest study areas. Within each plot I walked linear transects that were equivalent in size and distance to their forest fragment counterparts. There were a total of 75 phenology censuses conducted. In this chapter the data for the 1-ha, 10-ha, and 100-ha plots in the continuous forest were combined for one value (number of fruiting plants per 100 m) for each of the two continuous forest sites.

For each fruit and flower sighting along the transect, I classified the fruit state as ripe or unripe, classified the flower state as bud or open flower, recorded the GPS location of the tree, liana, or hemiepiphyte, measured the diameter at breast height (DBH) of each tree, and photographed each fruit or flower sample. I tallied the fruit abundance per 100 m for each transect (noted as the number of trees, lianas, and hemiepiphytes with fruit) during each of the five cycles to provide comparisons of seasonal fluctuations in fruit abundance. I then divided the cycle data into monthly averages in order to see the fruit fluctuations at a finer scale, as each cycle lasted for approximately 2.5 months. Flower abundance was recorded and tallied in the same manner as fruit abundance shown above.

Fragment data collection

I categorized the matrix surrounding each forest fragment by walking the perimeter of each of the forest fragments and categorizing the matrix at each forest edge as new clear-cut (barren ground), old clear-cut (pasture; height less than 10 cm), low secondary growth (height between 10 cm and 30 cm), medium secondary growth (height between 31 cm and 150 cm), tall secondary growth (height greater than 150 cm), and old growth forest. Each edge habitat was photographed and described to the fullest extent possible. It was possible to categorize the matrix for each side of a forest fragment because overall the manner in which a side of a forest fragment was isolated was consistent along the entire edge. Any changes in matrix composition along one side of a fragment were noted. These data were used to verify the classification data provided by the analysis of the satellite images (see below).

I then classified the matrix type by the use of three Landsat Thematic Mapper (TM) and one Landsat Enhanced Thematic Mapper (ETM+) satellite images (path 231, row 62) that spanned 22 years (June 1984, July 1992, July 2001, and June 2006). I chose cloud-free images taken during the dry season in order to minimize differences in vegetative cover due to phenological conditions. Images were geometrically and atmospherically corrected and rectified (Lu *et al.* 2002). I used Erdas Imagine 9.1 software (Leica Geosystems 2005) to perform supervised classifications on the four images using the bands 5, 4, and 1. I classified the land cover in the entire landscape, defined by the extent of the study area (210,000 ha). The land cover classes were old-growth forest, old secondary growth, medium secondary growth, new secondary growth, old clear-cut, and new clear-cut. These classes were used for comparisons between the 2006 satellite image and primate species richness data from 2005 and 2006, as I was able to compare the satellite classes with the findings from my research on the ground. Since it was not possible to go back in time and compare ground data and satellite data from 1984, 1992, and 2001, I combined the six land cover classes into three land-cover categories (old-growth forest, secondary growth, and clear-cut) for general analyses of the landscape in order to view overall patterns during a period of 22 years.

In order to describe the immediate surroundings of the forest fragments, I drew a 500-m buffer around each of the nine forest fragments and calculated the land cover percentiles of the buffer. Since areas of continuous forest and other forest fragments were often included in the buffer's area, I also determined the land cover characteristics for the matrix itself by excluding all old-growth forest areas of six pixels (0.54 ha) or larger. I defined forest patch as an area greater than or equal to six contiguous pixels because this was the minimum size of old-growth forest in the four fragments of the 1-ha size class from 1984 to 2006, and 0.50 ha was previously used to define a forest fragment in Mandujano *et al.* (2005).

I scored the degree of isolation of each of the forest fragments using four different criteria: shortest distance from fragment edge to continuous forest, shortest distance from fragment edge to a forested area of six pixels in area or greater (e.g., forest fragment or continuous forest), proportion of buffer area that was old-growth forest, and proportion of matrix that was old secondary growth. I measured the proportion of old secondary growth because a matrix of clear-cut area and a matrix of old secondary forest provide different degrees of isolation for the species inhabiting the forest fragments.

I combined my field and satellite data with BDFFP records (Bierregaard Jr. and Stouffer 1997, Gascon and Bierregaard Jr. 2001, Stouffer and Borges 2001) of the isolation and re-isolation history of each of the forest fragments in order to determine the age, history, and characteristics of the matrix.

Analysis

I analyzed the overall difference in primate distribution in the nine forest fragments from 2003-2006 using a Chi-Square Test, tallying the number of censuses (out of 46) that each species (n=6) had been spotted. Note in the subsequent analyses that “forest size class” refers to analysis of continuous forest, 100-ha, 10-ha, and 1-ha forest fragments, while “fragment size” refers to analysis of forest fragments, without data from continuous forest. I tested the effect of forest size class (continuous: n=2; 100 ha: n=2; 10 ha: n=3; 1 ha: n=4) and cycle (2003: n=1; 2005: n=4; 2006: n=1) on primate species richness using two-way analysis of variance (ANOVA), with a between-subjects variable of forest size class and a within-subject variable of cycle. I performed post-hoc one-way ANOVAs for significant effects in order to perform subsequent post hoc tests using a Student's *t* test, as standard post hoc tests were not possible with repeated-measures analysis. I also tested the effect of forest size class and cycle on fruit abundance (defined as the number of plants with fruit per 100 m) using two-way ANOVA, with forest size class as the between-subjects variable and cycle as the within-subject variable. Post-hoc tests were performed as above. I then tested the effect of forest size class and cycle on flower abundance (defined as the number of plants with flowers per 100 m) using the same statistical method as in the fruit abundance.

I examined total species richness from 1981 to 2006 across forest size classes using two-way ANOVA, with year as a within-subject's variable and size class as a between-subjects variable. Post-hoc comparisons were conducted as above.

I used my data from the classified satellite imagery to analyze land cover change in the buffer areas and matrices from 1984 to 2006 by performing a multivariate analysis of variance (MANCOVA), examining the effects of fragment size and year on the three land cover classes (i.e., old growth, secondary growth, and clear cut). These data were $\log_{10}$-transformed in order to meet normality assumptions.

To determine which factors predicted primate species richness, I examined attributes of the forest fragment (i.e., distance to forest patch greater than 0.50 ha, distance to continuous forest, proportion of the buffer that was old growth forest, proportion of the matrix that was clear cut, proportion of the matrix that was medium secondary growth, proportion of the matrix that was old secondary growth, and the $\log_{10}$-transformed size of the forest fragment) by running a stepwise multiple regression with forward entry of variables. I used $P=0.10$ for entry into the model, and $P=0.05$ as the limit to leave the variable in the model. Since the size of the forest fragment was correlated ($r=-0.81$, $n=9$, $P=0.0087$) to the distance to nearest forest patch greater than 0.50 ha (Fig. 6), I could not simultaneously include both variables in the analysis and therefore ran the multiple regression once without forest size (Model A) and once without distance to nearest forest patch (Model B), thereby generating two separate models.

I determined to what extent characteristics of the primate species (i.e., body weight, home range size, degree of frugivory) were predictive of their presence in the forest fragments by conducting a multiple regression analysis as above.

RESULTS

Primates (2003-2006)

The six primate species were not uniformly distributed across all nine forest fragments during the six full cycles of primate censuses ($\chi^2=41.93$, df=5, $P<0.001$), or when *ad libitum* data ($\chi^2=31.54$, df=5, $P<0.001$) were included for data collected in 2003, 2005, and 2006. Species richness was lowest in the smaller forest size classes during the censuses ($F_{3,7}$=106.90, P<0.0001; Fig. 7A), but neither cycle ($F_{4,4}$=2.09, P=0.25) nor the interaction between forest size class and cycle ($F_{12,11}$=1.56, P=0.24) affected primate species richness. This pattern of decreased primate richness with decreased forest size class held when I included *ad libitum* data ($F_{3,7}$=46.25, P<0.0001). In both datasets primate species richness was not significantly different between the 10-ha and 100-ha size classes.

Primate species richness was 6.00 in both continuous forest sites. Average primate species richness (±standard error) in the two 100-ha fragments during the primate censuses was 2.33 (±0.50), and 3.75 (SE±0.42) with *ad libitum* data included (Table 4). At one time or another, from 2003 to 2006, both 100-ha fragments supported all of the primate species, with the exception of the black spider monkey, which was never spotted. The five species present in the two fragments were not all permanent residents; I saw brown capuchin, northern bearded saki, and white-faced saki monkeys leaving both 100-ha fragments via tall secondary growth.

Average primate species richness in the three 10-ha fragments during primate censuses was 1.78 (±0.15), and 2.56 (±0.53) with *ad libitum* data. Howler and bearded saki monkeys were present in 100% of the censuses in two 10-ha fragments (#1202 and #2206). Although howler monkeys were present in the third 10-ha fragment (#3209) for 67% of the censuses times, bearded saki monkeys were never spotted in this fragment. White-faced saki monkeys traveled in and out of all three 10-ha fragments during the study. Golden-handed tamarin monkeys were present for 100% of the censuses of the 10-ha fragment at Dimona (#2206), they frequently entered and left the 10-ha Colosso fragment (#1202), and were found on one occasion foraging in the low secondary growth bordering the 10-ha fragment of Porto Alegre (#3209). Aside from one incident in September 2005 when a group of brown capuchin monkeys entered fragment #3209, traveled across it, and then left the fragment approximately 10 minutes after arriving, this species was not present in the 1-ha and 10-ha BDFFP forest fragments during these surveys.

Average species richness in the 1-ha fragments was 0.25 (±0.20) for both the census data and data including *ad libitum* primate sightings. Aside from the presence of a male bearded saki monkey in a 1-ha fragment (#2108) in 2003, the red howler monkey was the only species to inhabit 1-ha fragments from 2003-2006; however, the species was not a permanent resident of the two 1-ha fragments (#1104 and #2107) it frequented, and the remaining two 1-ha fragments (#2108 and #3114) never hosted primates during the study.

Overall the red howler monkey was the most prevalent primate species in the forest fragments: it was present throughout all three fragment size classes, and it was present in a greater proportion (61%) of the total censuses than any other species (Table 5). The black spider monkey was the least prevalent in the forest fragments (2% of the censuses). Aside from the brief presence of a juvenile black spider monkey in the 10-ha fragment #1202 in January 2005, black spider monkeys were not present in any of the forest fragments during 17 months of censuses; however, this species was present in both continuous forest sites throughout the study.

Primates (1980-2006)

The primate community has fluctuated from its original pre-isolation state, initial post-isolation state, and later post-isolation state. The pattern of greater species richness in the larger forest size classes from the 2003-2006 study held when all censuses from 1980 to 2006 were combined ($F_{3,7}$=33.68, P=0.0002; Fig. 7B), although there was a statistical difference in species richness only between the 1-ha forest fragments and the other size classes. Furthermore, the red howler monkey has been the most prevalent primate species since the initiation of the BDFFP study, while the black spider monkey has been the least often seen primate (Fig. 8).

Although there were no censuses of the 1-ha fragments during the 1980s, primates were absent from three of the four 1-ha fragments from 1991 until 2003. Howler and bearded saki monkeys first appeared in a second 1-ha fragment in 2003 (#2107), and the remaining two fragments have never hosted primates during censuses. There have been recent recolonizations in the 10-ha and 100-ha fragments; bearded saki monkeys were first noted in the two 100-ha fragments (#2303 and #3304) in 2001, and brown capuchin monkeys were first noted in the 10-ha fragment #3209 and the 100ha fragment #2303 in 2005.

Resource fluctuations

Fruit abundance during Cycle 2 (April-June 2005) and Cycle 3 (August-October 2005) was lower than during Cycle 1 (January-March 2005), Cycle 4 (October-December 2005), and Cycle 5 (January-March 2006; $F_{4,4}$=8.08, P=0.034; Fig. 9). Neither forest size class ($F_{3,7}$=1.70, P=0.25) nor the interaction between data cycle collection and forest size class ($F_{12,11}$=0.46, P=0.90) had an effect on fruit abundance. This relationship corresponded to greater fruit abundance during the period of November to February, and fruit scarcity during the months of June and August. No data were collected in July 2006 due to a month-long pause in the study. Overall, there was a correlation between the monthly precipitation total (mm) and the number of plants in fruit per 100 m (r=0.64, n=15, P=0.0099; Fig. 10).

Although flower abundance did fluctuate throughout this study, with Cycles 3 and 4 having the greatest abundance (Fig. 11), the differences among all five cycles were not significant at an alpha-level of 0.05 ($F_{4,4}$=5.83, P=0.058). Neither forest size class ($F_{3,7}$=2.09, P=0.19) nor the interaction between data cycle collection and forest size class ($F_{12,11}$=0.41, P=0.95) had an effect on flower abundance.

Landscape changes (1984-2006)

The landscape encompassing the study site area (210,000 ha) experienced a change from 1984 to 2006 (Fig. 12). Primary forest decreased from 91% to 88%, with the greatest difference in primary forest cover occurring between 1984 and 1992. The proportion of clear-cut areas also decreased, from 5% to 2%, with the greatest difference occurring between 1992 and 2001. Secondary growth forest cover increased from 3% in 1984 to 11% in 2006, with the greatest increase occurring between 1984 and 1992.

I classified a 500-m buffer area around each of the forest fragments in order to document whether old growth forest patches diminished in the proximity of the forest fragments from 1984 to 2006. Overall, the land cover of the buffers changed with time ($F_{9,44}$=6.40, P<0.0001); however, the changes were related to the increase in old growth forest and secondary growth in areas that were once clear cut, and a decrease in the proportion of area that was clear-cut (Fig. 13). Neither fragment size class ($F_{6,36}$=0.87, P=0.52) nor the interaction between fragment size class and year ($F_{18,51}$=0.38, P=0.99) had an effect on the buffers' land cover.

From 1984 to 2006, in the matrices surrounding the forest fragments, the amount of clear-cut land cover decreased and secondary growth increased ($F_{9,44}$=8.83, P<0.0001, Fig. 14). Neither fragment size class ($F_{6,36}$=035, P=0.91) nor the interaction between fragment size and year ($F_{18,51}$=0.23, P=1.00) were related to the land cover of the matrix.

Isolation distance of the forest fragments

Distance between the forest fragments and continuous forest varied from 0 m to 720 m in 2006 (Table 6). Due to regeneration of areas of the matrix, as of 2006 both 100-ha fragments (#2303, 3304) were connected to continuous forest by corridors of tall secondary growth, and therefore were not completely isolated. I witnessed the use of the corridors by primates in both 100-ha fragments. Some fragments such as the 1-ha fragment at Colosso (#1104) had tall secondary growth forest surrounding the original forest fragment, but satellite images indicated that the fragments were still isolated since the secondary growth did not continue uninterrupted to the continuous forest.

Distances between the nine forest fragments and the nearest forested area greater than 0.50 ha varied from 0 m to 150 m. Although distance to nearest forested area was correlated with size of the forest fragment (r=-0.81, n=9, P=0.0087), the variables distance to nearest forest patch and distance to continuous forest were not correlated (r=0.17, n=9, P=0.67).

Variables predicting primate presence

Because distance to forested area and fragment size were correlated, I ran separate multiple regressions involving these variables. Model A (excluding fragment size) found that distance to nearest forested patch predicted 80% of the variation in primate species richness ($F_{1,6}$=73.79, P=0.0001). The proportion of old secondary growth in the matrix surrounding each fragment explained an additional 12% ($F_{1,6}$=9.67, P=0.021; Table 7). When fragment size ($\log_{10}$-transformed) was added to the model in place of distance to forested area (Model B), only fragment size predicted primate species richness ($F_{1,7}$=32.23, P=0.0008), and it explained 82% of the variation (Table 7).

A separate multiple regression was run to test whether primate characteristics predict species' presence in forest fragments. None of the primate species' variables (i.e., body size, home range size, degree of frugivory) met the criteria for entry into the forward multiple regression model ($P>0.05$ for all).

DISCUSSION

This study demonstrates that a forest fragment's size, the configuration of nearby forest patches, and the extent of old secondary growth in its surrounding matrix are predictive of primate species richness. In contrast, factors such as distance to the continuous forest and proportion of clear-cut areas in the matrix were not indicative of richness. Furthermore, factors that are often used to categorize a species' vulnerability to fragmentation (e.g., body size, home range size, degree of frugivory) did not predict the presence of primates in fragments. These results therefore indicate that, in addition to preserving large tracts of land for primates, it is also necessary to take the surrounding landscape into consideration, as remnant patches of forest may assist with movements in and out of the study fragments. This relationship is especially appropriate in landscapes where deforestation continues, and where opportunities exist for the conversion of the matrix from clear-cut areas to secondary growth forest.

Fragment attributes

Large forest fragments had greater primate species richness than small forest fragments, which supported previous findings at BDFFP (Gascon *et al.* 2003), but the relationship between the two variables was not simple. Forest patch size did not predict the types of species (i.e., frugivorous, large-bodied, large-ranging) that were present or missing from a forest fragment at a given time. Furthermore, there was a strong negative correlation between fragment size and the distance to the nearest forested area greater than 0.50 ha. Due to this confound, I had to analyze the forest fragment size and distance to nearest forested area separately in multiple regressions examining the determinants of species richness. Neither of the variables, however, were correlated with distance to the continuous forest. According to the first model, the configuration of remnant forest patches and, secondarily, the amount of old secondary growth throughout a matrix, may positively affect primate species richness. Therefore, the arrangement of forest patches within the matrix and the condition of the matrix are important metrics to consider in terms of species management and conservation plans.

The importance of fragment size is evident when I compare the results of each of the fragment size classes. For instance, although the two 100-ha forest fragments were the closest to other forested areas, primate species richness was not significantly different between these 100-ha fragments and the 10-ha fragments (which were isolated); the main difference in species richness was seen when I compared the 1-ha fragments to the other size classes. This finding suggests that even with the low sample size and confounding variables, fragment size was still likely an important factor in the determination of primate species richness.

The proportion of old secondary growth in the matrices surrounding the fragments was related to primate species richness only in Model A, when forest fragment size was excluded. Therefore, it was not clear to what extent the matrices' proportion of secondary forest affected species richness. While the two 100-ha fragments had the lowest degrees of isolation, the proportion of their matrices composed of old secondary growth was mid-range when one looked at all nine forest fragments. The fragment with the greatest amount of old secondary growth in the matrix (#3209) was the most isolated of the nine forest fragments and had lower primate species richness than the other two fragments in its 10-ha size class. It's important to note that the two 100-ha fragments with corridors leading to continuous forest did not have greater species richness than the 10-ha fragments, none of which had corridors. Therefore, although some primate species used the tall secondary growth as a travel corridor, not all six species entered the two 100-ha fragments via these corridors, and some species entered and left forest fragments that did not have tall secondary growth surrounding the fragment edge. Although it isn't necessary for the entire matrix to be dominated by tall secondary growth in order for portions of the matrix to assist in travel in and out of the matrices, it does not appear to be the case that the proportion of secondary forest in the matrix is the prime driving force in determining species richness. It may be that the configuration of the matrix and its areas of various land cover types may play a more important role than the combined proportion of land cover types in the matrix.

Lastly, although fruit abundance varied seasonally, primate species richness did not vary throughout the data cycles. Therefore, I can infer that seasonal fluctuations in fruit abundance did not determine which primates occupied the forest fragments. Furthermore, due to the overall increase in primate species richness in the BDFFP forest fragments since the 1980s, it does not appear that El Niño Southern Oscillations are directly affecting primate species richness.

Isolation

With the exception of one fragment, the distances from the forest fragments to continuous forest in 2006 were similar to the distances reported in Bierregaard, Jr. and Stouffer (1997). This metric did not predict primate species richness in either of the models; instead the distance to nearest forest greater than 0.50 ha predicted primate species richness in Model A. This finding suggests that primates entered the isolated BDFFP fragments from other forested patches in the landscape, and did not rely solely on traveling from the continuous forest. Therefore, I stress the possible importance that matrix forest patches may have in the landscape. Further monitoring of the primates is necessary to determine the extent to which the primates use these other forested patches, as the loss of such patches may have a great effect on the future distribution and persistence of the primates in the fragments.

Land cover changes

Land cover changes were evident when I examined the entire BDFFP landscape, 500-m buffered areas surrounding each fragment, and the matrix between each forest fragment from 1984 to 2006. In all three categories, the proportion of secondary forest increased while the proportion of clear-cut area decreased. Due to the increase of secondary growth in locations that were once cleared of vegetation, the degree of isolation of some of the fragments have changed, with tall secondary forest in the matrix reaching the edge of some forest fragments.

Although only Model A found the proportion of old secondary growth to predict primate presence (along with distance to forested area), the conversion of the matrix to secondary growth may be enough to increase the travel of certain species in and out of the fragments (Bierregaard Jr. and Stouffer 1997). Furthermore, differences in matrix composition can result in other ecological changes within the forest fragment (Nascimento *et al.* 2006). Therefore, it will be important to continue monitoring the extent of secondary growth in the BDFFP matrices. The matrix is not dichotomous (habitat versus nonhabitat), as a continuum exists in terms of its composition, as well as the extent to which different primate species use it as habitat (McIntyre and Hobbs 1999).

While secondary growth forest has increased in the matrices, the amount of old growth forest in the BDFFP landscape decreased by 4% from 1984 to 2006. Furthermore, since June 2006 there has been an influx of people into the forests surrounding the BDFFP reserves, and with the Brazilian government’s plan of bringing more settlers to the area, further deforestation is inevitable (ATBC 2007, Laurance and Luizão 2007). Therefore, although the trend of an increase of secondary forest in the study area from 1984 until 2006 was present, I am not optimistic that the 1984-2006 pattern of regrowth of formerly clear-cut areas will continue or be sufficient to provide adequate resources for the primates at BDFFP. Furthermore, an increase of humans into the area could increase the amount of hunting; therefore, the safety of the primates, both outside and within the BDFFP reserves, could decrease with the rise in human population density.

Use of the matrix by primates

Some of the BDFFP primates did regularly use the tall secondary-growth forest as a means of a travel corridor, yet it was not known to what extent the species used different parts of the matrix. Previous tropical studies found correlations between a species’ abundance in the matrix and its presence in forest fragments (Laurance 1991a, Malcolm 1991). In 2005 and 2006 I noted, *ad libitum*, the presence of all six species in the secondary-forest areas within the BDFFP landscape (though not all of these areas were part of the fragments' initial matrix). Black spider monkeys were spotted least frequently, and red howler monkeys were spotted most frequently, though this could have been due to a bias towards the red howler monkeys living near the study's camps, and differences in species density. Further studies about the use of secondary forest by these primates are necessary to determine the prevalence of their use of the secondary forest, and whether these areas should become a conservation priority.

Although some of the primate species used tall secondary-growth forest as a corridor to travel in and out of the 100-ha fragments, some also appeared sporadically in fragments that were surrounded by low secondary growth. Therefore, the persistence of primate species may depend greatly on the species' ability to cross low-growth areas of the matrix.

Primate attributes

Neither body weight, nor home range size, nor degree of frugivory predicted primate presence in the forest fragments, findings similar to Onderdonk and Chapman (2000). For instance, the two largest species, black spider and red howler monkeys, responded differently to the forest fragments, as howler monkeys were the most prevalent in the fragments and spider monkeys were the least often seen.

Although red howler monkeys, with one of the smallest home ranges, occupied the smaller fragments more frequently than the other five primate species, white-faced saki and golden-handed tamarin monkeys, which both have small home ranges, were not found in the 1-ha and 10-ha fragments as often. The presence across fragments of different size of the three species with the largest home ranges, brown capuchin, bearded saki, and black spider monkeys, varied as well.

The most folivorous species, the red howler monkey, was present in forest fragments of all sizes, and had a greater presence in the fragments than any other primate species in the study. While the red howler monkey data matched the prediction that folivorous-frugivorous species would be present more often than highly frugivorous species, the highly frugivorous species—black spider, bearded saki, and white-faced saki monkeys—did not follow a strict pattern in their distribution across the landscape. While black spider monkeys were absent from most of the forest fragments, bearded saki monkeys were present in all three size classes (though its presence in the 1-ha fragments was minimal), and white-faced saki monkeys were intermittently present in all three 10-ha fragments and both 100-ha fragments. These differences may be attributable to the high proportion of seeds in the northern bearded saki (Chapter 3) and white-faced saki diets. Therefore, discrimination between fruit consumption and seed consumption may be important when comparing primate species.

Keep in mind that the diets of primates are not static (Chapman and Chapman 1990). In this study I quantified a species' degree of frugivory by compiling data from studies of the species in undisturbed habitats because there exist no detailed studies of the diet of *all* six species living in anthropogenic, mainland forest fragments. Therefore, it is unknown to what extent these six species demonstrate plasticity in their foraging and feeding behavior.

Red howler monkey

Red howler monkeys had a greater distribution and persistence throughout the forest fragments than any other primate species in the area. The frequent presence of howler monkeys did not support the prediction that larger-bodied primates are less likely to reside in forest fragments, but the predictions relating to diet and home range size were supported by the data, as howler monkeys have small home range sizes and can have highly folivorous diets. Other studies have also found howler monkeys (genus *Alouatta*) to fare better than their highly frugivorous counterparts (Ferrari and Diego 1995, Estrada and Coates-Estrada 1996, Bicca-Marques 2003, Ferrari *et al.* 2003). Howler monkeys used all three forest size classes, and traveled in and out of many of the fragments during my study. Although they were present only intermittently in two of the four 1-ha fragments, infants were noted in one of the 1-ha fragments and in two of the 10-ha fragments, suggesting that red howler monkeys are doing better reproductively than other species in the smaller forest fragments (i.e., bearded saki monkeys). Furthermore, I frequently noted the presence of red howler monkeys *ad libitum* in the secondary growth forest near the forest fragments and the BDFFP camps.

Overall howler monkeys have fared the best in the BDFFP forest fragments; however, one must be cautious in drawing conclusions on the health of their populations. Howler monkeys (genus *Alouatta*) living in forest fragments or confined habitats oftentimes have high parasite loads (Gilbert 1994, Cruz *et al.* 2000), and are susceptible to hunting (de Souza-Mazurek *et al.* 2000, Peres 2001) and diseases such as yellow fever (Mondet *et al.* 2002, Sallis *et al.* 2003).

Northern bearded saki monkey

Northern bearded saki monkeys were the second most-prevalent species in the BDFFP forest fragments during the 2003-2006 study. The species left the forest fragments after the initial isolation in the early 1980s, which led Rylands and Keuroghlian (1988) to conclude that bearded saki monkeys would not recolonize the forest fragments due to their diet and home range size requirements. Gilbert and Setz (2001) came to similar conclusions; however, such conclusions have not been supported by recent data. In my study northern bearded saki monkeys were spotted intermittently in six of the nine fragments, and were permanent residents of two of the three 10-ha forest fragments throughout the 18-month study period (2005-2006). The groups present in the two 10-ha forest fragments in 2003 had the same group size and sex-ratio as the groups in January 2005; however, I was unable to verify that these groups contained the same individuals.

At first glance it appears unusual that two of the 10-ha forest fragments could support permanent resident groups of bearded saki monkeys, but that the two 100-ha fragments did not. One would expect that if the animals leave a forest fragment of 100 ha, they would also leave one that is one-tenth its size. One possible explanation for this is that the two 100-ha fragments are no longer completely isolated, as they are connected to continuous forest by areas of tall secondary growth, thereby allowing a forested corridor for travel in and out of the fragments. Since the bearded saki monkeys are permanent residents of the two isolated 10-ha forest fragments, and were not spotted intermittently in any of the other isolated forest fragments in 2005 and 2006, I suggest that this species is not as likely to cross open gaps in the matrix. Viega (2006) never witnessed terrestrial travel in bearded sakis (*Chiropotes satanas*) living in a forest fragment, or on an island in Tucuruí Reservoir, Pará, Brazil.

The continued presence of the species in two of the 10-ha fragments suggests that bearded sakis are relatively flexible in their ability to adjust to drastic habitat changes. This contention is supported by further evidence of bearded saki monkeys (*Chiropotes* spp.) living in forest fragments and on small islands in Venezuela (Norconk 1996, Peetz 2001) and northeastern Brazil (Port-Carvalho and Ferrari 2004, Vieira 2005, Viega 2006).

It appears that bearded sakis can exist in small, disturbed habitats; however, the lack of migration from these areas raises concerns about the population's long-term viability in the BDFFP landscape. Although bearded saki groups in the 100-ha and continuous forest had new births in 2005, no births were recorded for either of the two groups in the 10-ha forest fragments from January 2005 until June 2006, and no infants were present in 2003. Therefore, I suggest that while species such as bearded saki monkeys are present in small forest fragments, the health and future of the local population may be greatly compromised due to the genetic isolation of the small social groups (Dobson and Lyles 1989, Pope 1996, Dietz *et al.* 2000). Furthermore, since *Chiropotes* spp. face hunting pressure in other areas of the Amazon (de Souza-Mazurek *et al.* 2000, Cormier 2006), northern bearded saki monkeys may be hunted in the BDFFP area.

Golden-handed tamarin monkey

Golden-handed tamarin monkeys were spotted relatively frequently in the BDFFP forest fragments. The species was present in three of the forest fragments immediately following isolation in the 1980s, and during the 2003-2006 study the primates resided in both 100-ha fragments and one 10-ha fragment; however, the golden-handed tamarin monkeys were transient in a second 10-ha fragment and were spotted only once on the border of the third 10-ha fragment. These results suggest that in general 10-ha fragments may not be of adequate size for golden-handed tamarin monkeys, despite the species’ small body size, relatively small home range, and medium-level degree of frugivory. It is also possible, however, that fluctuations in the species’ presence are a result of the species’ habitat preferences.

Golden-handed tamarins are found in a variety of habitats ranging from primary forest to secondary forest (Oliveira and Ferrari 2000, Trolle 2003), and at times, logged forest (Oliveira and Ferrari 2000). The species frequently entered and left some of the isolated BDFFP fragments, and was found foraging in the low underbrush bordering the fragments in 2006, as well as previously by Gilbert (2003). This evidence suggests that golden-handed tamarin monkeys may not be reluctant to cross open areas, and that the areas of secondary growth in the matrix surrounding the forests may provide habitat for the species.

Hunting of tamarin monkeys occurs in other parts of the Amazon, but these report are rare (de Thoisy *et al.* 2005, Cormier 2006). Peres (1990) found that hunters in the western Amazon did not bother with animals weighing less than 3 kg. Lopes and Ferrari (2000) suggest that the species benefits from forest disturbance, as they regularly eat insects, are not often hunted, and do not have to compete with the larger-bodied primates for resources. My data do not support the notion that the species has benefited from forest fragmentation at BDFFP, as it was common in only four of the fragments. Further study will be necessary on the species’ use of the matrix in order to determine the overall status of the BDFFP populations.

White-faced saki monkey

White-faced saki monkeys have not been consistently present in the BDFFP forest fragments during the past two decades. Although the species has been present in all of the 10-ha and 100-ha fragments at some time, they were not permanent residents in any of the fragments during my study and had the third lowest persistence score in the forest fragments. This suggests that white-faced saki monkeys, similar to golden-handed tamarin monkeys, are leaving and re-entering the forest fragments, including some of the fragments that were fairly isolated in terms of their distance to continuous forest and the status of the surrounding matrix. I noticed white-faced saki monkeys *ad libitum* in the tall secondary growth areas surrounding the Porto Alegre camp on several occasions. Therefore, in order to come to a conclusion regarding the conservation status of this species, future studies should also monitor the matrix and other forested areas not part of the BDFFP reserves in order to determine the range and habitat use of the white-faced saki monkeys.

White-faced sakis are hunted in other areas of the Amazon; however they do not appear to be hunted as much as larger primates such as spider monkeys, howler monkeys, and capuchin monkeys (de Thoisy *et al.* 2005). Further study is needed in the BDFFP areas to determine whether or not local hunting influences the population densities of white-faced saki monkeys.

Brown capuchin monkey

Brown capuchin monkeys do not appear to have adjusted well to forest fragmentation in the BDFFP study area. This species was present in the study area prior to the isolation of the forest fragments (Rylands and Keuroghlian 1988), and it was encountered in the continuous forest sites in 2003, 2005, and 2006. Aside from the quick sighting of a group in a 10-ha fragment in September 2005, brown capuchin monkeys have never been present in any of the 10-ha or 1-ha BDFFP fragments. The species recently re-colonized one of the 100-ha fragments, and it frequently travels in and out of both 100-ha fragments via the tall secondary-growth matrix. Mittermeier and van Roosmalen (1981) concluded that of eight monkeys species in Suriname (where all six BDFFP primate species are represented), the brown capuchin monkey is the most adaptable of all eight species since it was found in all of the forest types, as well as edge habitat. My results indicate that this species is not as adaptable to habitat change as earlier thought, especially when its habitat has decreased extensively.

Furthermore, it is possible that hunting may affect the presence of the brown capuchin monkey, as this species is hunted throughout South America (Peres 1990, de Souza-Mazurek *et al.* 2000, de Thoisy *et al.* 2005, Lehman *et al.* 2006).

Black spider monkey

Aside from an intermittent appearance in one of the 10-ha fragments, black spider monkeys have been absent from the BDFFP forest fragments for almost three decades. The species was present in the study area prior to isolation of the forest fragments, and it was also spotted in both continuous forest sites in 2003, 2005, and 2006. Therefore, I conclude that this large-bodied, highly frugivorous species with a large home range was negatively affected by forest fragmentation at BDFFP, as expected. It is unclear why the black spider monkey has appeared on several occasions in one of the 10-ha fragments during the last few decades when it does not use any other the other forest fragments, including the 100-ha fragments with tall secondary-growth corridors.

Spider monkeys are commonly hunted in the tropics (Silva-López *et al.* 1988, Lara and Jorgenson 1998, de Souza-Mazurek *et al.* 2000, Lehman *et al.* 2006), though as with other species, the hunting intensity varies among localities and local beliefs (Peres 1990, Alvard *et al.* 1997). Therefore, it is possible that black spider monkeys are hunted near the BDFFP reserves, which could decrease the pool of animals that could potentially enter the BDFFP fragments.

Although spider monkeys (*Ateles* spp.) exist in neotropical forest fragments (Gonzalez-Kirchner 1999, Ramos-Fernández and Ayala-Orozco 2003, Zamora and Mandujano 2003), and have been sighted in one 10-ha

BDFFP fragment, I conclude that black spider monkeys in the BDFFP study area have not responded well to forest fragmentation. This conclusion is consistent with previous findings that spider monkeys (*Ateles* spp.) are restricted in terms of their use of habitats (Mittermeier and van Roosmalen 1981, Gonzalez-Kirchner 1999), and are not commonly found in fragmented environments (Estrada and Coates-Estrada 1996). Nonetheless, one must be cautious in identifying the main factor for their low visibility. Black spider monkeys are large-bodied, highly frugivorous primates with large home ranges, factors that have been used to explain the absence of such species from the forest fragments (Rylands and Keuroghlian 1988); however, bearded saki monkeys are also highly frugivorous and have large home ranges, yet they were consistently present in many of the forest fragments. Therefore, although these factors may play a role in the high sensitivity of the black spider monkey to forest fragmentation, I do not think that there are adequate data indicating that these factors are the main driving force in determining the species' presence or absence in forest fragments.

Conclusions

To preserve biodiversity in areas experiencing human disturbance, it is important to understand how habitat modifications may alter the behavioral ecology, and consequently the survival, of the local fauna. While my data provided insight into the fluctuations of primate presence in the forest fragments, I stress the need for 1) continued monitoring of the BDFFP primates in order to contribute to the analysis of long-term patterns in primate presence; 2) continued monitoring of the land cover in order to discern both long-term patterns and sudden changes in land cover surrounding the forest fragments; and 3) research on the behavioral ecology of the primate species that have never been studied thoroughly in the forest fragments (e.g., golden handed tamarin monkey, brown capuchin monkey, and black spider monkey). Furthermore, I suggest that future studies monitor areas in addition to the forest fragments (e.g., matrices) in order to determine how the six primate species are using the BDFFP landscape, as scale is important in monitoring a species' conservation status (Kattan and Murcia 2003, Anderson *et al.* 2007). Understanding the role of the matrix in primate ecology would be much improved by following the primate groups that frequently leave and enter the fragments, as these animals are not restricted to the scale of the forest fragments. Such a study would provide insight into the extent to which the species use the matrix (e.g., travel corridors, feeding sites, sleeping sites), as well as dietary and home range comparisons between groups utilizing the matrix, and those groups that do not utilize the matrix.

While the BDFFP reserves are technically protected from hunting, the forest surrounding the reserves is not protected. Furthermore, in recent years there has been an increase of illegal use of the BDFFP reserve by hunters (Laurance and Luizão 2007), and shotgun blasts were heard in close proximity during data collection in one of the 10-ha fragments and in one of the continuous forest study sites. Therefore, human pressure on the primates exists both in terms of the landscape's land cover change and hunting. An important aspect of future studies of the BDFFP primates would be to assess the degree to which primates are hunted in and around the BDFFP reserves via interviews with the local landowners.

Overall, the six primate species are not equally represented in the BDFFP reserves. I think there is serious conservation concern regarding the future of these species, in particular the ones that are virtually absent from the majority of the forest fragments (i.e., black spider monkeys, brown capuchin monkeys), those that appear to be severely isolated from other groups due to their hesitance to cross a young matrix (i.e., bearded saki monkeys), and those that may be currently under hunting pressure in the immediate areas surrounding the BDFFP reserves (i.e., black spider monkeys, red howler monkeys, and brown capuchin monkeys). Although there was more secondary forest regrowth in the matrix in 2006 than in previous years, the proportion of old-growth forest in 2006 was less than previous years, and it does not appear that the pattern of deforestation of old growth forest will abate, especially if the recolonization plans for the BDFFP area are realized. Therefore, I conclude that the current and future deforestation practices in the area, resulting in habitat loss for the species, will be the primary factors affecting the future viability and conservation of these primate populations.

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TABLE 3. Characteristics of the primates at the BDFFP.

	Weight (kg)[1]			Group Size[2]	Home Range (ha)[2]	Day Range (km)		Diet (%)			
	♂	♀	Av.			Range	Mean	Fruit	Flower	Leaf	Other[3]
Alouatta seniculus 4,5,6, 7,8	7.2	5.6	6.8	4-17 (8.2)	4-166 (53)	0.3-1.6	0.8	40.4	6.4	48.1	5.1
Ateles paniscus 9,10,11, 12,13,14,15,16	7.5	8.8	7.8	12-18 (14.3)	153-255 (224)	0.5-5.0	2.2	88.7	3.8	6.1	1.4
Cebus apella 9,11,14,17,18,19,20,21	3.1	2.4	2.6	6-23 (14.3)	250-850 (429)	1.7-4.6	2.9	65.0	1.4	2.7	30.9
Chiropotes sagulatus 10,18, 22,23,24	3.1	2.6	2.8	8-44 (21.8)	200-559 (336)	2.5-4.5	3.3	87.9	5.7	5.8	0.6
Pithecia pithecia 18,25,26, 27,28,29,30	1.7	1.5	1.7	1-12 (3.4)	10-287 (103)	0.9-2.0	1.9	86.4[34]	2.1[34]	8.7[34]	2.8[34]
Saguinus midas 11,18,31,32, 33	0.6	0.4	0.5	3-8 (5.7)	28-43 (33)	n/a	0.4	66.0	1.9	0.8	31.3

Notes: [1]Ford and Davis (1992) used for all body weight references; [2]Mean is in parentheses; [3]High values for "other" represents a high proportion of insects in the diet; [4]Gaulin and Gaulin (1982); [5]Julliot and Sabatier (1993); [6]Julliot (1996); [7]Palacios and Rodriguez (2001); [8]Sekulic (1982); [9]Guillotin and Dubost (1994); [10]Kinzey and Norconk (1990); [11]Mittermeier and van Roosmalen (1981); [12]Norconk and Kinzey (1994); [13]Simmen (1992); [14]Simmen and Sabatier (1996); [15]Symington (1988); [16]van Roosmalen (1985); [17]Izawa (1980); [18]Norconk *et al.* (2003); [19]Peres (1993); [20]Spironello (2001); [21]Zhang (1995); [22]Ayres (1981); [23]Boyle *et al.* (In press); [24]van Roosmalen *et al.* (1981); [25]Homborg (1997); [26]Kinzey and Norconk (1993); [27]Lehman *et al.* (2001); [28]Norconk (1996); [29]Oliveira *et al.* (1985); [30]Vie *et al.* (2001); [31]Day and Elwood (1999); [32]Kessler (1995); [33]Oliveira and Ferrari (2000); [34]Due to lack of data in continuous forest, these data include studies from an island.

Table 4. Average primate species richness from 2003-2006.

	100 ha	10 ha	1 ha
Census data	2.33 (±0.50)	1.78 (±0.15)	0.25 (±0.20)
Census + *ad libitum* data	3.75 (±0.42)	2.56 (±0.53)	0.25 (±0.20)

Notes: Average primate species richness (±SE) for each fragment size class (100: *n*=2; 10: *n*=3; 1 ha: *n*=4) was calculated using the census data, as well as the census data with *ad libitum* primate sightings. Six primate species resided in the continuous forest sites.

TABLE 5. Primate persistence in the forest fragments from 2003-2006.

	100 ha (%)		10 ha (%)			1 ha (%)				Overall (%)
	2303	3304	1202	2206	3209	2107	1104	2108	3114	
Alouatta	100	100	100	100	67	67	17			61
Chiropotes	100*	50*	100	100		17				41
Saguinus	100	83	50	100	17*					39
Pithecia	67*	33	50	33	50					26
Cebus	50*	67*			17*					15
Ateles			17							2

Notes: The persistence of the six primate species in each of the nine forest fragments is indicated by the percentage of data cycles (*n*=6) in which the species were present. Overall persistence is the percentage of the total censuses (*n*=54) that the species was located in each of the nine fragments during the six cycles. Species witnessed leaving the forest fragments are indicated by *.

TABLE 6. Degree of isolation of the forest fragments in 2006.

			Distance			
Fragment	Size class (ha)	Isolated	Forest >0.50 ha	Continuous forest	Buffer: % old-growth forest	Matrix: % old-growth forest
2303	100	N	0	0	44.95	51.35
3304	100	N	30	42	18.25	48.20
1104	1	Y	85	85	36.41	33.65
2206	10	Y	30	120	46.94	44.52
2107	1	Y	85	145	31.02	44.89
3114	1	Y	150	150	33.68	63.71
2108	1	Y	85	360	25.31	40.27
1202	10	Y	30	600	27.49	33.19
3209	10	Y	90	720	9.10	71.18

Notes: A fragment's degree of isolation was measured in terms of its distance to the closest forested area larger than 0.50 ha, the shortest distance to continuous forest, the percentage of a 500-m buffer surrounding each fragment that was old growth forest, and the percentage the fragment's matrix that was old secondary growth forest. Data are presented from lowest to highest isolation.

TABLE 7. Predicting primate species richness with forest fragment variables.

	Variables' results	Overall model
Model A		
Distance to forest >0.50 ha	$F_{1,6}$=73.79, P=0.0001	r^2=0.92, P=0.0004
% secondary forest in matrix	$F_{1,6}$=9.67, P=0.021	
Model B		
Log_{10} fragment size	$F_{1,7}$=32.23, P=0.0008	r^2=0.82, P=0.0008

Notes: Distance to the nearest forested area greater than 0.50 ha and proportion of the matrix that was old secondary growth forest explained 92% of the variation in Model A (fragment size excluded). Distance to fragment by itself explained 80% of the variation. In Model B (distance to forest patch excluded), fragment size ($\log_{10}$-transformed) predicted primate species richness, explaining 82% of the variation. Distance to continuous forest and proportion of clear cuts in the matrix did not affect primate species richness. None of the primate characteristics (i.e., body weight, home range size, degree of frugivory) were found to explain primate presence in a separate multiple regression analysis.

FIG. 6. Correlation between variables. The size of the forest fragment was strongly correlated with the distance to the closest forest patch with an area greater than 0.50 ha (*r*=-0.81, *n*=9, *P*=0.0087). As a result, the two confounding variables were included separately into multiple regression analyses of primate species richness.

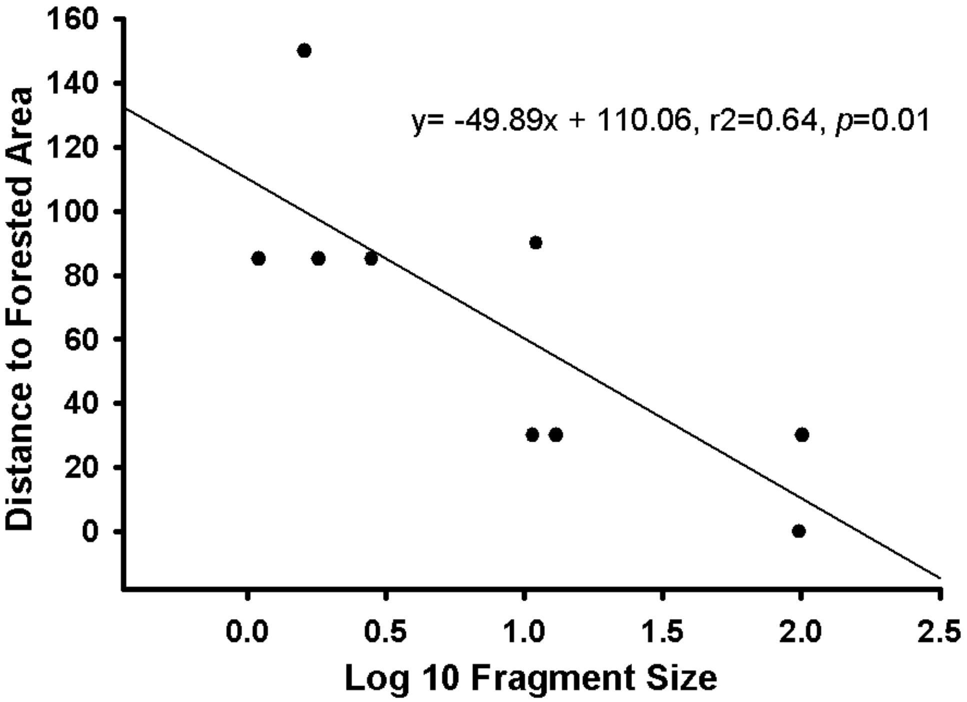

160
140
120
100
80
60
40
20
0
Distance to Forested Area
y= -49.89x + 110.06, r2=0.64, p=0.01
0.0
0.5
1.0
1.5
2.0
2.5
Log 10 Fragment Size

FIG. 7. Primate species richness. As fragment size decreased, so did (A) average primate species (±standard error) richness in nine BDFFP fragments from 2003-2006 ($F_{3,7}$=106.90, P<0.0001) and (B) average species richness during primate censuses at BDFFP from 1980-2006 ($F_{3,7}$=33.68, P=0.0002). Data prior to 2003 were based on census data by Rylands and Keuroghlian (1988), Schwarzkopf and Rylands (1989), and Gilbert (2003).

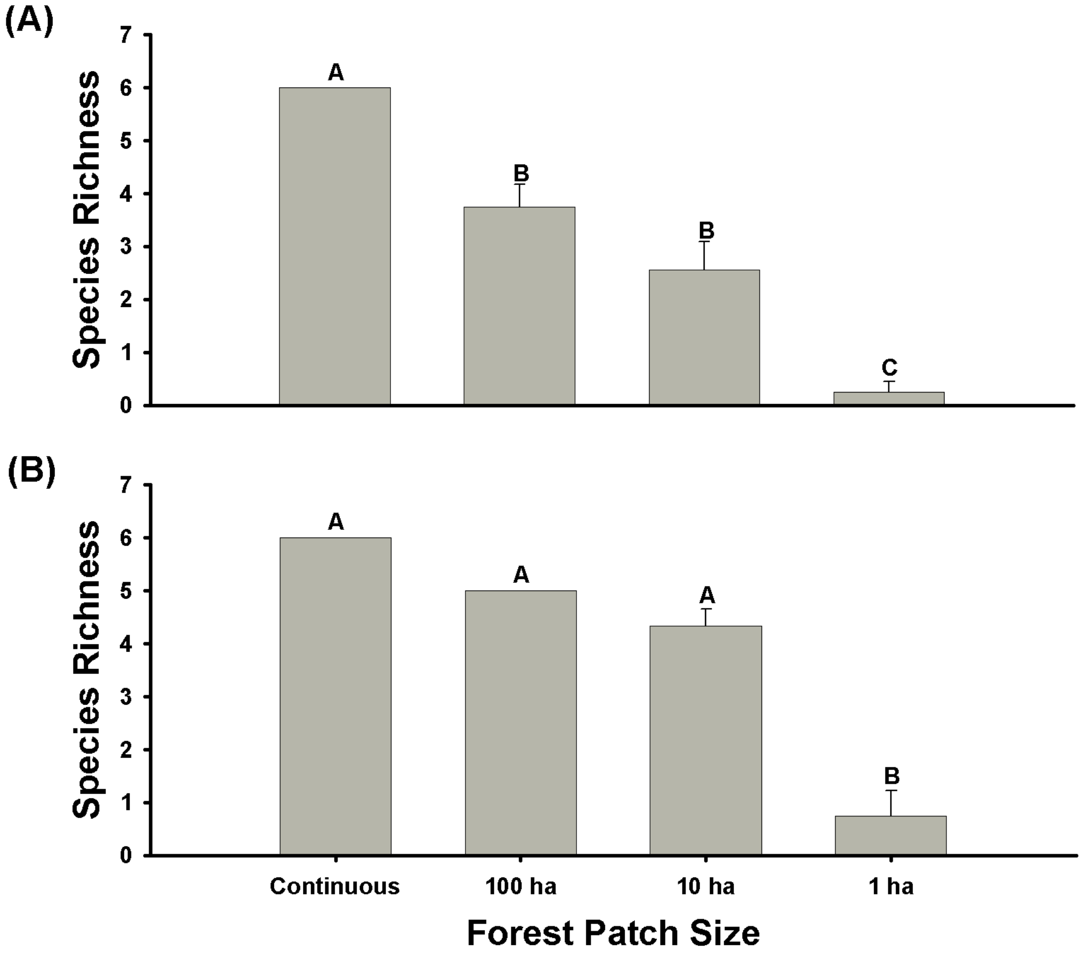

(A)
7
6
5
4
3
2
1
0
Species Richness
A
B
B
C
(B)
7
6
5
4
3
2
1
0
Species Richness
A
A
A
B
Continuous
100 ha
10 ha
1 ha
Forest Patch Size

Fig. 8. Primate distribution and colonization 1980-2006. Six primate species inhabited the BDFFP landscape. Since the initial isolation of the forest fragments, there have been changes in primate distribution and re-colonization of the forest fragments. Lightning bolts indicate the initial isolation of the forest fragment. Solid lines represent continued presence of the species since its initial presence. Dotted lines represent intermittent presence of the species. Species are noted as the following: *Alouatta seniculus* (AL), *Ateles paniscus* (AT), *Cebus apella* (CE), *Chiropotes sagulatus* (CS), *Pithecia pithecia* (PI), and *Saguinus midas* (SA). Data prior to 2003 were based on census data by Rylands and Keuroghlian (1988), Schwarzkopf and Rylands (1989), and Gilbert (2003).

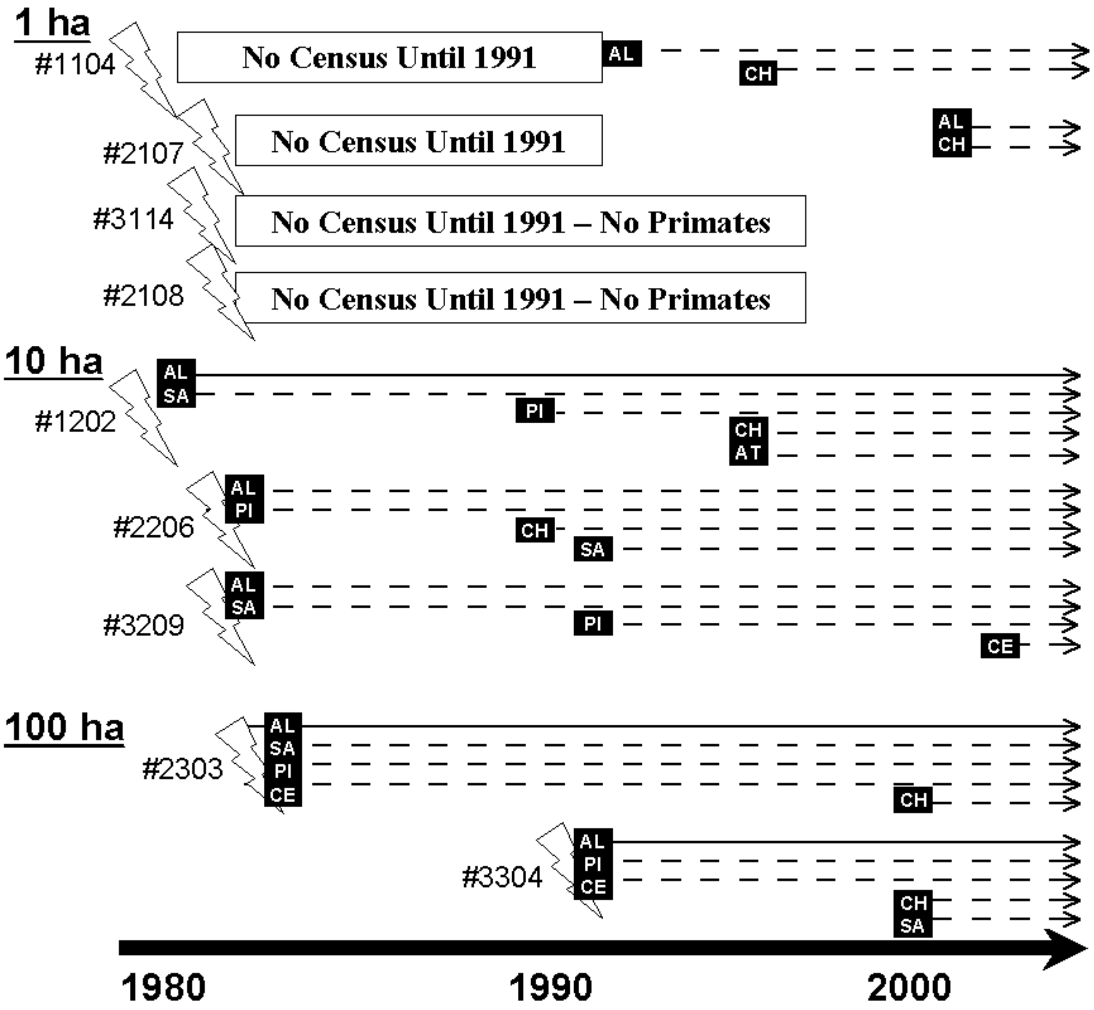
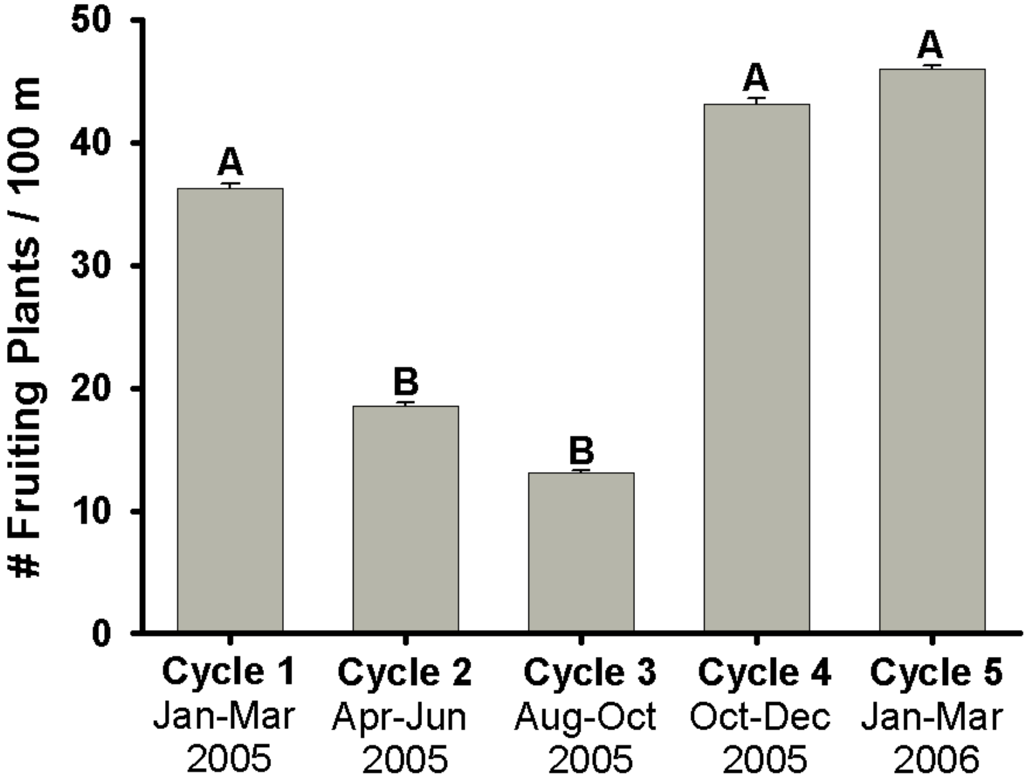

1 ha
#1104
No Census Until 1991
AL
CH
#2107
No Census Until 1991
AL
CH
#3114
No Census Until 1991 – No Primates
#2108
No Census Until 1991 – No Primates
10 ha
#1202
AL
SA
PI
CH
AT
#2206
AL
PI
CH
SA
#3209
AL
SA
PI
CE
100 ha
#2303
AL
SA
PI
CE
CH
#3304
AL
PI
CE
CH
SA
1980
1990
2000

FIG. 9. Fruit abundance fluctuation. The number of fruiting trees, lianas, and hemiepiphytes per 100 m (mean ±standard error) fluctuated seasonally, with Cycles 2 and 3 having lower fruit abundances than other cycles ($F_{4,4}$=8.08, P=0.034).



Fruiting Plants / 100 m
0
10
20
30
40
50
A
B
B
A
A
Cycle 1
Jan-Mar
2005
Cycle 2
Apr-Jun
2005
Cycle 3
Aug-Oct
2005
Cycle 4
Oct-Dec
2005
Cycle 5
Jan-Mar
2006

FIG. 10. Resource and precipitation fluctuation. Abundance of fruiting trees (per 100 m) and monthly precipitation totals were positively correlated (*r*=.64, *n*=15, *P*=0.0099).

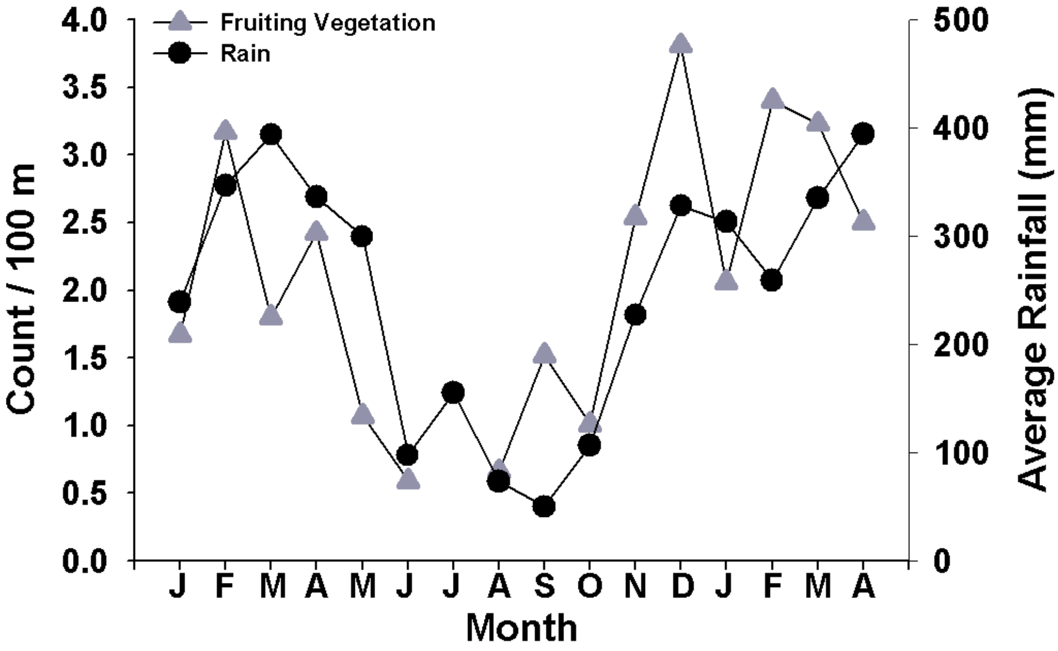
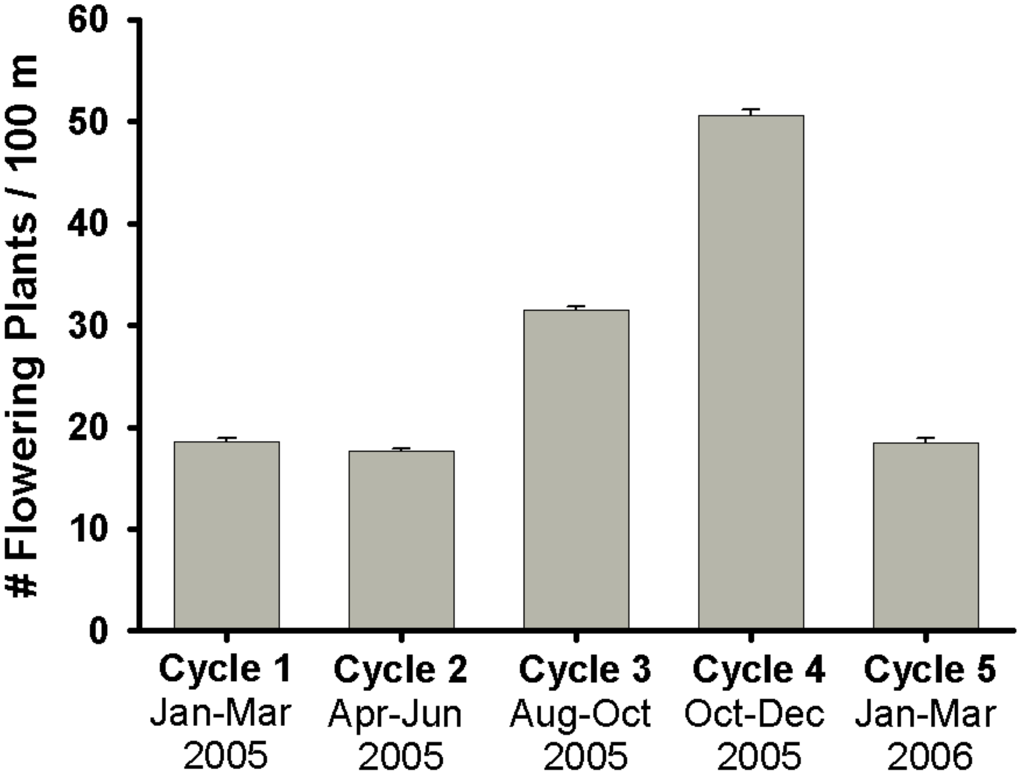

Fruiting Vegetation
Rain
Count / 100 m
Average Rainfall (mm)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
0
100
200
300
400
500
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
Month

FIG. 11. Flower abundance throughout the study cycles. The number of flowering trees, hemiepiphytes, and lianas per 100 m (mean ±standard error) fluctuated throughout the study period, but the differences were not statistically significant ($F_{4,4}$=5.83, P=0.058).



Flowering Plants / 100 m
0
10
20
30
40
50
60
Cycle 1 Jan-Mar 2005
Cycle 2 Apr-Jun 2005
Cycle 3 Aug-Oct 2005
Cycle 4 Oct-Dec 2005
Cycle 5 Jan-Mar 2006

FIG. 12. Landscape change. From 1984 to 2006, the area of primary forest in the BDFFP landscape decreased by 4%. Clear-cut areas decreased by 69%, and the amount of secondary growth increased by 321%.

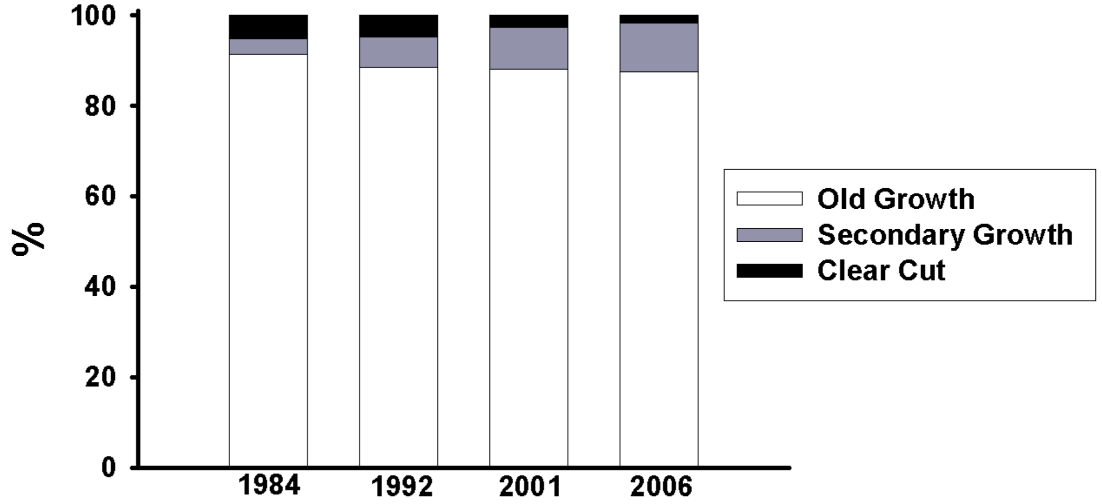

100
80
60
40
20
0
%
1984
1992
2001
2006
Old Growth
Secondary Growth
Clear Cut

FIG. 13. Land cover change in the fragments' buffers. These data represent the land-cover classifications of a 500-m buffer surrounding each of the nine forest fragments at the Colosso (A), Porto Alegre (B), and Dimona (C) ranches from 1984 to 2006. Overall the proportion of old growth forest and secondary growth forest in the buffer increased, and the proportion of clear-cut areas decreased ($F_{9,44}$=6.40, P<0.0001). A large proportion of old growth forest indicates that in general the forest fragment was close to other forest fragments, forested corridors, or continuous forest. Data do not exist for the four Dimona fragments in 1984 because these fragments were isolated after the June 1984 satellite image was taken.

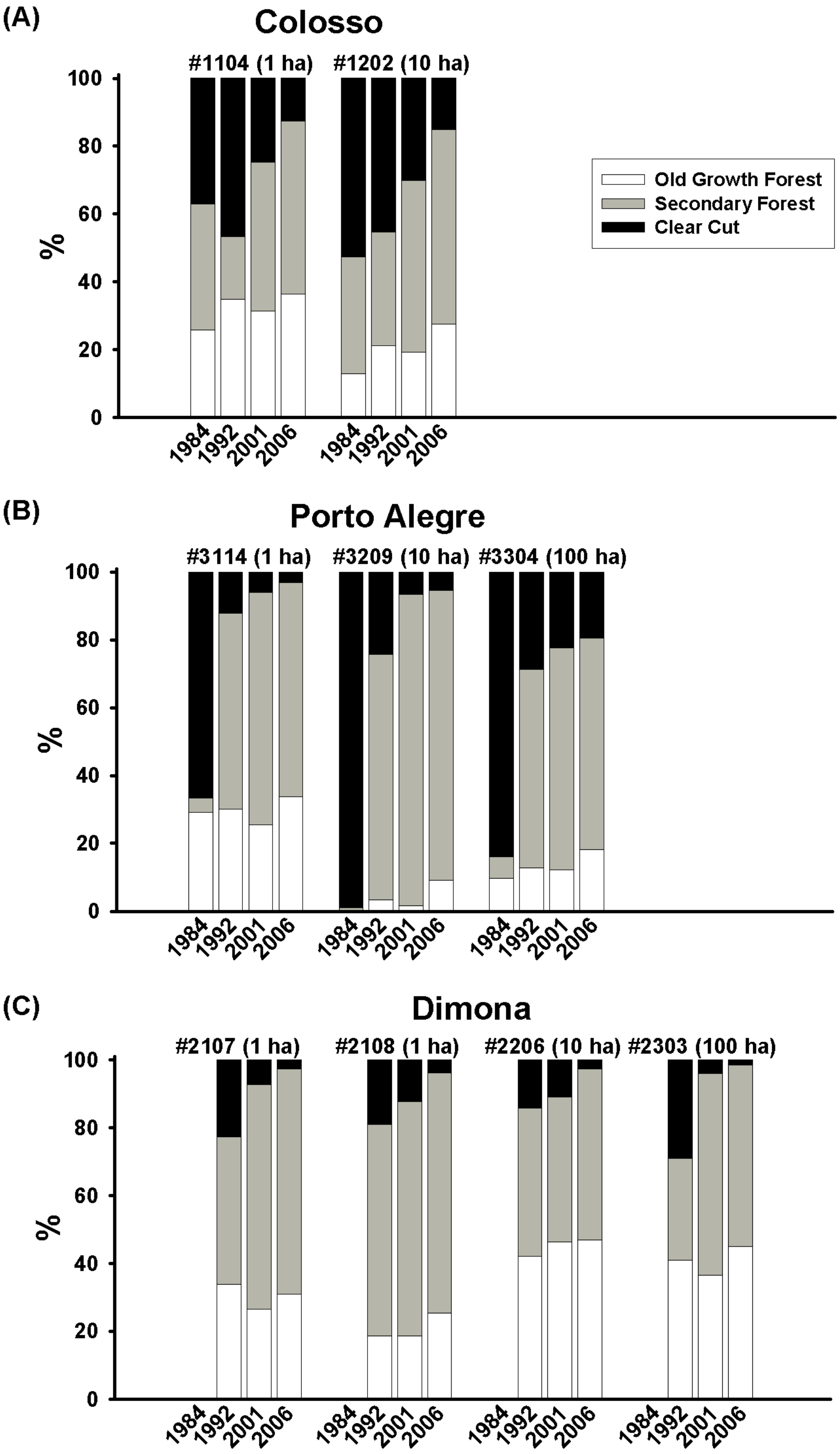
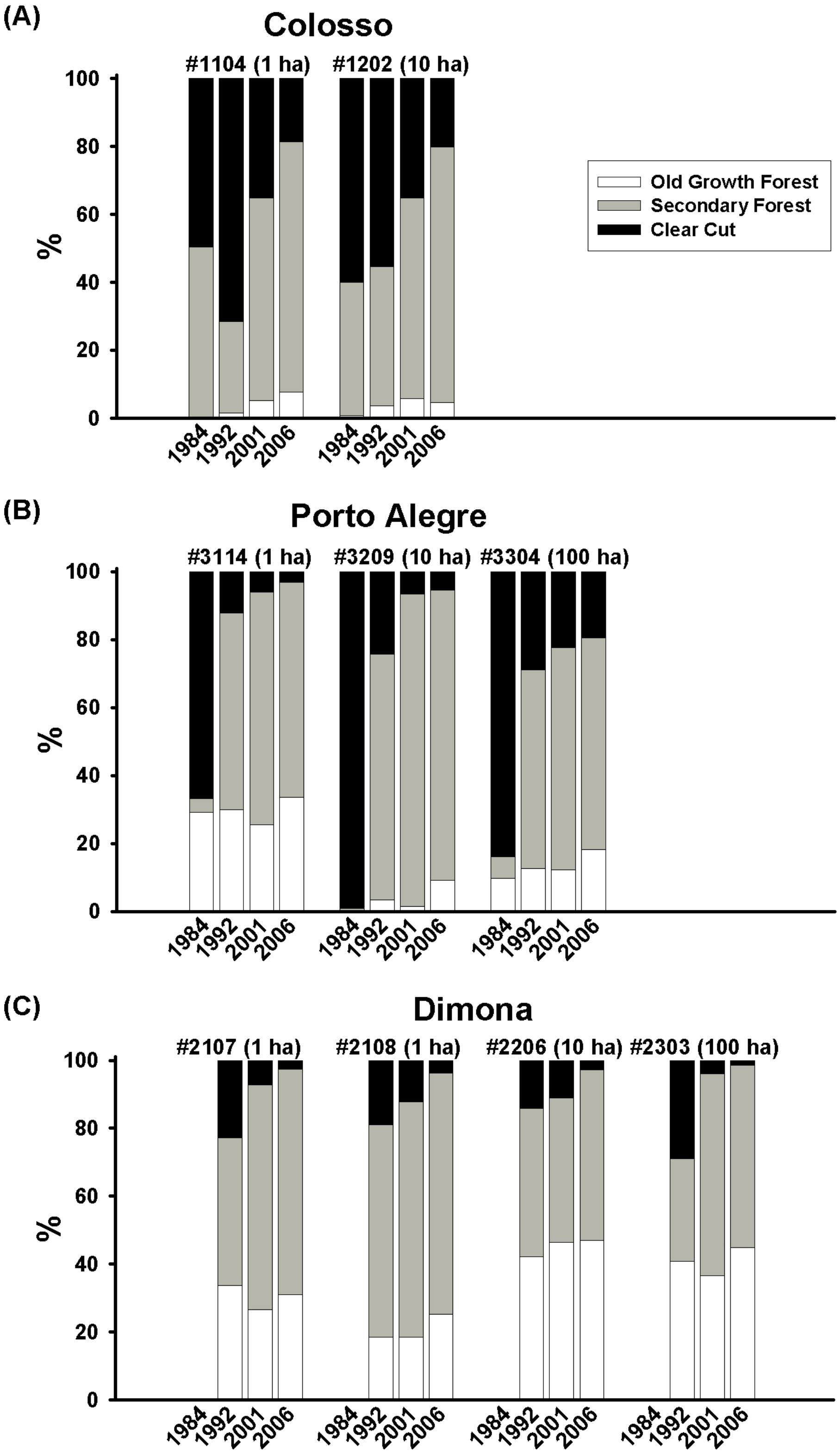

(A)
Colosso
#1104 (1 ha)
#1202 (10 ha)
%
100
80
60
40
20
0
1984
1992
2001
2006
1984
1992
2001
2006
Old Growth Forest
Secondary Forest
Clear Cut
(B)
Porto Alegre
#3114 (1 ha)
#3209 (10 ha)
#3304 (100 ha)
%
100
80
60
40
20
0
1984
1992
2001
2006
1984
1992
2001
2006
1984
1992
2001
2006
(C)
Dimona
#2107 (1 ha)
#2108 (1 ha)
#2206 (10 ha)
#2303 (100 ha)
%
100
80
60
40
20
0
1984
1992
2001
2006
1984
1992
2001
2006
1984
1992
2001
2006
1984
1992
2001
2006

FIG. 14. Land cover change in the matrix. From 1984 to 2006, the proportion of clear-cut areas in the matrices decreased while areas of secondary growth increased ($F_{9,44}$=8.83, P<0.0001) surrounding the nine forest fragments at the Colosso (A), Porto Alegre (B), and Dimona (C) ranches. There are no data from the Dimona fragments in 1984 due to the fact that these fragments were isolated after June 1984.


(A)
Colosso
#1104 (1 ha)
#1202 (10 ha)
%
0
20
40
60
80
100
1984
1992
2001
2006
Old Growth Forest
Secondary Forest
Clear Cut
(B)
Porto Alegre
#3114 (1 ha)
#3209 (10 ha)
#3304 (100 ha)
(C)
Dimona
#2107 (1 ha)
#2108 (1 ha)
#2206 (10 ha)
#2303 (100 ha)

CHAPTER 3

EFFECTS OF FOREST FRAGMENTATION ON THE SOCIAL AND FEEDING ECOLOGY OF THE NORTHERN BEARDED SAKI MONKEY (*CHIROPOTES SAGULATUS*)

Abstract. Forest fragmentation is one of the primary threats to primate conservation. This chapter investigates how fragmentation affects the social and feeding ecology of the northern bearded saki monkey (Chiropotes sagulatus). It was predicted that group size, behavior, and feeding strategies would differ based on the size of the forest available to the monkeys. Nine forest fragments of three size classes (1 ha, 10 ha, 100 ha) and two areas of continuous forest were surveyed for primates at the Biological Dynamics of Forest Fragments Project (BDFFP) study area, located approximately 80 km north of Manaus, Amazonas, Brazil. Data were collected in six research cycles from July-August 2003 and January 2005-June 2006. When northern bearded saki monkeys were present in a study area during a cycle, the group was followed from dawn until dusk for three consecutive days. Behavioral scans and GPS locations were taken every five minutes. If a monkey was eating during the behavioral scan, the food item was noted and the tree from which it came was marked so to allow for species identification after the behavioral study was completed. Bearded sakis were present in all three fragment size classes; however, the monkeys were only permanent residents of two of the nine forest fragments. Bearded saki group sizes were smallest in the two smallest fragment size classes ($F_{3,3}$=43.80, P=0.0056), but density was nevertheless greater in the two smaller fragment size classes than in the largest fragment size class or continuous forest ($F_{3,3}$=35.75, P=0.0076). The bearded sakis ate 244 plant species, of which 65% were consumed by a single group at a single site. Although the bearded saki diet in

forest fragments was limited to plant species present in the fragment, bearded sakis did not consume all species of available fruit, but instead chose only certain taxa. These results indicate that northern bearded saki monkeys are more flexible in their social groupings and dietary choices than previously thought. Such behavioral variability may enable bearded saki monkeys to reside in small forest fragments; however, groups residing in such areas may have problems associated with resource depletion, disease, and lower reproductive success.

INTRODUCTION

Forest fragmentation is one of the primary threats to primate conservation in the tropics (Estrada and Coates-Estrada 1996, Chapman *et al.* 2007). Forest fragmentation occurs when sections of contiguous forest are cleared, thereby leaving a mosaic of patches surrounded by a non-forested matrix. As deforestation for agriculture or urban development continues, the remaining forest becomes increasingly patchy, affecting local climate (Bierregaard Jr. *et al.* 1992, Achard *et al.* 2002), species richness (Bierregaard Jr. *et al.* 1992, Malcolm 1997), predator-prey interactions (Asquith *et al.* 1997), seed dispersal (Chapman and Onderdonk 1998, Estrada *et al.* 1999), and habitat suitability (Laurance *et al.* 2000b, Gascon *et al.* 2001).

Primates vary morphologically, behaviorally, and ecologically (Napier and Napier 1967, Milton and May 1976, Dunbar 1988). Past studies have examined primate characteristics (e.g., home range size, diet, diet flexibility, ability to travel across forest gaps) in order to determine a species' vulnerability to habitat destruction (Skorupa 1986, Johns and Skorupa 1987, Onderdonk and Chapman 2000). Two of these factors, diet (Skorupa 1986, Johns and Skorupa 1987) and diet flexibility (Estrada and Coates-Estrada 1988, Horwich 1998, Sussman 1999, Clarke *et al.* 2002), have received considerable attention. Leaves, for example, can comprise 25-79% of a howler monkey's (*Alouatta*) diet (Gaulin and Gaulin 1982, Julliot and Sabatier 1993, Palacios and Rodriguez 2001), and such a diet has been linked to their ability to subsist in small areas (Ferrari and Diego 1995, Estrada and Coates-Estrada 1996, Bicca-Marques 2003, Ferrari *et al.* 2003). In contrast, large-bodied, frugivorous primates typically require large home ranges (Milton and May 1976, Clutton-Brock and Harvey 1977, Johns and Skorupa 1987, Onderdonk and Chapman 2000), and some authors have concluded that a highly frugivorous diet and a large home range limits, or excludes, such primates from forest fragments (Rylands and Keuroghlian 1988, Gilbert and Setz 2001). Studies relating a primate species' degree of frugivory and its presence within forest fragments, however, have yielded differing results, and currently there is no consensus regarding the use of primate characteristics to predict the vulnerability of a species in fragmented habitat (Johns and Skorupa 1987, Estrada and Coates-Estrada 1996, Onderdonk and Chapman 2000, Marsh *et al.* 2003).

I focused this research on the northern bearded saki monkey (*Chiropotes sagulatus*). Currently there are discrepancies regarding taxonomy in the genus *Chiropotes* (Hershkovitz 1985, Silva and Figueiredo 2002, Bonvicino *et al.* 2003).

Prior to the recent taxonomic revision, the species found in this area of the Amazon Basin was considered *C. satanas chiropotes*. In this study I follow the taxonomy proposed by Silva and Figueiredo (2002) because it is currently the preferred taxonomy among researchers studying this species. Natural history data for *C. sagulatus* are presented here, and were based on data for *C. satanas chiropotes*, the previous classification of this species.

The northern bearded saki monkey was of interest to study because it 1) is a medium-bodied monkey with an average weight of 2.81 kg (Ford and Davis 1992); 2) lives in large social groups comprised of an average of 21.8 individuals (van Roosmalen *et al.* 1981, Kinzey and Norconk 1990, Norconk *et al.* 2003, Boyle *et al.* In press); 3) is highly frugivorous, obtaining approximately 88% of its diet from fruit, a majority of which is seed material (Ayres 1981, van Roosmalen *et al.* 1981, Kinzey and Norconk 1990); 4) travels long daily distances, averaging 3.3 km (van Roosmalen *et al.* 1981, Norconk *et al.* 2003, Boyle *et al.* In press); and 5) occupies large home ranges of 200-559 ha (Ayres 1981, van Roosmalen *et al.* 1981, Boyle *et al.* In press). Therefore, this study allowed me to examine how a medium-bodied, social, frugivorous species adjusts its behavioral ecology when living in forest fragments that are considerably smaller than the species' average home range.

Furthermore, few publications have examined *Chiropotes* in human-altered habitats (Ferrari *et al.* 1999, Peetz 2001, Port-Carvalho and Ferrari 2004, Veiga 2006, Veiga and Ferrari 2006), and much of this research has focused on forested islands that resulted from hydroelectric dam construction and flooding (Peetz 2001, Santos 2002, Veiga 2006, Veiga and Ferrari 2006), and not mainland populations of *Chiropotes*.

Therefore, the aim of this study was to determine to what extent the social and feeding ecology of bearded saki groups inhabiting mainland forest fragments of three size classes (1, 10 and 100 ha) differed from bearded saki groups living in continuous forest. The specific areas of interest involved monitoring the study groups in order to determine 1) the extent to which the bearded saki monkeys occupied the forest fragments; 2) variation in group size of bearded sakis living in forest fragments versus in continuous forest; 3) feeding behavior patterns of the study groups in forest fragments and continuous forest; 4) overall diet composition of the bearded sakis, as well as comparisons of diet between the different study groups; and 5) whether differences in diet between the study groups were a result of plant species availability in the forest fragments.

I predicted that the bearded saki monkeys living in forest fragments would have smaller group sizes than those monkeys living in continuous forest due to the reduction in habitat space, and the consequent reduction in resources. Furthermore, living in smaller areas would lead to differences in the monkeys' behavioral activity budgets, as monkeys living in a restricted area would be expected to travel less and rest more than those monkeys in continuous forest. Lastly, it was expected that diets would differ among the bearded saki groups due to the restricted resources that are available in a forest fragment.

METHODS

Study site

I collected data during a preliminary study in July-August 2003, and then from January 2005-June 2006, at the Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km north of Manaus, Amazonas, Brazil (2°30'S, 60°W). BDFFP is the site of a long-term project on fragmentation, facilitated by the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil. The forest fragments, which are categorized into size classes of 1, 10 and 100 ha, were initially isolated from the continuous forest by distances of 70-1000 m (Laurance *et al.* 2006b). The first isolation of the forest fragments began in 1980. Gascon and Bierregaard, Jr. (2001) provide a detailed history of BDFFP, and Chapter 2 of this dissertation provides an overview of the current isolation distance of each forest fragment, as well as the condition of the matrix surrounding each forest fragment. The most abundant plant families are Lecythidaceae, Leguminosae, Sapotaceae, Burseraceae, and Euphorbiaceae (Laurance 2001).

There are six primate species in the BDFFP study area: red howler monkey (*Alouatta seniculus*), black spider monkey (*Ateles paniscus*), brown capuchin monkey (*Cebus apella*), northern bearded saki monkey (*Chiropotes sagulatus*), white-faced saki monkey (*Pithecia pithecia*), and golden-handed tamarin monkey (*Saguinus midas*). Chapters 1 and 2 of this dissertation provide a history of these six species in the BDFFP study area, as well an analysis of their vulnerability to forest fragmentation.

After the initial isolation of the BDFFP forest fragments, the bearded saki was absent from all fragments, and it was predicted that the species would not recolonize the fragments due to its large home range and highly frugivorous diet (Rylands and Keuroghlian 1988, Gilbert and Setz 2001). These predictions have not held true, as the bearded sakis returned to several of the forest fragments 7-19 years after the initial isolation of the forest fragments (Gilbert and Setz 2001, Gilbert 2003, Boyle *et al.* In press). This recolonization may have been driven by changing conditions in the matrix surrounding the forest fragments during the period of recolonization. Overall, there was an increase of secondary growth in the matrix, and a decrease in clear-cut areas. Chapter 2 of this dissertation provides additional information regarding the recolonization of forest fragments by primates and the landscape changes in the BDFFP study area.

Bearded saki data collection

Nine forest fragments were surveyed for primates and fruit and flower abundance at the Dimona, Esteio and Porto Alegre ranches—four 1-ha (#1104, #2107, #2108, and #3114), three 10-ha (#1202, #2206, and #3209), and two 100-ha fragments (#2303 and #3304)—and two areas of continuous forest (Km41 and Cabo Frio). Each cycle consisted of a rotation through the nine forest fragments and two continuous forest sites. It took approximately 2.5 months to complete each cycle. I conducted one primate census cycle in July-August 2003, four cycles in 2005, and one cycle in 2006 in order to account for annual and seasonal fluctuations. The durations of the cycles were as follows: January-March 2005 (Cycle 1), April-June 2005 (Cycle 2), August-October 2005 (Cycle 3), October-December 2005 (Cycle 4), January-March 2006 (Cycle 5). Additional data collection was conducted in April 2006 for a sixth cycle of the 10-ha fragment #1202 because the study group in this fragment was the best documented group in terms of contact hours and diet identification. Comparisons were made between the cycles in order to determine seasonal differences in fruit abundance and primate species richness. Data from 2003 were not included in these seasonal comparisons because phenological data were collected only in 2005 and 2006. Therefore, the 2003 data are referred to by the year 2003, and do not have a corresponding cycle name.

On the first day in each study area I conducted a primate census by walking line transects along already established trails, following the methods of Rylands and Keuroghlian (1988) and Gilbert (2003). Chapter 2 provides additional information on the methods and results for each of the primate species during these censuses. If bearded sakis were present in the forest fragment during the primate census, they were designated the focal study group for that fragment's cycle, and upon completion of the primate census, subsequently relocated and followed for three consecutive days. In total, the primate censuses spanned 253 hours and 195.2 km. During the behavioral study there were 70 full days (≥8 hours) of bearded saki follows, 604 contact hours with the monkeys, and an additional 582 hours devoted to locating the monkeys in the continuous forest.

Upon locating a group of bearded sakis, I tracked the same group from the time they awoke in the morning until the time they settled down for the night (approximately 0530 to 1730). Using group scan sampling techniques (Altmann 1974), every five minutes I recorded the group’s GPS coordinates, group size and composition, as well as the activity of each individual in sight. Activities included eating, traveling, moving, resting, and “other” (Table 8). Moving behavior was defined as vertical or horizontal movement within a single tree, but not explicitly associated with obtaining food items. The category “other” included all other behaviors that were not classified as eating, traveling, moving, or resting. All behaviors were tallied for each day of observation, and for each study cycle.

If individuals were eating fruit, flowers, or leaves, the tree or liana was marked with plastic flagging and assigned a unique number. The number identification system allowed for the subsequent identification of the plant species upon completion of the period of following the monkeys. It also assisted in monitoring the monkeys’ revisits to feeding trees during each cycle, as well as over the entire study period. Furthermore, I noted each tree’s GPS coordinates and diameter at breast height (DBH), as well as the condition of the fruit (ripe, unripe), flowers (adult, buds), or leaves (mature, immature) that were consumed.

Once the behavioral data collection was complete in April 2006, all flagged trees, hemi-epiphytes, and lianas were relocated using maps produced from the GPS data. Plant material samples were collected in order to identify the bearded saki's food sources. Identifications were conducted both in the field and the INPA herbarium in Manaus, Brazil.

It was possible to confirm that the bearded saki groups were the same each day during a cycle because they were tracked from the start to the end of their day's activity; however, as a result of large group sizes in the 100-ha fragments and continuous forest, as well as the tall, dense canopy cover, it was not possible to identify each individual. Therefore, it is not known whether there were fluctuations in group members throughout the cycles. It was possible to confirm that the general group was the same throughout each cycle (based on the appearance of particular infants, juveniles, and adults) for all study sites except for the continuous forest site Cabo Frio. Due to the configuration of the forest fragments, there was little probability that bearded saki monkeys from one forest fragment traveled into any other of this study's forest fragments.

Phenological data collection

Phenological data were also collected during each study cycle in 2005 and 2006 in order to account for seasonal changes in fruit and flower abundance. This fruit and flower census was conducted on the same day as the primate census, but neither census interfered with data collection for the other census. Trees, lianas, and hemiepiphytes with fruits and/or flowers were counted and identified along two parallel transects (approximately 10 m width) that were located in each of the 1-ha and 10-ha forest fragments. One transect bisected the forest fragment, and the other transect was located approximately halfway between the middle transect and the forest fragment's edge. In the 100-ha fragments data were collected along one long, linear transect instead of two due to the length (1000 m) of one transect. In order to compare the phenological surveys in the continuous forest and forest fragments, 1-ha, 10-ha, and 100-ha study plots were demarcated in both continuous forest study areas. Within each plot, linear transects were walked that were equivalent in width, length, and distance to study plot edge as their forest fragment counterparts. I conducted the phenology censuses along linear transects in order to account for plant species found both near and far from the forest fragments' edges. A total of 75 phenology censuses were conducted. In this chapter the phenological data for each of the two continuous forest sites was noted as one value (the number of fruiting plants per 100 m), instead of three values (1 ha, 10 ha and 100 ha censuses) for each continuous forest site, as there were no differences in fruit abundance per 100 m among the nine forest fragments and two continuous forest sites.

For each fruit and flower sighting along the transect, I classified the fruit state as ripe or unripe, classified the flower state as bud or open flower, recorded the GPS location of the tree, liana, or hemiepiphyte, measured the DBH of each tree, and photographed each fruit or flower sample. Fruit and flower abundance were separately tallied per 100 m for each transect during each of the five cycles to provide comparisons of seasonal fluctuations in fruit and flower abundance.

Diet comparisons between study sites

In order to determine whether differences in diet between the study groups were a result of plant species availability in the forest fragments, I checked the availability of the dietary tree species in the forest fragments by using the BDFFP tree database. This database, overseen via a long-term monitoring project currently managed by W. F. Laurance, provided the scientific names for a sample of trees in each of the four forest fragments where bearded saki monkeys resided. I examined the records for 21,033 trees in the four fragments where bearded saki monkeys were present in 2005-2006, although the number of entries in the database varied (#1202: 6454 trees, #2206: 2296 trees, #2303: 6251 trees, and #3304: 6032 trees).

For each unique dietary species, defined as a plant species that was consumed by only one bearded saki group at a single study site, I calculated the presence of the species in each of the four forest fragments using the BDFFP database. These comparisons did not include the two continuous forest sites because there were not enough data available in the database. Once comparisons between the bearded saki monkeys' diet and the presence of the diet species in the forest fragments were complete, I compared the dietary plant species with the phenological data that were collected in each forest fragment during each study cycle to determine whether or not these plant species produced fruit during the study. This comparison was essential because often individuals of the same plant species do not fruit at the same time, so the presence of a species in a forest fragment does not necessarily mean that the species was in fruit during the study period, or that the species would provide fruit in all locations.

Analysis

I tested whether forest size class (continuous forest, 100 ha, 10 ha, 1 ha) determined bearded saki group size, subgroup size, or density using Analysis of Variance (ANOVA) and I used Student's *t* to determine post hoc differences between forest size classes. Average group size, subgroup size, and density were calculated for each study site (*n*=7) that hosted bearded saki monkeys in 2003, 2005, or 2006, and these values were used in the ANOVA, based on the study area's size class (*n*=4). Average subgroup size was determined as the proportion of the average group size that was present during each behavioral scan. Data were arcsin square root transformed. Average densities were computed using the actual size of each forest fragment, and the home range size for the two continuous forest study sites. Home range size was calculated using the minimum convex polygon method from the Home Range Extension for ArcView (Rodgers and Carr 2002). Chapter 4 and Boyle *et al.* (In press) give further detail on how home range sizes were calculated. Note that analysis of forest size class involves forest fragments and continuous forest comparisons, while analysis of fragment size class involves only comparisons among forest fragments.

I used the Shannon-Wiener Index of Diversity H_s (Shannon 1948, Zar 1999, Peetz 2001) to determine a value for the diet diversity, based on feeding records for each study site (n=6) where the monkeys were present in 2005 and 2006. I did this in order to compare diet diversity between BDFFP sites, as well as to later compare this study's results to previous studies of *Chiropotes* (Ayres 1989, Peetz 2001, Veiga 2006). Comparisons of diet diversity among bearded saki groups living in three forest size classes were completed using ANOVA. Seasonal comparisons of diet diversity were also made among the data cycles with repeated-measures ANOVA. Such seasonal comparisons were completed only for bearded saki groups that were present in their study area during all five data collection cycles.

A measure of evenness, J', was also computed for the bearded saki monkeys' diets (Zar 1999, Peetz 2001). Evenness measured the homogeneity of the plant species consumed. Values approaching 1 indicated homogeneity among the feeding records. Diet evenness was analyzed among bearded saki groups living in three forest size classes using ANOVA, and among data cycles using repeated-measures ANOVA. I tested whether there was a difference in the DBH of the feeding trees based on the forest size class using ANOVA. I used a *G* test to analyze the distribution of the unique dietary species among the six study sites. Comparisons between the species that were fruiting and the species that were eaten by the bearded saki monkeys were analyzed across all forest size classes using ANOVA.

I conducted regressions between the independent variable forest size and the dependent variables eating, traveling, resting, moving, and “other.” Forest size was defined as the actual size of the forest fragment. In the continuous forest, forest size was defined as the home range size for the bearded saki monkeys, since the monkeys did not use the entire area of continuous forest. Forest size data were $\log_{10}$-transformed in order to meet normality assumptions. Sample sizes were unequal because the monkeys left and re-entered some of the forest fragments, and group size varied greatly between study sites and within a group throughout the day. Therefore, I standardized the behavioral scans by calculating the number of observations of the particular behavior per individual per hour. Seasonal variations in activity budget were analyzed based on three-month periods using repeated-measures ANOVA.

The proportion of fruit, flowers, insects, and leaves in the bearded saki monkeys’ diets was determined for each study group. Data were arcsin square root transformed. Differences in the proportion of fruit in the diet across forest size classes were determined using ANOVA. Seasonal differences in the proportion of fruit in the diet were analyzed using repeated measures ANOVA.

RESULTS

Presence in Fragments

Bearded saki groups were present in five of the nine forest fragments (one 1-ha, two 10-ha, and two 100-ha fragments); however, only the groups in the 10-ha fragments were permanent residents during the study period (Table 9). There were no bearded sakis in any of the four 1-ha fragments, with the exception of the presence of one sub-adult male in a 1-ha fragment (#2107) in July-August 2003. It is not known whether this individual left the forest fragment or died.

Two of the 10-ha fragments (#1202 and #2206) each contained one bearded saki group. These two groups were always present in the fragments in July-August 2003 and January 2005-April 2006. I never witnessed either group leaving the forest fragment. Bearded sakis monkeys were never present during censuses of the remaining 10-ha fragment (#3209) at Porto Alegre.

Each 100-ha fragment hosted one bearded saki group. Although one 100-ha fragment (#2303) had a bearded saki group present in each of the study cycles, the monkeys frequently left and re-entered this forest fragment. The monkeys also left and re-entered the other 100-ha forest fragment (#3304), and they were present for only two data cycles during the course of this study.

Group size

Bearded saki group size varied from 1 to 35 individuals. As forest size class increased, so did group size ($F_{3,3}$=43.80, P=0.0056). Average group size (±standard error) was 22.89 (±5.09) in the two continuous forest sites, 12.15

(±1.44) in the 100-ha fragments, 3.79 (±0.21) in the two 10-ha fragments that hosted bearded sakis, and 1 (±0.00) in the 1-ha fragment in 2003 (Fig. 15). There was no statistical difference between bearded saki group size in the 10-ha and 1-ha fragments, but all other pairwise comparisons between forest size classes were significant. Group size at the 10-ha fragment #2206 remained constant at four individuals during the 2003 and 2005-2006 study periods. Group size also remained constant at four individuals for the group inhabiting the 10-ha fragment #1202 until October 2005 when the adult female disappeared. The female was never spotted again, and it is unknown whether she left the fragment or died. No new individuals joined either of the "permanent" bearded saki groups in the 10-ha fragments.

Single offspring births occurred from mid-October to early-November 2005 (early wet season) in groups that frequented the 100-ha fragments, as well as in groups from the continuous forest. During the study period from 2003-2006, there were no births with successful infant survival in either of the two bearded saki groups residing in the two 10-ha fragments.

All groups were multi-male and multi-female in composition throughout the study, except for the lone subadult male in the 1-ha fragment in 2003, and the group in fragment #1202 that lost an adult female in October 2005.

The average proportion of the group that was present throughout the day's behavioral scans was 37.3% (±12.08) in continuous forest, 54.56% (±0.16) in 100-ha fragments, 67.57% (±1.52) in 10-ha fragments, and 100% (±0.00) in the

1-ha fragment. Bearded saki monkeys in the smaller forest size classes had a greater proportion of the group present during scans than did the monkeys in the larger forest size classes ($F_{3,3}$=18.01, P=0.02). There was no statistical difference between bearded saki densities in the continuous forest, and 100-ha and 10-ha fragments, but all pairwise comparisons between the 1-ha fragment and the other size classes were significant. When the data from the 1-ha fragment were omitted from the analysis, the differences were not significant at an alpha level of 0.05 ($F_{2,3}$=4.53, P=0.12).

Density

Of the seven study areas where bearded sakis were found from 2003-2006, the smaller forest size classes had greater densities of bearded saki monkeys than the larger forest size classes ($F_{3,3}$=35.75, P=0.0076; Fig. 16). When the monkeys were present in a study area, average density (±standard error) was 0.05 (±0.018) individuals/ha in the continuous forest, 0.12 (±0.012) in the 100-ha fragments, 0.32 (±0.050) in the two 10-ha fragments, and 0.56 (±0.00) in the one 1-ha fragment. Home ranges were calculated as 300 ha and 559 ha in the two continuous forest sites. There was no statistical difference between bearded saki densities in the 100-ha fragments and the continuous forest, but all other pairwise comparisons between forest size classes were significant.

Diet

There were 993 trees, lianas, and epiphytes that provided food for bearded sakis during the behavioral observations in 2005-2006. These included 47 families, 115 genera, and 244 species (Appendix A). Identification was not successful for 19 of the 933 specimens.

The families Sapotaceae, Lecythidaceae, Chrysobalanaceae, and Euphorbiaceae were most prevalent in the bearded sakis' diet (Table 10) in 2005-2006. Lianas and epiphytes represented 17.02% of the overall bearded saki diet, and there was no difference in the proportion of lianas and epiphytes in the diet across forest size classes ($F_{2,3}$=0.27, P=0.78).

There was little dietary overlap across all six inhabited sites (four forest fragments and two areas of continuous forest) in 2005-2006 (Table 11). Bearded sakis consumed only four species (1.64% of the pooled flora) in all six study areas. These species were *Ecclinusa guianensis* (Sapotaceae), *Eschweilera truncata* (Lecythidaceae), *Hevea guianensis* (Euphorbiaceae), and *Micropholis guyanensis* (Sapotaceae). Sixty-five percent (n=158) of all species eaten were consumed by bearded saki monkeys in only one of the six study sites. These species are designated as "unique species" in this chapter. There was no relationship between the proportion of a bearded saki group's diet that was unique and the forest size class in which the group resided ($F_{2,3}$=0.61, P=0.60).

Of the 158 unique species, 15 (9.49%) were species that were fruiting in at least on other occupied study site, but were not part of the diet of the bearded saki monkeys that resided in that study site. Of these 15 species, 11 (73.33%) were from 10-ha fragment #1202, which represented 22% of that study site's unique species (the other study sites had 0-8% of their unique species in fruit elsewhere). Eleven (6.96%) of the unique species were tree species that were not present in any other forest fragment, according to the BDFFP database. Of these 11 species, 10 (90.91%) were found solely in the continuous forest. This distribution was not random (G=26.64, df=5, P<0.001).

Overall, lianas and hemi-epiphytes comprised 28% of the unique species. Because the BDFFP database only represents trees with a DBH of 10 cm or greater, it was not possible to perform a comparison of the presence of lianas and hemi-epiphytes in the study areas that was as detailed as that completed with trees.

DBH of all of the feeding trees in 2005-2006 ranged from 9-134 cm, with an average (±standard error) overall DBH of 37.91 (±0.59) cm overall. Average DBH did not differ among forest size classes ($F_{2,3}$=0.013, P=0.99). Average DBH was 38.46 (±0.87) cm in continuous forest, 37.76 (±1.03) cm in 100-ha fragments, and 37.48 (±1.15) cm in the two 10-ha fragments where bearded saki monkeys ate. Of the 933 trees, hemiepiphytes, and lianas that were consumed by the bearded saki monkeys, 94.12% served as a fruit resource for the monkeys, 5.03% as a flower resource, and 0.86% as a leaf resource.

Diet diversity was relatively high, ranging from H_s=3.05 to H_s=3.85. Diet diversity did not differ among forest size classes ($F_{2,3}$=0.26, P=0.79). There were no seasonal differences in diet diversity ($F_{4,1}$=5.31, P=0.31). There were inadequate data to compare diet seasonally in the fragment #3304, as bearded saki monkeys were present in only two of the five cycles. Evenness, the measure of homogeneity among plant species in the diet, ranged from J'=0.71 to J'= 0.92, indicating that bearded saki groups consumed the species fairly evenly. There was no difference in evenness among groups inhabiting different forest size classes ($F_{2,3}$=0.12, P=0.89), nor was there any difference in evenness between seasons ($F_{4,1}$=1.21, P=0.59).

Phenology and diet

Fruit abundance during Cycle 2 (April-June 2005) and Cycle 3 (August-October 2005) was lower than during Cycle 1 (January-March 2005), Cycle 4 (October-December 2005), and Cycle 5 (January-March 2006; $F_{4,4}$=8.08, P=0.034). Neither forest size class ($F_{3,7}$=1.70, P=0.25) nor the interaction between cycle and forest size class ($F_{12,11}$=0.46, P=0.90) had an effect on fruit abundance, defined as the number of trees with fruit per 100 m (not the number of trees in fruit in each study area uncorrected for area size). Overall, the trend in fruit abundance paralleled the amount of rainfall during that time period ($F_{1,13}$=9.15, P=0.0098; See Fig. 10 from Chapter 2).

Bearded saki monkeys did not consume all species of available fruit in the forest. Overall, of the 141 plant species in fruit during the phenological surveys of the six study sites where the species was present in 2005-2006, 51 (36.17%) of the plant species were never part of the monkeys' diet in any of the study sites.

Bearded saki monkeys were never noted eating the fruit from 24 genera of trees, hemi-epiphytes, and lianas that were in fruit during the censuses (Table 12). There was no difference among size classes in the proportion of fruit in the censuses that was not eaten by the monkeys in the particular study site ($F_{2,3}$=1.15, P=0.42), the proportion of fruit in the censuses that was never eaten by any bearded saki groups ($F_{2,3}$=1.28, P=0.40), or the proportion of fruit in the censuses that was not eaten at the site but was part of another group's diet elsewhere ($F_{2,3}$=1.72, P=0.32).

Activity budget

In 2003, 2005, and 2006, the overall behavioral activity budget (±standard error) for all seven bearded saki groups included: resting 46.56% (±5.17), eating 24.95% (±2.87), traveling 21.34% (±3.95), moving 3.58% (±0.44), and "other" 3.55% (±0.99). "Other" consisted of vocalizations (95.53%), defecation and/or urination (3.02%), and grooming, copulating, play behavior, and aggressive displays (1.45% combined). Copulations were witnessed in a continuous forest site (Cabo Frio) on June 18, 2005, and twice on August 20, 2005 in a 100-ha forest fragment (#2303).

When the activity budgets were compared among forest size classes, most of these budgets deviated from the overall activity budget presented above. Groups living in smaller forest size classes rested more often ($F_{1,5}$=6.84, r=-0.75, P=0.047), traveled less frequently ($F_{1,5}$=79.63, r=0.97, P<0.001), and exhibited "other" behaviors ($F_{1,5}$=10.46, r=0.82, P=0.023) less frequently than did bearded saki groups inhabiting larger forest size classes (Fig. 17). Vocalizations, which comprised almost 96% of the "other" behaviors, were then analyzed separately from the "other" behaviors, and groups in larger forest size classes vocalized more often than did groups inhabiting smaller forest size classes ($F_{1,5}$=10.41, r=0.82, P=0.023). There was no relationship between forest size class and time spent feeding ($F_{1,5}$=0.001, r=0.016, P=0.97) or moving ($F_{1,5}$=0.18, r=0.19, P=0.69). There were no seasonal differences in eating ($F_{3,1}$=1.77, P=0.49), resting ($F_{3,1}$=0.32, P=0.83), traveling ($F_{3,1}$=0.73, P=0.67), moving ($F_{3,1}$=4.85, P=0.32), and "other" ($F_{3,1}$=4.65, P=0.33) behavior.

Based upon combined feeding scans for all bearded saki groups, the monkeys ate seeds (83.30%), fruit (16.70%), flowers (4.31%), insects (2.4%), leaves (0.47%), and unknown substances (2.4%). The seeds and fruit consumed were from unripe (54.59%) and ripe (45.41%) fruits. There were no differences in the proportion of fruit (fruit and seed material combined) in the diets among forest size classes ($F_{2,3}$=0.91, P=0.49; Fig. 18). When seed and fruit material were analyzed as separate items, there were no differences in either the proportion of seeds and fruits in the diet ($F_{2,3}$=2.00, P=0.28) or the proportion of ripe and unripe fruits ($F_{2,3}$=2.30, P=0.25) among forest size class. Diets did not differ significantly with respect to the proportion of flowers, insects, and leaves eaten in the different forest size classes (P>0.05 for all). Although the proportion of fruit in the diet was greatest during Cycles 1, 2, and 5, there were no seasonal differences in fruit consumption (fruits and seeds combined) by the bearded sakis

($F_{4,1}$=3.01, P=0.41). Taken separately, there also were no seasonal differences in either the proportion of seeds in the diet (P>0.05), or the proportion of unripe fruit in the diet (P>0.05).

DISCUSSION

Although frugivores are often assumed not to be able to survive in small forest fragments, this study shows that some species are capable of residing in areas that are drastically smaller than the species' home range size in continuous forest. However, northern bearded saki monkeys living in such fragments showed extreme variability with respect to their social group size and density, dietary species consumed, and relative frequency of traveling, resting, and "other" behavior. Such flexibility allowed them to reside in forest fragments that corresponded to as little as 2% of the species' characteristic home range size. Other aspects of the species' feeding behavior, such as the proportion of fruit in its diet, diet diversity values, and proportion of time spent feeding, did not differ between groups living in continuous forest and those living in forest fragments. Although the monkeys that were restricted to 10-ha fragments ate as frequently and as diverse a dietary selection as their continuous forest counterparts, notable differences between the consumption of preferred plant species existed. This outcome might result in differential nutrient value of the animals' diet. Overall, the reliance on a forest fragment's limited sample of trees and the physical isolation of a group of monkeys from the rest of the population could have deleterious consequences on the future health and viability of the population.

Social groups

Northern bearded saki monkey groups were drastically smaller when forest size was limited. This finding was true even when the one individual that resided in the 1-ha forest fragment during the study period in 2003 was omitted from the analysis. The average group size in a 10-ha forest fragment was almost one-sixth of the average group size in the continuous forest. This result was not a surprise, as a smaller area has limited resources and would not be expected to support as many individuals as a larger area could (Chapman 1990).

Density of individuals was greater in small forest fragments than larger areas. A study of birds in the BDFFP fragments found density to increase immediately after isolation of the fragments, and then decrease (Lovejoy *et al.* 1986). In the case of bearded saki monkeys, none of the forest fragments hosted the species immediately after isolation of the forest fragments, and it took 7-19 years for northern bearded saki monkeys to recolonize these forest fragments. Although some of the forest fragments provided resources to the monkeys, at least temporarily, there may be long-term consequences of living in these fragments. Higher density groups living in forest fragments are often more prone to parasites (Gilbert 1994) and, in some animal taxa, disease (Allan *et al.* 2003), than are animals living in undisturbed areas. Furthermore, an overabundance of fauna can lead to changes in tree recruitment patterns (Terborgh *et al.* 2001), thereby affecting the fragment's plant composition.

Diet

During the course of this study, bearded saki diets consisted primarily of fruits (seeds, endocarp and mesocarp), but flowers, insects, and young leaves were also present. Although a trend existed for fruit consumption to be greater during the wet season, with flower and leaf consumption greater in the dry season, the proportion of fruit in the diet remained high even during periods of low fruit abundance. This result stresses the importance of fruit in the bearded saki diet, and suggests that fruit resources were adequate throughout the year to support the monkeys, even in relatively small forest fragments.

The diets of primates are not static (Chapman and Chapman 1990). The fact that 64% of the total plant species consumed were eaten by only one of the six bearded saki groups in this study indicates that these monkeys are capable of consuming a large variety of plant types. Overall, the families, genera, and species that were most often consumed by the bearded saki monkeys were those from the most common plant families in the study area; however, this pattern did not hold for all study groups. For example, the most frequently consumed species in both 10-ha fragments was *Protium hebetatum* (Burseraceae), yet none of the bearded saki groups from the 100-ha fragments or continuous forest sites ate this species or genus regularly, even though *Protium* was both present and producing fruit in all of the other study sites. This observation suggests that some species, such as those in the genus *Protium*, may not be a preferred food when other options are available, as was the case in the large forested areas.

Further evidence indicates that bearded saki monkeys are not completely generalist frugivores, as the monkeys never consumed plant material from 17 genera that produced fruit during the study. Additional research is needed in order to determine whether similarities exist (i.e., chemical compounds, feeding accessibility) between the 17 genera that were avoided by the monkeys.

Comparisons with other studies of bearded saki monkeys also suggest regional differences in feeding patterns. Consumption of fruits from lianas and epiphytes was greater in this study (17%) than by the bearded saki monkeys studied by van Roosmalen *et al.* (1988) in Suriname, although the sample size was greater in my study (6,495 feeding observations representing 244 species of plant consumed compared with 217 feeding observations of 85 plant species consumed in the study by van Roosmalen *et al.* (1988)). Comparisons of the dietary overlap between the two studies, measured by the percentage of the diet in the Suriname population compared with that in my study, showed an 80% overlap in families, a 40% overlap in genera, and a 16% overlap in species. Dietary similarity between the BDFFP bearded saki monkeys and bearded saki monkeys in Venezuela (Peetz 2001) was low. Of the 94 identified species in Peetz (2001), 51% of the families, 22% of the genera, and 2% of the species were also eaten by the bearded saki monkeys in my study. Furthermore, BDFFP bearded saki monkeys exhibited a greater dietary diversity and greater dietary evenness than bearded saki groups in Venezuela (Peetz 2001) and eastern Brazil (Veiga 2006). Therefore, overall, there appears to be regional flexibility in food consumption patterns.

Seed predation

Bearded saki monkeys (*Chiropotes* spp.) have dental adaptations associated with seed predation, such as widely flaring canines that aid in opening hard fruits (Kinzey and Norconk 1990) and uneven dental enamel infused with Hunter-Schreger bands that assist during chewing and prevent tooth wear (Kinzey 1992, Martin *et al.* 2003). Some seeds are a nutritious dietary resource, high in lipids, proteins, and sugars (Norconk *et al.* 1998), but the concentration of nutritional material varies among plant species, and bearded saki monkeys consume seeds of varying quality (Kinzey and Norconk 1993, Norconk *et al.* 1998).

Frugivores typically have large home ranges, and often highly frugivorous species are not found in areas of intense disturbance and forest fragmentation (Skorupa 1986, Johns and Skorupa 1987). In contrast, bearded sakis were found throughout forest fragments ranging in 1-100 ha in size, and they were always located in two 10-ha forest fragments during the entire study. It is possible that the high proportion of seeds in their diet helps bearded sakis during periods of low food availability (Norconk 1996, 2007). Furthermore, seed-eating can minimize competition with other frugivores for resources (van Roosmalen *et al.*

1988). Therefore, it may be that the high incidence of seed predation allows bearded saki monkeys to reside in forest fragments that are smaller than the species' natural home ranges. Other species with high proportions of fruit in their diet that are not typically found in forest fragments (i.e., *Ateles*) primarily eat ripe fruit (Estrada and Coates-Estrada 1996). By eating seeds of unripe and ripe fruit, as well as the endocarp and mesocarp of ripe fruit, bearded sakis manage to obtain fruit resources throughout the year. In my study, northern bearded saki monkeys consistently ate a high proportion of seeds from unripe and ripe fruit

Activity budget

There was great variation in the activity budgets of the northern bearded saki monkeys. Travel time increased with forest size. This was expected, as bearded sakis have large home ranges and typically travel long distances daily. Resting behavior increased as forest size decreased, which is not surprising since these animals were not traveling as frequently. A third behavior that differed between bearded saki groups was "other," which was primarily behavior associated with sociality, such as vocalization, grooming, and copulation. Vocalization comprised almost 96% of all "other" behaviors, and this behavior was more often exhibited in larger forest size classes than smaller forest size classes. In continuous forest and large forest fragments, bearded saki monkeys lived in large social groups that split and re-joined throughout the day, and thus vocalizations would provide a way to communicate between the subgroups. In smaller patches where there were fewer individuals, and these individuals could better keep track of one another visually, these behaviors decreased in frequency. Although the monkeys in the 10-ha fragments did spread out during the day, with two individuals often remaining together, vocalizations occurred less frequently than in larger areas where the monkeys would have more difficulty keeping monitoring the location of the other group members visually. Overall, it appeared that subgroups were forming more frequently in the larger forest size classes, as the monkeys vocalized more and the proportion of the actual group size that was present during the behavioral scans throughout the day was greater in the smaller forest fragments. Alternatively, the data on the proportion of the group present for the behavioral scans may have been influenced by the size of the social group, as it would be more difficult to keep track of 35 individuals than 1 individual. Although it is likely that there was a bias towards more accurate subgroup counts in the 10-ha fragments because total group size was ≤4, the average number of individuals present during a behavior scan in the continuous forest was one-third of the total group size. I think that it was very unlikely that so many individuals (approximately 10-15 monkeys) were overlooked in the behavioral scans in the continuous forest.

Note, however, that there was no difference between bearded saki groups in terms of the amount of time spent feeding. The animals living in smaller, restricted areas fed just as frequently as those in continuous forest, although their traveling time between trees was reduced.

Conclusions

Although northern bearded saki monkeys were present in forest fragments that were fractions of their typical home ranges in continuous forest, the monkeys did not reside in all of the available fragments. Furthermore, they left and re-entered both 100-ha fragments on several occasions during this study, suggesting that the monkeys used these areas opportunistically. Both 100-ha fragments were connected to continuous forest via corridors of tall secondary growth forest (see Chapter 2 for details and analysis), therefore the animals were not restricted to the 100-ha fragments as were the monkeys living in the more isolated 10-ha fragments. Given the large home ranges in continuous forest, and the movement of bearded saki monkeys in and out of the 100-ha fragments, the two bearded saki groups that were restricted to 10-ha fragments appeared to face movement barriers due to the isolation of their forest remnants. These barriers are not necessarily absolute, as in the 1990s, bearded saki monkeys traveled across the matrices in order to enter the two 10-ha fragments.

Continued monitoring of the bearded saki groups living in the two 10-ha fragments is necessary, as the 10-ha fragments may not be providing adequate long-term resources. Also there is a need for further attention to reproductive patterns. Copulations were witnessed in June and August 2005, and infants were noted in both 100-ha groups and both continuous forest groups in November and December 2005 (early wet season). Bearded saki monkeys reach sexual maturation at approximately 36 months, and interbirth interval is greater than 24 months (Peetz 2001). Given the lack of young juveniles in the 10-ha fragments since 2003, it would appear that there had not been a successful birth in either 10-ha group for at least 3.5 years (November 2002 to June 2006). Terborgh *et al.* (2001) found howler monkey reproduction was repressed on small islands with high howler monkey densities.

Finally, although no differences were found in the proportion of time spent feeding and the diversity and evenness of the bearded saki monkeys' diets at BDFFP, it is important to note two major findings from this study. First, monkeys residing in the small forest fragments lived in uncharacteristically small social groups and at a greater density than their counterparts living in continuous forest. Second, monkeys residing in the small forest fragments were restricted by the forest fragment's plant composition, and thereby appeared to consume certain plant species that were present, but not consumed as frequently, if at all, by northern bearded saki groups living in larger areas. Future changes in resource abundance due to both abiotic and biotic factors could severely affect such groups.

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TABLE 8. Ethogram.

Behavior	Description
Eating	Consumption or handling of food items.
Traveling	Movement between two trees.
Moving	Movement (horizontal or vertical) within one tree. Not explicitly associated with obtaining food items.
Resting	Remaining in one location, and not exhibiting any other behaviors. In sitting or prone positions.
Other	All other behaviors. Included vocalization, copulation, grooming, defecation, and urination.

Notes: Behavioral scan sampling was conducted every five minutes for each bearded saki individual in sight.

TABLE 9. Bearded saki monkey presence in forest fragments from 2003-2006.

	Present	Persistence (%)	Status	Absent
100-ha fragments	#2303	100	Nomadic	
	#3304	33	Nomadic	
10-ha fragments	#2206	100	Permanent	#3209
	#1202	100	Permanent	
1-ha fragments	#2107	17	2003 only	#1104 #2108 #3114

Notes: Bearded saki monkeys were present in all three size classes of forest fragments; however, the species was permanently resident in only two forest fragments during the study period. Persistence is defined as the percentage of censuses that a bearded saki group was present in the forest fragment.

TABLE 10. Plant species commonly consumed by northern bearded saki monkeys.

Family	% Diet (*n*)	Genus	% Diet (*n*)	Species	% Diet (*n*)
Sapotaceae	23 (207)	*Eschweilera* (Lecythidaceae)	12 (109)	*Micrandropsis scleroxylon* (Euphorbiaceae)	5 (47)
Lecythidaceae	14 (131)	*Pouteria* (Sapotaceae)	11 (95)	*Eschweilera truncata* (Lecythidaceae)	4 (41)
Chrysobalanaceae	8 (71)	*Licania* (Chrysobalanaceae)	6 (54)	*Ecclinusa guianensis* (Sapotaceae)	3 (26)
Euphorbiaceae	7 (68)	*Micrandropsis* (Euphorbiaceae)	5 (47)	*Licania heteromorpha* (Chrysobalanaceae)	3 (23)
Leguminosae	6 (56)	*Pourouma* (Cecropiaceae)	4 (38)	*Eschweilera wachenheimii* (Lecythidaceae)	2 (22)

Notes: Number of feeding trees for each category (*n*) is presented.

TABLE 11. Dietary comparisons among forest size classes.

	Continuous forest sites		
Continuous forest Km41	%	Continuous forest Cabo Frio	%
Xylopia callophylla	11.40	*Micrandropsis scleroxylon*	19.38
Eschweilera cyathiformis	7.80	*Ecclinusa guianensis*	9.30
Manilkara bidentata	6.60	*Eschweilera truncata*	7.75
Ecclinusa guianensis	5.16	*Coeupia longipendula*	6.98
Anacardium spruceanum	3.78	*Dulacia guianensis*	6.98
	100-ha fragments		
Fragment #2303	%	Fragment #3304	%
Licania lata	26.18	*Pourouma bicolor*	7.95
Xylopia polyantha	11.99	*Moutabea guianensis*	7.95
Xylopia calophylla	10.37	*Micrandropsis scleroxylon*	7.28
Licania heteromorpha	7.19	*Couratari stellata*	6.62
Eschweilera truncata	2.85	*Chrysophyllum sanguinolentum*	6.62
	10-ha fragments		
Fragment #2206	%	Fragment #1202	%
Protium hebetatum	20.60	*Protium hebetatum*	7.94
Miconia burchelli	10.20	*Inga splendens*	7.79
Eschweilera truncata	8.01	*Croton lanjouwensis*	4.08
Eschweilera coriacea	6.97	*Qualea labouriauna*	4.08
Osteophloeum platyspermum	4.89	*Swartzia recurva*	4.01

Notes: Presented are the top five dietary species for each study area, and the percent of feeding records in the study area that the plant species represent.

TABLE 12. Uneaten plant genera.

Family	Genus
Annonaceae	*Ephedranthus* *Guatteriopsis*
Apocynaceae	*Aspidosperma* *Tabernaemontana*
Aracaceae	*Astrocaryum* *Euterpe* *Oenocarpus* *Socratea*
Bignoniaceae	*Cuspidara*
Cecropiaceae	*Cecropia*
Cyclantaceae*	*Asplundia*
Lauraceae	*Licaria* *Mezilaurus*
Leguminosae	*Dinizia*
Moraceae	*Sorocea*
Myristicaceae	*Virola*
Myrtaceae	*Calyptranthes* *Eugenia*
Passifloraceae	*Dilkea*
Rubiaceae	*Coussarea* *Isertia*
Sapindaceae*	*Talisia*
Sterculiaceae*	*Theobroma*
Violaceae	*Rinorea*

Notes: Bearded saki monkeys never consumed plant material from 24 genera of plants that produced fruit during the phenological censuses in the six study sites where bearded saki monkeys were present in 2005-2006. Three plant families (indicated by *) were never consumed by the monkeys.

FIG. 15. Average group size. Bearded saki group size was greater in larger forest size classes than smaller ones ($F_{3,3}$=43.80, P=0.0056). There was no statistical difference between group size in the 10-ha fragments and the 1-ha fragment. Mean group size and standard error bars are presented.

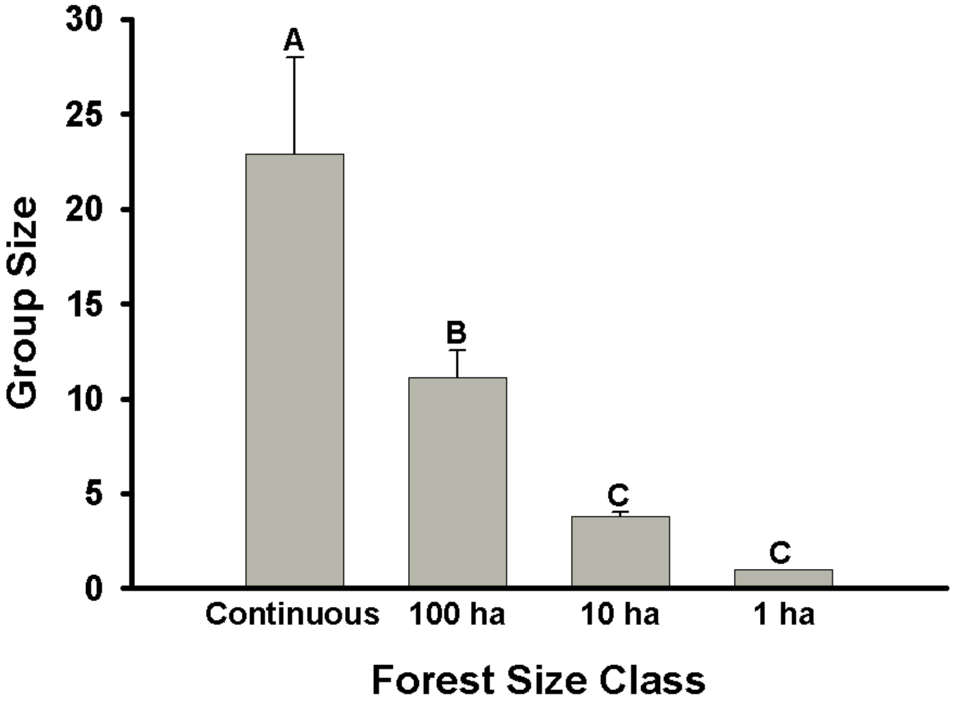

30
25
20
15
10
5
0
Group Size
A
B
C
C
Continuous
100 ha
10 ha
1 ha
Forest Size Class

FIG. 16. Bearded saki monkey density. Bearded saki density was greater in smaller forest fragments than in 100-ha fragments and continuous forest ($F_{3,3}$=35.75, P=0.0076). There was no statistical difference between densities in the 100-ha fragments and the continuous forest. Mean density and standard error bars are presented.

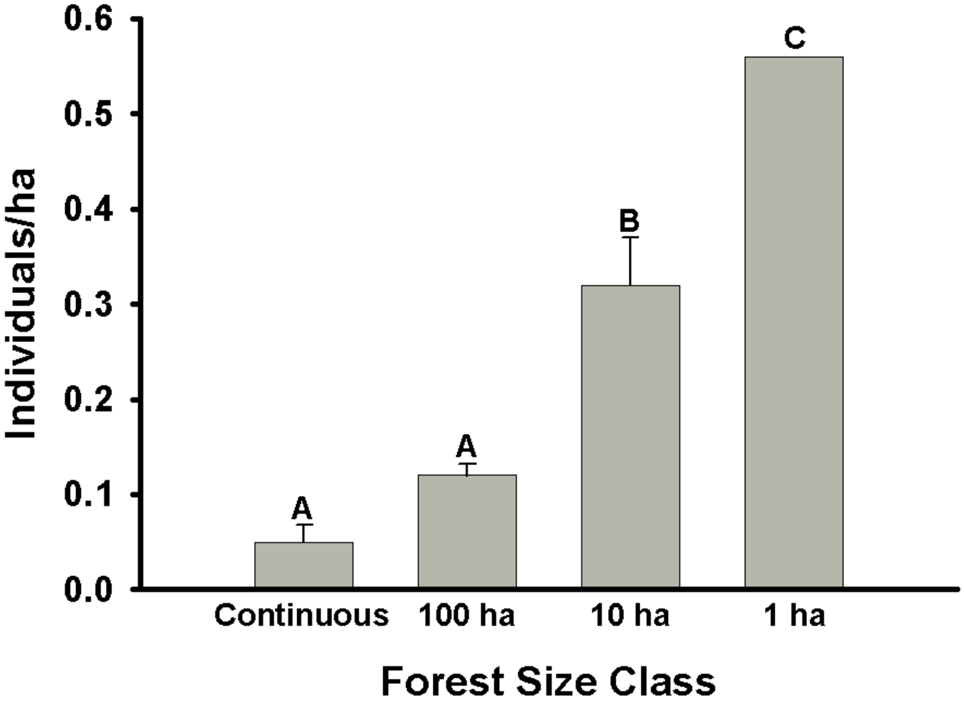

0.6
0.5
0.4
0.3
0.2
0.1
0.0
Individuals/ha
A
A
B
C
Continuous
100 ha
10 ha
1 ha
Forest Size Class

FIG. 17. Bearded saki monkey behavior. The frequency of traveling and "other" behavior decreased with decreases in forest size class, while the frequency of resting behavior increased with decreases in forest size class. Eating and moving frequencies did not correlate to forest size ($p>0.05$). Behaviors that varied with forest size are indicated with *. Means and standard error bars are presented.

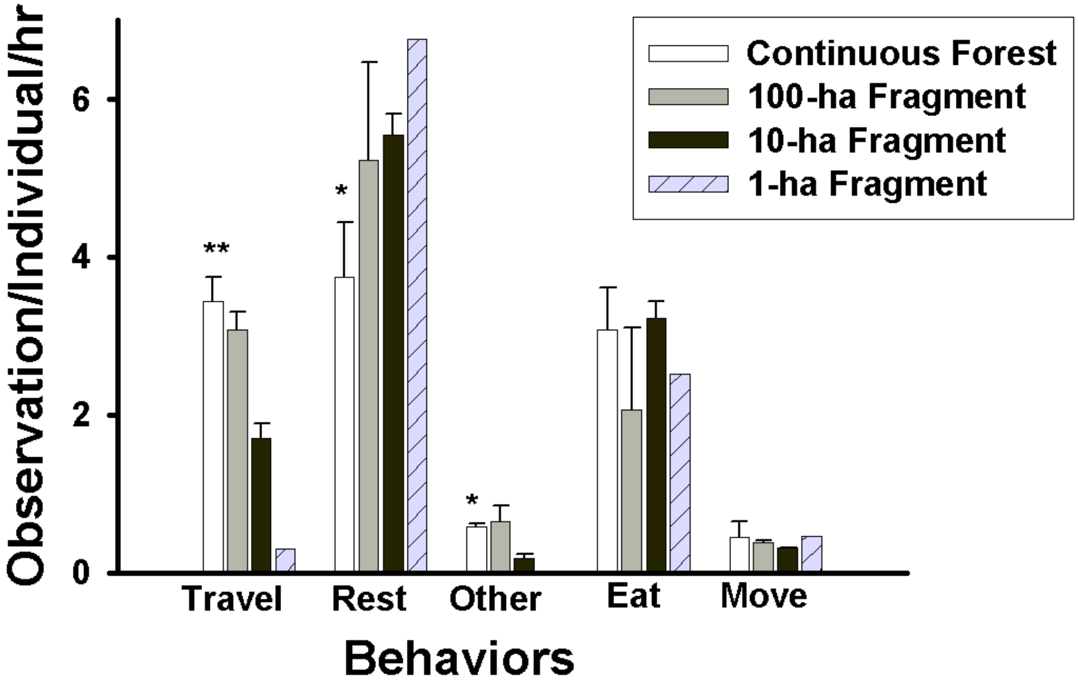
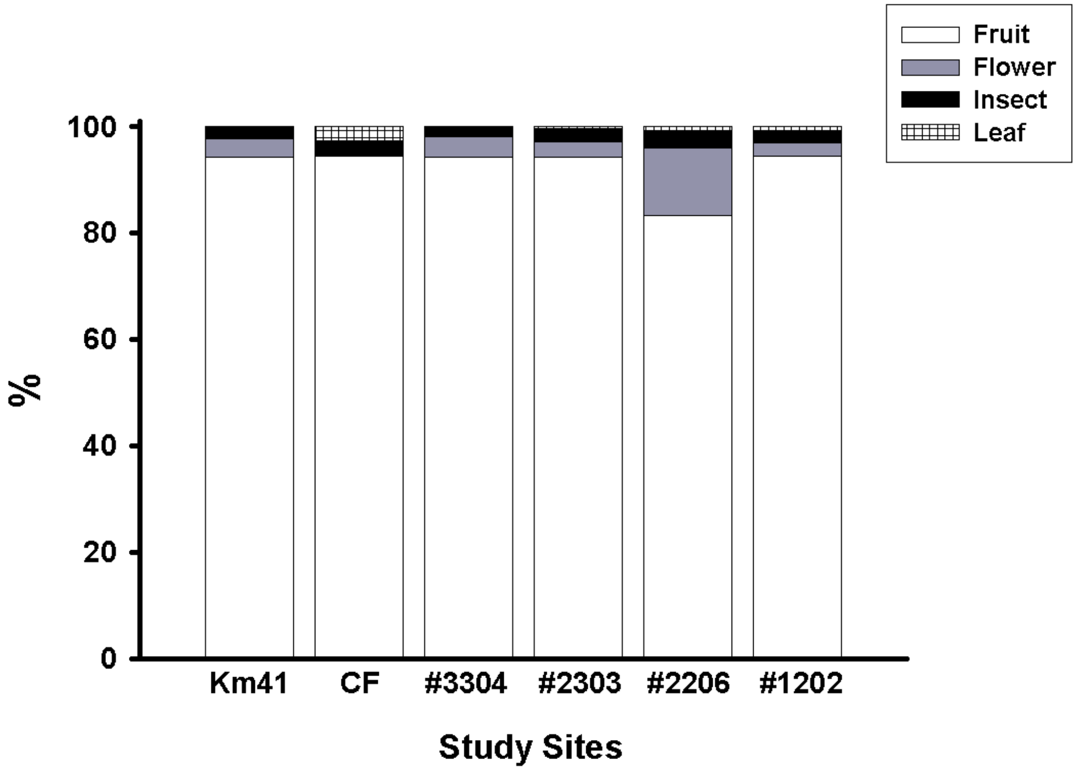

Observation/Individual/hr
0
2
4
6
**
*
*
Travel
Rest
Other
Eat
Move
Behaviors
Continuous Forest
100-ha Fragment
10-ha Fragment
1-ha Fragment

FIG. 18. Bearded saki monkey diet. There was no difference in diet composition among groups compared by forest size class (*P*>0.05). (Continuous forest sites: KM41 and CF; 100-ha fragments: #3304 and #2303; and 10-ha fragments: #2206 and #1202).


Fruit
Flower
Insect
Leaf
100
80
60
40
20
0
%
Km41
CF
#3304
#2303
#2206
#1202
Study Sites

CHAPTER 4

SPATIAL USE OF FOREST FRAGMENTS BY NORTHERN BEARDED SAKI MONKEYS (*CHIROPOTES SAGULATUS*) IN THE BRAZILIAN AMAZON

Abstract. Northern bearded saki monkeys (*Chiropotes sagulatus*) are medium-bodied frugivores with large home ranges; however, they can reside in forest fragments that are significantly smaller than the species' characteristic home range size. This chapter examines how the spatial use of forest differs between groups living in forest fragments of three size classes (1 ha, 10 ha, and 100 ha) versus continuous forest. Data were collected in six research cycles from July-August 2003 and January 2005-June 2006 at the Biological Dynamics of Forest Fragments Project (BDFFP), approximately 80 km north of Manaus, Brazil. For each cycle, the monkeys were followed from dusk until dawn in each of the study sites for three consecutive days. Every five minutes the location of the group was noted using a handheld GPS. Analyses of the monkeys' travel patterns were conducted using the Home Range Extension and Animal Movement Spatial Analysis for ArcView. Bearded saki monkeys living in small fragments had smaller day ranges, traveled shorter daily distances, revisited a greater percentage of feeding trees, and traveled in more circular patterns than their counterparts in the continuous forest. Furthermore, animals in the smaller fragments used the forest fragments uniformly, while animals in the 100-ha and continuous forest had clumped distributions of ranging activities. In addition, bearded saki monkeys did not use all habitat types equally; therefore, it is important to consider a species' habitat preferences when establishing conservation and management plans.

INTRODUCTION

A home range is the area in which an individual engages in its regular activities (Burt 1943). There are many methods for estimating home range (Worton 1987, Harris *et al.* 1990, Powell 2000), as well as various applications of home range size and use measures. These applications include, but are not limited to, determining relationships between home range size and species' characteristics (Harvey and Clutton-Brock 1981, Mace and Harvey 1983, Haskell *et al.* 2002), habitat preferences (Cederlund and Okarma 1988, Gese *et al.* 1988, Tufto *et al.* 1996), seasonal and annual fluctuations (Li *et al.* 2000, Wiktander *et al.* 2001, Börger *et al.* 2006b), and sex differences (Attuquayefio *et al.* 1986, Fedigan *et al.* 1988), as well as applications to conservation and management (Bull and Holthausen 1993, Bingham and Noon 1997, Linnell *et al.* 2001). Furthermore, home range size is often used to predict a species' vulnerability to habitat loss, although the strength of such predictions have varied (Skorupa 1986, Johns and Skorupa 1987, Onderdonk and Chapman 2000).

One means by which a species' habitat is destroyed is through forest fragmentation. During this process, forested areas are cleared, consequently leaving a mosaic of forest patches surrounded by a non-forested matrix. Often these remaining forest patches are smaller than what is characteristically required for survival by some fauna. For example, large-bodied, frugivorous primates typically require large home ranges (Milton and May 1976, Clutton-Brock and Harvey 1977, Johns and Skorupa 1987, Onderdonk and Chapman

2000). Therefore, some researchers have stated that a highly frugivorous diet and a large home range limits, or excludes, the presence of such primate species in forest fragments (Rylands and Keuroghlian 1988, Gilbert and Setz 2001).

In this chapter I focus on the northern bearded saki monkey (*Chiropotes sagulatus*)[1], a medium-bodied (Ford and Davis 1992), highly frugivorous (Ayres 1981, van Roosmalen *et al.* 1981, Kinzey and Norconk 1990) monkey that lives in large social groups (van Roosmalen *et al.* 1981, Kinzey and Norconk 1990, Norconk *et al.* 2003, Boyle *et al.* In press) and has large home ranges (Ayres 1981, van Roosmalen *et al.* 1981, Boyle *et al.* In press). Therefore, this study allowed me to examine the spatial use of forested area by a highly frugivorous species living in forest fragments that are considerably smaller than the species' characteristic home range size. As documented in Chapter 3, northern bearded saki monkeys had smaller group sizes and were found in greater density in small forest fragments than in large forested areas. Furthermore, these monkeys spent more time resting, and less time traveling and engaging in social behaviors than their continuous forest counterparts. Therefore, I predicted that bearded saki monkeys would also vary in their spatial use of the forest fragments.

Previous studies of bearded sakis have found that the species' home range varies from 200-250 ha (Ayres 1981, van Roosmalen *et al.* 1981) in continuous forest; however, research in Pará, Brazil (Silva 2003, Veiga 2006) and Venezuela

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[1] Currently there are discrepancies regarding taxonomy in the genus *Chiropotes* (Hershkovitz 1985, Silva and Figueiredo 2002, Bonvicino *et al.* 2003). Prior to the recent taxonomic revision, the species found at BDFFP was considered *C. satanas chiropotes*. In this study I follow the taxonomy proposed by Silva and Figueiredo (2002). See Chapter 2 for additional taxonomic information.

(Peetz 2001) revealed that bearded sakis on islands (resulting from hydroelectric dam construction) occupied areas of 16-250 ha. Furthermore, these monkeys have inhabited forest fragments ranging in size from 1 ha to 100 ha at the Biological Dynamics of Forest Fragments Project (BDFFP) sites in the central Brazilian Amazon (see Chapter 3). Therefore, the species' home range size appears to be somewhat flexible, particularly in areas altered by humans.

The presence of bearded saki monkeys in BDFFP forest fragments provided a unique opportunity to examine groups living in forest fragments that were a fraction of the size of the previously calculated home ranges for the species in continuous forest (Ayres 1981, van Roosmalen *et al.* 1981). Through the use of Geographic Information Systems (GIS) technology, it was possible to analyze the animals' travel patterns and use of space, as well as the relationship between the monkeys' movement patterns and the distribution of their food resources.

The objectives of this study were to 1) compare home ranges and day ranges of bearded saki groups in forest fragments of various sizes and in continuous forest; 2) quantify differences in travel patterns (i.e., distance, movement paths) between these groups; 3) compare the spatial distribution of feeding trees, and their frequency of use by the monkeys, between the different forested areas; 4) determine the proportion of a forest fragment that is used by the monkeys, and its extent of use; and 5) analyze seasonal fluctuations in movement patterns.

I predicted that bearded saki monkeys living in small forest fragments would maximize their use of forest by regularly using all areas of the fragment. Animals in the continuous forest would not be constrained by forest size, and therefore I expected that such animals would concentrate their efforts in a patchier distribution, according to the presence of preferred dietary trees. Furthermore, I expected monkeys in the small fragments to travel shorter daily distances and resort to revisiting feeding trees more often than those monkeys living in the continuous forest. Lastly, I predicted that there would be seasonal differences in the travel patterns of bearded saki monkeys in all of the study sites due to seasonal fluctuations in fruit abundance.

METHODS

Study site

Data were collected in July-August 2003, and then from January 2005-June 2006, at the Biological Dynamics of Forest Fragments Project (BDFFP), located approximately 80 km north of Manaus, Brazil (2°30'S, 60°W). BDFFP is the site of a long-term project on fragmentation, facilitated by the Instituto Nacional de Pesquisas da Amazônia (INPA) in Manaus, Brazil and the Smithsonian Tropical Research Institute (STRI). The forest fragments are categorized into size classes of 1, 10 and 100 ha, and were initially isolated from the continuous forest by distances of 70-1000 m (Laurance *et al.* 2006b). Gascon and Bierregaard, Jr. (2001) provide a detailed history of BDFFP and a review of the research conducted at the site. The isolation distance and the condition of the matrix surrounding each forest fragment as of 2006 is provided in Chapter 2.

Six primate species reside in the BDFFP study area: red howler monkey (*Alouatta seniculus*), black spider monkey (*Ateles paniscus*), brown capuchin monkey (*Cebus apella*), bearded saki monkey (*Chiropotes sagulatus*), white-faced saki monkey (*Pithecia pithecia*), and golden-handed tamarin monkey (*Saguinus midas*). A history of these six species in the BDFFP study area, as well an analysis of their vulnerability to forest fragmentation, can be found in Chapters 1 and 2.

The bearded saki monkey was present in the BDFFP study area prior to the creation of the study site; however, it was absent from all of the study's forest fragments immediately after the initial isolation process (Rylands and Keuroghlian 1988). Although the species recolonized several of the forest fragments 7-19 years later, some of the fragments have never hosted bearded sakis (Gilbert and Setz 2001, Gilbert 2003, Boyle *et al.* In press). Recolonization of some of the BDFFP fragments may have been driven by the increase of old secondary growth in the surrounding matrix (see Chapter 2). Alternatively, the continued absense of bearded saki monkeys in some fragments may be due to the size of the forest patch and the continued isolation (e.g., large distance to nearest forested patch, low proportion of old secondary) of the fragment.

Bearded saki data collection

Nine forest fragments—four 1-ha (#1104, #2107, #2108, and #3114), three 10-ha (#1202, #2206, and #3209), and two 100-ha fragments (#2303 and #3304)—and two areas of continuous forest were surveyed for bearded saki monkeys. Each cycle consisted of a rotation through the nine forest fragments and two continuous forest sites. It took approximately 2.5 months to complete each cycle. I conducted one census cycle in July-August 2003, four cycles in 2005, and one cycle in 2006. The durations of the cycles were as follows: July-August 2003 (Cycle 2003), January-March 2005 (Cycle 1), April-June 2005 (Cycle 2), August-October 2005 (Cycle 3), October-December 2005 (Cycle 4), January-March 2006 (Cycle 5). Additional data were collected in April 2006 for a sixth cycle of the 10-ha fragment #1202 because the study group in this fragment was the best documented group in terms of contact hours and diet identification. Comparisons were made between the cycles in order to determine seasonal differences in the monkeys' spatial use of the forest fragments.

On the first day in each study area for each cycle, I conducted a primate census by walking line transects along already established trails, following the methods of Rylands and Keuroghlian (1988) and Gilbert (2003). Chapter 2 provides additional information on the methods and results for each of the primate species during these censuses. If bearded sakis were present in the forest fragment during the primate census, they were designated the focal study group for that fragment’s cycle, and subsequently relocated and followed for three consecutive days.

Upon locating a group of bearded sakis, I tracked the same group from the time they awoke in the morning until the time they settled down for the night (approximately 0530 to 1730). Using group scan sampling techniques (Altmann 1974), every five minutes I recorded the group’s GPS coordinates, group size and composition, as well as the activity of each individual in sight. An analysis of the bearded saki monkey’s activity budget is provided in Chapter 3.

If individuals were eating fruit, flowers, or leaves, the tree or liana was marked with plastic flagging and assigned a unique number. This system allowed for subsequent identification of the plant species, as well as the monitoring of revisits by monkeys to feeding trees during a cycle and throughout the year. Also recorded were each tree’s GPS coordinates and diameter at breast height (DBH), and the part of the plant that was consumed (fruit, flower, leaf). An analysis of the bearded saki monkey’s diet is provided in Chapter 3.

Spatial analysis – Home and day range

Daily travel routes and the animals’ feeding trees were mapped using ArcView 3.3. I determined daily home range, day range, and distance traveled using the Home Range Extension (Rodgers and Carr 2002) for ArcView. Home range size and day range size were calculated using minimum convex polygon (Odum and Kuenzler 1955). Kernel density estimators (Worton 1987), another method for estimating home range, were not used for calculating day range because they were inconsistent and overestimated the size of the area when sample size was low (see Appendix B).

Home range size was calculated for the bearded saki groups in the two continuous forest sites, and the two groups in two 10-ha fragments (#1202 and #2206), based on the GPS points taken every five minutes. Home range size was not determined for the groups in the two 100-ha fragments because these groups frequently left and re-entered the fragments, and therefore it was not possible to monitor their overall use of the BDFFP landscape. Home range was also not calculated for the sole individual in the 1-ha fragment. This was due to the fact that this bearded saki was present for only one cycle in 2003. Additional data were needed to determine the extent of this individual's home range, as it was not known whether he left the fragment or died.

Day range size (ha) and area used per hour (ha/hr) were calculated for each day in each study site. An hourly average was determined in addition to the daily area total because contact hours with the monkeys varied daily and between groups. All forest fragments (*n*=5) and continuous forest sites (*n*=2) used by bearded saki monkeys were included in the analyses of day range. Comparisons of each dependent variable among forest size classes were analyzed using ANOVA, with Student's *t* post-hoc analyses. I examined area used per hour across cycles using repeated measures ANOVA with a Greenhouse-Geisser correction for data not meeting sphericity assumptions. Because there were differences among forest size classes in overall analyses, I also included fragment size here as a between-subjects factor in repeated-measures analyses. These seasonal comparisons were determined only with data from study sites (*n*=4) where bearded saki monkeys were present during all of the study cycles.

I calculated the percentage of each forest fragment used by bearded saki monkeys using a minimum convex polygon for all bearded saki data points. Since minimum convex polygon does not provide data on the proportion of time spent in various areas of the home range, I used kernel density estimators to illustrate the overall core areas used by the bearded saki monkeys, and categorize the location of the core areas within the forest fragment. Since these calculations were based on total points for each study site, kernel density estimators performed well, due to large sample sizes. The average percent difference between the two methods of home range estimation (±standard error) was 4.5% (±1.13).

I then classified the spatial distribution of the bearded saki monkeys within each forest fragment and area of continuous forest as fitting a clumped, random, or uniform pattern (Fig. 19) by conducting a Nearest Neighbor Analysis in the Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView. This same procedure was also followed for the trees that were used for food by bearded saki monkeys. In forest fragments the entire fragment area was used for these analyses, whereas the home range extent for groups living in the continuous forest served to denote boundaries of the area for analysis. In order to determine the pattern of resource use, an *R* statistic was calculated. *R* is the ratio of the actual average distance between the nearest neighbor points and the expected average distance between points. An *R*-value of 1 indicates a random pattern, an *R*-value less than one indicates a clumped pattern, and an *R*-value greater than one indicates a uniform pattern. A *z*-score indicates whether the deviation from randomness is significant at the alpha level of 0.05. If *z* is greater than 1.96 or less than –1.96, the pattern is significantly different from the random pattern (Lee and Wong 2001).

Spatial analysis – Travel patterns

I calculated the daily distance traveled (km) and distance traveled per hour (km/hr) for each day of data. Comparisons of travel distance among forest size classes were made using ANOVA. I tested to see if there were differences in the distance traveled per hour across data cycles using repeated measures ANOVA with a Greenhouse-Geisser correction. Forest size class was again included as a between-subjects factor since distance traveled varied with size class in overall analyses. This analysis only included study sites (*n*=4) where bearded saki monkeys were present for all of the data cycles.

Daily travel patterns were scored on a continuum from straight-line paths to circular paths based on the distance between the start and stop endpoints for the day, divided by the total distance traveled. A value of 1 indicated a straight line from start to finish, and a value of 0 indicated that the individual had fully returned to its starting point (Fig. 20). Data were log-transformed in order to meet the assumption of normality. Differences between the size classes were analyzed using ANOVA. I also calculated the percentage of the feeding trees that were revisited throughout the day, and compared the results between forest class sizes using ANOVA. In order to compare the distance traveled and area of forest used daily, I divided distance (m) by area (ha) in order to provide a measurement in the amount of space used versus distance being traveled. Forest size classes were compared with ANOVA.

Spatial analysis – Feeding tree distribution

Distance from each of the feeding trees to the closest edge of the forest fragment was calculated in ArcView 3.3. Distance from the feeding trees to the fragment's edge was compared among fragment size classes with ANOVA. I tested whether the trees' distance to edge varied among study cycles with a repeated measures ANOVA, with a Greenhouse-Geisser correction, and including forest fragment size as a between-subjects factor. Only forest fragments (*n*=3) that had bearded saki monkeys during all data cycles were used in this analysis.

Since larger fragments have a greater possible distance to edge than smaller fragments, I also calculated the proportion of each forest fragment within four distance-to-edge categories (<50 m, 50-100 m, 100-150 m, and >150 m). Percentage data were arcsin square-root transformed, and ANOVA was used to determine if there was a difference in the percentage of feeding trees within 50 m of the fragment's edge between fragment size classes (100 ha, 10 ha, and 1 ha). I then calculated the expected distribution of the feeding trees within each category, based on its proportional representation within the forest fragment's size, and compared the observed versus expected distribution in the four categories using a Chi-square test.

I also examined the distance of the feeding trees to the edge of the forest fragment based on their location within the overall size of the forest fragment. Each fragment was partitioned into four equal areas (representing 25% of the forest fragment's total size) based on concentric buffers around the edge of the forest fragment. The number of feeding trees in each area (from closest-to-edge to farthest-from-edge) was tallied, and the proportion of trees in each category was determined. Percentage data were arcsin square-root transformed, and ANOVA was used to determine if there was a difference in the proportion of feeding trees near the outer edge of the forest fragments between fragment size classes. I then calculated the expected distribution of the feeding trees within each category, based on the forest fragment's size, and compared the observed versus expected distribution in the four categories using a Chi-square test.

RESULTS

Presence in forest fragments

Northern bearded saki monkeys were present in five forest fragments (#3304, #2303, #2206, #1202, and #2107) and two areas of continuous forest during the study; however, of the five forest fragments, only two (#1202 and #2206, both in the 10-ha fragment size class) continuously sustained the monkeys during each of the study cycles in 2003, 2005 and 2006 (Table 13). The species was present in both 100-ha fragments (#3304 and #2303), but groups left and re-entered both sites frequently, and fragment #3304 hosted bearded sakis for only two of the data collection cycles. One individual was present in a 1.8 ha fragment (#2107) in 2003, but there were no sightings of bearded saki monkeys in any fragments in the 1-ha size class during 2005-2006.

Home and day ranges

Bearded saki home range in continuous forest was 559 ha at the KM41 study area and 300 ha at the Cabo Frio study area. The home range of the groups that did not leave the forest fragments #2206 (fragment area of 13.96 ha) and #1202 (fragment area of 13.67) was 12.05 ha and 13.67 ha, respectively. It was not possible to calculate home range for the bearded saki groups in the 100-ha fragments because they frequently left and re-entered the fragments. It was also not possible to calculate home range size for the individual in the 1-ha fragment in August 2003 because one cycle of data collection was not adequate to calculate a home range.

Bearded saki monkeys occupied a larger daily area in the continuous forest than the 10-ha and 1-ha forest fragments ($F_{3,3}$=10.61, P=0.042; Fig. 21A). Average daily area used (±standard error) was 32.92 (±4.27) ha in the continuous forest, 23.40 (±0.46) ha in the 100-ha fragments, 4.87 (± 0.02) ha in the 10-ha fragments, and 0.43 (± 0.00) ha in the 1-ha fragment (Table 14). When average area used per hour was computed, in order to account for differences in daily contact hours with the bearded saki groups due to some groups leaving and re-entering the forest fragments, there was an even greater difference between forest size class ($F_{3,3}$=52.20, P=0.0043; Fig. 21B). When the data were compared across five study cycles for the study sites (n=4) where bearded saki monkeys were present in all of the cycles, there was a difference between cycles ($F_{1,1}$=356.31, P=0.0034; Fig. 22), with area use increasing in Cycle 2, the April-June 2005 time period immediately preceding the dry season. The interaction between cycle and size was marginally significant ($F_{2,1}$=186.06, P=0.052), with the seasonal effect being most pronounced in the continuous forest sites and virtually absent in the 10-ha fragments.

Spatial use of the forest fragments

Bearded saki monkeys used 83.46% of the available area in the100-ha fragment #2303 (Fig. 23A), 54.27% in the 100-ha fragment #3304 (Fig. 23B), 100.00% in the 10-ha fragment #1202 (Fig. 23C), 86.28% in the 10-ha fragment #2206 (Fig. 23D), and 36.89% in the 1-ha fragment #2107 (Fig. 23E).

The monkeys also did not use the available habitat evenly in the continuous forest and the large forest fragments. Nearest Neighbor Analysis showed that the geographic locations of the bearded saki groups (sampled every five minutes) were distributed in a clumped pattern in the continuous forest sites (n=2) and in the 100-ha fragments (n=2), and in a uniform pattern in the 10-ha fragments (n=2) and the 1-ha fragment (n=1; Table 15). Seasonal patterns, represented by cycles, in the three forest fragments (#2303, #2206, and #1202) and one area of continuous forest (Km41) where bearded saki monkeys were present throughout the study indicate that the patterns of bearded saki locations did not vary much by cycle (Table 16A). Clumped patterns were present in 100% of the cycles of the continuous forest site (Km41) and the 100-ha fragment (#2303). Uniform patterns were present in 80% of the cycles in both 10-ha fragments (#1202 and #2206).

Travel patterns

Bearded saki monkeys traveled greater daily distances in the continuous forest and 100-ha fragments than in the smaller fragments ($F_{3,3}$=58.97, P=0.0036; Fig. 24A). Average daily distance traveled (±standard error) was 2.99 (±0.02) km in the continuous forest, 2.83 (±0.22) km in the 100-ha fragments, 1.72 (±0.09) km in the 10-ha fragments, and 0.41 (±0.00) km in the 1-ha fragment. When comparisons were standardized by distance traveled per hour, differences between the forest size classes were even greater ($F_{3,3}$=155.13, P=0.0009; Fig. 24C). There was no difference in distance traveled per hour between cycles ($F_{1,1}$=1.44, P=0.44), nor in the interaction between cycle and size ($F_{2,1}$=2.62, P=0.40; data not shown).

There was daily variation in the travel patterns of the bearded saki monkeys within each forest size class, as indicated in Fig. 25 by four study days of 8 hr or more, with diagrams A, B, and C showing similar daily ranging distance (km). Overall, monkeys in the continuous forest traveled more in a straight-line path (value close to 1) than the monkeys in the 100- ha and 10-ha fragments, which followed more circular (value close to 0) daily routes ($F_{2,3}$=14.37, P=0.029; Fig.

26). When the individual in the 1-ha fragment was considered with the other bearded saki groups, there was still an overall difference between size classes ($F_{3,3}$=9.58, P=0.048), but the 1-ha fragment values (from 2 days of data) were not statistically different from the values of the other size classes. Furthermore, bearded saki monkeys revisited a smaller percentage of feeding trees in continuous forest and 100-ha fragments than in the smaller fragments ($F_{3,3}$=103.34, P=0.0016; Fig. 27). Even when the 1-ha size class was not considered, the monkeys still revisited a smaller percentage of trees in the continuous forest and 100-ha fragments than in the 10-ha fragments ($F_{2,3}$=15.72, P=0.026). Multiple visits to the same tree throughout one day occurred for 1.95% (±1.95) of the feeding trees in the continuous forest, 5.54% (±2.45) of the feeding trees in 100-ha fragments, 15.88% (±0.46) of the feeding trees in the 10-ha fragments, and 54.29% (±25.71) of the feeding trees in the 1-ha fragment.

Although bearded saki monkeys traveled greater absolute distances in larger forest fragments and continuous forest than in the small forest fragments (Figs. 24A and 24B), the monkeys traveled greater distances per ha in the smaller fragments ($F_{3,3}$=431.78, P=0.0002; Fig. 24C). For example, even when monkeys in continuous forest and in 10-ha fragments traveled relatively long distances (more than 3 km), the average day area covered was 57.18 (±23.58) ha in continuous forest, 40.98 (±9.32) ha in 100-ha fragments, and 8.84 (±1.42) ha in 10-ha fragments.

Feeding tree distribution and use

Nearest neighbor analysis indicated that feeding trees were located in clumped patterns in continuous forest sites (*n*=2), clumped patterns in 100-ha fragments (*n*=2), in clumped (*n*=1) and random (*n*=1) patterns in 10-ha fragments, and in a clumped pattern in a 1-ha fragment (*n*=1; Table 15). When the three forest fragments and one continuous forest site that had bearded saki monkeys present in all five data cycles were analyzed for seasonal changes in distribution patterns, there was a clumped distribution in 100% of the data cycles in the continuous forest site Km41, a clumped distribution of feeding trees in 100% of the data cycles for the 100-ha fragment (#2303), and a mixture of clumped (20%, 60%) and random (80%, 40%) distributions in the two 10-ha fragments (#1202 and #2206, respectively).

Average distance from the feeding trees to the fragment edge was greater in the 100-ha forest fragments than in the 10-ha and 1-ha forest fragments ($F_{2,2}$=37.65, *P*=0.026; Fig. 28). Average distance was 164.36 (±13.32) m in the two 100-ha fragments, 65.60 (±5.55) m in the two 10-ha fragments, and 28.88 (±0.00) m in the 1-ha fragment. There was no difference in the distance of feeding trees to the edge between cycles ($F_{1,1}$=15.79, *P*=0.16), nor was there an interaction of cycle and fragment size ($F_{1,1}$=84.09, *P*=0.069). Although all forest fragments had feeding trees located within 50 m of the edge, the proportion of trees within 50 m of the edge was greater for the smaller fragments than for the larger fragments ($F_{2,2}$=35.68, *P*=0.027; Fig.29A). However, the percentage of the fragment represented by edge area was also greater in smaller fragments (Fig. 29B). When the percent of the area was taken into account, there was a difference between the observed and the expected distribution of the feeding trees for one 100-ha fragment (#2303; χ^2=17.10, df=3, P<0.001), one 10-ha fragment (#2206; χ^2=16.86, df=3, P<0.001), and the 1-ha fragment (#2303; χ^2=9.55, df=3, P<0.025; Fig. 29C). There was no difference between the observed and expected distribution of feeding trees for the remaining 100-ha (#3304; χ^2=1.59, df=3, P=0.75) and 10-ha (#1202; χ^2=6.34, df=3, P=0.10) fragments.

Alternatively, when the size of the forest fragment was taken into account by delineating four buffers of equal area (0-25%, 25-50%, 50-75%, 75-100%) around the forest edge, there was no difference between fragment sizes in the percentage of feeding trees located within the buffer closest to the forest edge ($F_{2,2}$=0.49, P=0.67; Fig. 20). All five fragments had between 16.67% and 26.19% of their feeding trees located within this buffer area. Within each forest fragment, there was a difference between the observed and expected distributions of feeding trees throughout all four buffer areas in one 100-ha fragment (#2303; χ^2=10.97 df=3, P<0.025) and one 10-ha fragment (#2206; χ^2=13.50, df=3, P<0.005). There was no difference between the observed and expected distribution of feeding trees for the remaining 100-ha (#3304; χ^2=3.38, df=3, P=0.50), 10-ha (#1202; χ^2=0.62, df=3, P=0.90), and 1-ha (#2107; χ^2=5.27, df=3, P=0.25) fragments.

DISCUSSION

It is not uncommon for primates to occupy smaller home ranges in forest fragments than they do in undisturbed habitat (Tutin 1999, Onderdonk and Chapman 2000). In this study, however, I found extreme spatial variations between bearded saki monkeys living in small forest fragments and those monkeys living in continuous forest. Home ranges in continuous forest were 26-46 times larger than home ranges of two groups living continuously in the two forest fragments in the 10-ha size class. Bearded saki monkeys living in smaller forest fragments also occupied smaller daily areas, traveled shorter distances daily, revisited a larger percentage of feeding trees throughout the day, followed more circular paths, and moved in a more uniform pattern throughout their habitat than bearded saki monkeys living in the 100-ha fragments and continuous forest. Furthermore, in the majority of the fragments, the monkeys did not obtain food resources from all areas of available forest. These results indicate that forest fragment size influences the spatial use of the patch by bearded saki monkeys, but also other characteristics of the fragment (e.g., tree composition and canopy openness) may affect a forest fragment's potential to provide adequate resources for the species.

Home range

The home range size of the bearded saki groups in the BDFFP continuous forest ranged from 300 ha at the Cabo Frio site to 559 ha at the Km41 site. It is likely that the estimate of the home range at Cabo Frio was low due to fewer contact hours with the bearded saki monkeys at this site than at the Km41 site. Data collection at the Km41 site was more thorough, and contact time with the monkeys increased the home range estimates. Since average daily area used and distance traveled were similar at the two continuous forest sites, it is possible that the bearded saki monkeys at Cabo Frio had a home range that approached the size of the home range at Km41. There were no outlier points in the data sets that would have influenced home range estimates.

Both home range estimates from this study, 300 ha at Cabo Frio and 559 at Km41, exceeded the previously stated home ranges for bearded saki monkeys of 200-250 ha (Ayres, 1981; van Roosmalen *et al.*, 1981). However, van Roosmalen *et al.* (1981) states that their estimate was conservative, and that “home range was not accurately calculated,” and day range estimates were based on only five days of data. Therefore, difficulties in following bearded saki monkeys may lead to lower estimates of the area used by the monkeys. It is also possible that the home range size of the species varies with geographic region. A previous study of the brown capuchin monkeys (*Cebus apella*) at Km41 estimated home range size to be much larger than published accounts in other areas of the Amazon (Spironello 2001). Spironello attributed these variations to duration and extent of the field studies, and to ecological differences between study sites. Differences in environmental factors (e.g., plant community, soil fertility) also have been suggested to explain differences in home range size estimates for *Lagothrix lagotricha*, the woolly monkey (Defler 1996).

Even though there was variation in estimated home range size in the continuous forest sites, the figures of 300 ha and 559 ha were between 26 and 46 times greater than the 12.05 ha and 13.67 ha occupied by two bearded saki groups in the forest fragments #2206 and #1202, respectively. These extreme differences in total forest area use also are accompanied by changes in the spatial distribution and travel patterns of the monkeys, as described below.

Use of space

Bearded saki monkeys living in small forest fragments used smaller daily areas, and covered smaller areas per hour. Although this is to be expected, as animals living in a 10-ha fragment would not have more than 10 ha available to them, the average area covered per hour was nine times greater in the continuous forest than in the 10-ha fragments. Furthermore, it is interesting to note that the bearded saki monkeys' average daily area used in the forest fragments (1 ha, 10 ha, and 100 ha) was only a fraction of the available space. For example, in the two 10-ha forests, the average daily area used by the monkeys was approximately one-third of the fragment's total area. In fact, the monkeys in the 10-ha fragments used 50% or more of the fragment's area only 17% of the time, even though the monkeys in the 100-ha fragments and continuous forest sites had average day ranges of 27.70 ha and 34.63 ha, respectively.

Even when all data for the study period were combined, just one (#1202) of the five forest fragments was fully used by the bearded saki monkeys. Only portions of 100-ha fragments #3304 and #2303, 10-ha fragment #2206, and 1-ha fragment #2107 were used during this study.

In both 100-ha fragments, bearded saki monkeys followed a clumped distribution, and concentrated their daily activities in core areas, while completely avoiding other areas (Figs. 23A and B). The clumped distribution indicated that the monkeys were concentrating their efforts on particular areas of the forest fragment, and were not surveying the entire area. Because bearded saki monkeys left and re-entered both 100-ha fragments, they were not constrained to these sites, and did not have to obtain resources from sub-optimal areas. Had the monkeys been isolated in the 100-ha fragments, their spatial use of the fragments may have been very different. For instance, in 100-ha fragment #2303 (Fig. 23A), the main portion of the fragment that was not used by the bearded saki monkeys was alongside a stream that flooded frequently, and the area had a high concentration of palms (Arecaceae), which were rarely utilized as a food resource by the monkeys (see Chapter 3). Had the animals been restricted to the forest fragment, they may have traveled through and possibly foraged in a greater proportion of the forest fragment.

Bearded saki monkeys in both 10-ha fragments followed a uniform pattern of distribution. This means that overall, each bearded saki group traveled fairly evenly throughout its 10-ha fragment. The bearded saki group in fragment #1202 used 100% of the forest fragment during the study period (Fig. 23C). Although the group in fragment #2206 also traveled in a uniform pattern, it only used 86%

of the available forest fragment (Fig. 23D). In this forest fragment, the area that was not used by the monkeys was a large open area in the northern section of the fragment, where there had been several tree falls. Without a connective canopy, it would not be possible for the monkeys to travel through this area. Furthermore, the map of this fragment shows four areas of high use by the monkeys, but the area between these western and eastern sides has a relatively low concentration of bearded saki location data. This area of lower concentration of bearded saki presence corresponds to another stream, surrounded by steep banks on the western and eastern sides. Within this area, which represented just over 10% of the area used by the bearded saki monkeys, there were only 4% of the monkeys' feeding trees. The areas of the forest fragment that were most widely used were on the top of these embankments, above the stream. Therefore, the steep embankments and stream corridor were used primarily as travel routes to and from the top of the embankments.

The bearded saki monkey in the 1-ha fragment used only 36% of the available area (Fig. 23E); however, there were only two days of data for this fragment in 2003, during a pilot study. Due to the fact that no bearded saki monkeys were found in any of the 1-ha fragments during the 2005-2006 study period, it was not possible to explore how a bearded saki monkey would use a 1-ha fragment, and for how long a 1-ha forest fragment would support a bearded saki monkey. Since there were only two days of data, and during August, which is a period of low fruit productivity, it is likely that had it been possible to track this individual for a longer time, the total area used by the monkey would have been greater than the amount presented here. Unfortunately, it is not known for how long the monkey had been in the fragment prior to the pilot study, and it is not known for how long the monkey remained in the forest fragment after August 2003.

Travel patterns

Average daily distance and distance traveled per hour were shortest for bearded saki monkeys living in the small forest fragments. This was expected, since the amount of travel area available was smaller in forest fragments. It was not expected, however, that monkeys in the 10-ha and 1-ha fragments would travel greater distances than predicted, based on the size of the forest fragment. This means that bearded saki monkeys are traveled more per ha in the smaller forest fragments than their counterparts did in 100-ha fragments and continuous forest. This point was illustrated further on days when the animals traveled more than 3 km. Although average daily distance in continuous forest was 2.98 km, average daily distance in the 10-ha fragments was 1.72 km, and only 11% of the data collection days in continuous forest had distances greater than 3 km, at times the monkeys in the 10-ha fragments traveled distances that were equivalent to the average daily distance traveled in continuous forest sites. Using 3 km as a lower limit, it was possible to compare area used when distance traveled was similar. Monkeys in smaller fragments covered smaller areas (average area covered: 8.84 ha) during their long expeditions than monkeys in continuous forest (average area covered: 57.18 ha).

The notion that bearded saki monkeys in the small forest size classes traveled greater daily distances than what was expected was also supported by these monkeys revisiting a greater percentage of feeding trees throughout the day than did monkeys living in 100-ha and continuous forest. Therefore, the animals were returning multiple times to areas throughout the day. The return rates of 2% for continuous forest, 6% for 100-ha fragments, 16% for 10-ha fragments, and 54% for 1-ha fragments indicate the differences in resource use between the bearded saki groups. The results for 100-ha and continuous forest groups followed Norconk and Kinzey (1994), who found that *Chiropotes* reused less than 10% of its feeding trees in a day.

These results were surprising, as I had originally expected that bearded saki monkeys would minimize their effort in the smaller forest fragments by traveling the minimum amount and maximizing their food intake. Although the monkeys traveled shorter distances in the smaller fragments, these distances were greater than expected. By revisiting feeding trees throughout the day and traveling through the forest fragment in a uniform pattern, the monkeys appear to be continuously monitoring the status of the trees in the forest fragments, and they do not appear to be depleting the tree of its fruit during a feeding session, as they oftentimes returned a couple hours later to feed again.

The direction and path of the travel patterns varied daily as well. The monkeys in continuous forest did not travel in one direction, forming a straight line; however, they traveled in a straighter pattern than the monkeys living in 10-ha fragments. This pattern follows with the other findings, that bearded saki monkeys revisited areas throughout the day in the 10-ha fragments, they traveled greater distances per area, and they often ended their day close to where they began their day. These patterns were not evident in the continuous forest. Although bearded saki monkeys did regularly return to a sleeping site at Km41 throughout the study, the monkeys often traveled in other areas for days before returning to the sleeping site again.

Seasonal variation

During times of resource scarcity, some primates species travel longer distances than during times of high resource abundance, while other species travel shorter distances, and still other species do not vary in their travel distances; thus, primates deal with resource scarcity in various ways, and many variables and behavioral adjustments may be involved, aside from overall fluctuations in range (Di Fiore 2003). I found in this study that bearded saki monkeys had seasonal variations in the daily area covered. The animals covered the largest areas in the period leading up to the dry season, in both the 100-ha and continuous forest sites. The monkeys in the 10-ha fragments, however, did not show much variation in the area used between study cycles. These results indicate that the monkeys living in uncharacteristically small habitats did not alter the amount of area used during any part of the year.

Although there were differences in the daily area covered, there were no differences in the daily distance traveled between study cycles. Daily variations existed, but overall the bearded saki monkeys traveled similar distances throughout the year. Furthermore, the spatial patterns were consistent throughout the study. The bearded saki monkeys were consistently clumped in parts of the continuous forest and 100-ha sites, while the animals in the two 10-ha fragments were distributed in a uniform pattern 80% of the time.

Resource distribution and use

The main component of the bearded saki monkey's diet was fruit (primarily seeds, and primarily unripe fruit), although the monkeys also consumed flowers, leaves, and insects (Chapter 3). The trees, lianas, and hemiepiphytes that provided food resources for the monkeys were located throughout the forest fragments. The distance of the feeding trees to the edge of the forest fragments was greatest in 100-ha fragments, and smallest in 1-ha fragments, as one would expect. When the feeding trees were analyzed in groups (<50 m, 50-100 m, 100-150 m, and >150 m from the fragment edge), all forest fragments had feeding trees located within 50 m of the forest fragment's edge, although small patches had a greater proportion of feeding trees within 50 m of the edge. Again, this was not a surprise, as the area covering a distance of 50 m from the edge varies greatly between large and small fragments. When comparisons were made between the observed number of feeding trees and the expected distributions based on the percentage of the fragment near the fragment’s edge, all five fragments had fewer feeding trees than expected within 50 m of the fragment’s edge, and there were significant differences in the overall distribution of feeding trees in one 100-ha, one 10-ha and one 1-ha fragment.

When the location of the feeding trees was categorized into four buffer areas of equal size, significant differences or trends in four of the five forest fragments exhibited a lower than expected percentage of feeding trees in the outer 25% buffer. The exception was #1202 (the 10-ha fragment with the highest diversity index and random distribution of feeding trees).

Bearded saki travel patterns (clumped, random, uniform; see “Use of space”) matched the distribution of feeding trees only in the continuous forest and 100-ha sites. Feeding trees also were located in clumped distributions in one 10-ha fragment (#2206) and the 1-ha fragment as well, even though the distribution of the monkeys throughout the forest fragments was not clumped (as true for the 100-ha fragments and continuous forest sites). Possible explanations for the differences in bearded saki patterns and the feeding tree patterns are provided below.

The differences between the two 10-ha fragments are interesting because in fragment #2206, the animals traveled in a uniform pattern, and used 86% of the forest fragment, yet they fed on trees that were distributed in a clumped pattern. Therefore, these monkeys were traveling throughout the fragment, but only using certain areas as feeding sites. In contrast, the monkeys in the other 10-ha fragment (#1202), while also traveling in a uniform pattern across the fragment, fed on trees that were distributed in a random pattern. Therefore, the monkeys were not concentrating their feeding efforts in particular areas overall.

In the 10-ha fragment #2206, where the feeding trees were in a clumped distribution, the monkeys may have concentrated their feeding efforts on preferred species that were located in clumps throughout the fragment, thereby ignoring other species that may have provided food under dire circumstances. Another possibility is that the only available resources present during the study were distributed in a clumped pattern, and therefore although the monkeys traveled throughout the fragment, only certain areas of the fragment provided food for the monkeys. As noted earlier, this forest fragment had a stream that ran through the middle of the fragment, and few feeding trees were located along this riparian area. Therefore, the clumped distribution of the feeding trees may have been due to the physical characteristics of the forest fragment and the possible aversion of bearded saki monkeys to tree species in the riparian area.

The bearded saki monkeys in fragment #1202, who fed from feeding trees in a random distribution, may not have been as picky in their diet and may have been consuming items that monkeys in larger areas with more resources would have ignored. Or, it may have been that the resources were not patchily distributed in the forest fragment, as there were no streams present and overall the habitat was similar throughout the fragment. In either case, the bearded saki monkeys in this fragment ate a more diverse diet than groups in any other forest fragment in the study, and had the greatest proportion of unique species in their diet, as well as the greatest proportion of unique species that were fruiting in other study sites but not eaten by any other groups (see Chapter 3). Therefore, these monkeys in fragment #1202 may have consumed sub-optimal food.

While there were overall differences between the spatial distribution of feeding trees in the 10-ha fragments, when the data were analyzed by cycle, both fragments had a mixture of clumped and random patterns. Therefore, although overall fragment #1202 had a random distribution of feeding trees, and overall fragment #2206 had a clumped distribution, there were some fluctuations with season.

Conclusions

When bearded sakis were living in forest fragments that were a fraction of their characteristic home range size, they drastically changed their travel patterns and spatial habitat use. One of the goals in many conservation studies is to determine the minimum fragment size needed to sustain a species (Lovejoy and Oren 1981). While it is important to understand a species' spatial and habitat needs, the size of the habitat is not the only consideration.

In this study, bearded saki monkeys did not utilize all the area available to them. Sites that had many tree falls, and areas dominated by riparian or variably flooded habitats, were avoided. Only in fragment #1202, where there were no streams present, and the habitat was fairly homogenous, did the monkeys use all parts of the forest fragment. Therefore, even though a 10-ha fragment may be available to the species, it may not provide 10 ha of appropriate habitat. If there are stochastic events, such as increased tree falls and tree mortality due to heavy wind or storms, even less of the fragment may be available as habitat. Furthermore, in years of low resource productivity, some small patches may not provide the minimum amount of resources, or the food resources may be of lower value. Therefore, the reserve may not be suited to the conservation needs of the species.

ACKNOWLEDGEMENTS

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TABLE 13. Bearded saki monkeys in BDFFP forest fragments.

Fragment size	Present	Absent
100 ha	#3304† #2303*†	
10 ha	#2206* #1202*	#3209
1 ha	#2107	#1104 #2108 #3101

Notes: Bearded saki monkeys occupied five of the nine forest fragments during the study period (2003, 2005-2006). (*) indicates that there were bearded saki monkeys present in the forest fragment during all study cycles. (†) indicates that the monkeys left and re-entered the forest fragments during the study.

TABLE 14. Home range, day range, and daily travel distances

	Continuous forest	100-ha fragments	10-ha fragments	1-ha fragment
Home Range (ha)				
Mean (±S.E.)	429.5 (±129.5)	n/a[1]	12.36 (±0.31)	n/a[2]
Range	300-559		12.05-13.67	
Day Range (ha)				
Mean (±S.E.)	32.92 (±4.27)	23.40 (±0.46)	4.87 (±0.02)	0.43 (±0.00)
Range	28.65-37.18	17.39-29.41	4.56-5.19	n/a
Area/Hr (ha)				
Mean (±S.E.)	5.28 (±0.26)	3.01 (±0.46)	0.57 (±0.02)	0.05 (±0.00)
Range	5.02-5.54	2.55-3.47	0.55-0.59	n/a
Daily Distance (km)				
Mean (±S.E.)	2.99 (±0.02)	2.83 (±0.22)	1.72 (±0.09)	0.41 (±0.00)
Range	2.97-3.01	2.61-3.05	1.71-1.73	n/a
Daily Distance (km/hr)				
Mean (±S.E.)	0.42 (±0.01)	0.36 (±0.01)	0.20 (±0.01)	0.04 (±0.00)
Range	0.40-0.43	3.54-3.75	1.89-2.09	n/a

Notes: [1] Monkeys were not permanent residents of the forest fragments during this study, therefore it was not possible to calculate accurate home ranges. [2] One bearded saki monkey was present in 2003, but never in 2005-2006. Data were not adequate to calculate home range, given the uncertainty of the individual (i.e., left fragment, death).

TABLE 15. Spatial patterns of bearded saki monkeys and feeding trees.

		Feeding Trees				Bearded Saki Locations			
Site	Size	Pattern	R	z	n	Pattern	R	z	n
KM41	Continuous	Clumped	0.53	-13.89	251	Clumped	0.55	-20.19	586
Cabo Frio	Continuous	Clumped	0.58	-6.21	61	Clumped	0.73	-9.37	326
#3304	100 ha	Clumped	0.65	-4.78	51	Clumped	0.73	-10.22	387
#2303	100 ha	Clumped	0.80	-5.50	208	Clumped	0.90	-5.29	798
#2206	10 ha	Clumped	0.84	-3.67	144	Uniform	1.22	15.42	1359
#1202	10 ha	Random	1.03	0.71	155	Uniform	1.56	47.11	1944
#2107	1 ha	Clumped	0.72	-2.55	22	Uniform	1.10	2.67	192

Notes: The spatial distribution of the bearded saki monkeys' feeding trees and the geographic locations of the monkeys were classified to be in random, clumped, or uniform patterns, using the R-value obtained from nearest neighbor analysis ($R=1$ indicates a random pattern, $R<1$ indicates a clumped pattern, and $R>1$ indicates a uniform pattern). The pattern was determined to deviate significantly from a random pattern at the *alpha* level of 0.05 if $z>1.96$ or $z<-1.96$.

TABLE 16. Seasonal spatial patterns.

(A)	KM41 (cont)	#2303 (100 ha)	#2206 (10 ha)	#1202 (10 ha)
Cycle 1 (*n*)	Clumped (29)	Clumped (108)	Uniform (124)	Uniform (185)
R	0.34	0.86	1.33	1.23
z	-6.79	-2.84	7.03	5.96
Cycle 2 (*n*)	Clumped (100)	Clumped (63)	Uniform (212)	Uniform (445)
R	0.31	0.53	1.11	1.76
z	-13.29	-7.13	2.89	29.39
Cycle 3 (*n*)	Clumped (111)	Clumped (423)	Uniform (436)	Random (180)
R	0.30	0.94	1.07	1.02
z	-14.07	-2.36	2.87	0.42
Cycle 4 (*n*)	Clumped (52)	Clumped (147)	Uniform (269)	Uniform (403)
R	0.16	0.64	1.22	1.08
z	-11.61	-8.44	6.89	3.01
Cycle 5 (*n*)	Clumped (126)	Clumped (124)	Random (291)	Uniform (387)
R	0.22	0.50	1.03	1.06
z	-16.82	-10.69	1.12	2.10

(B)	KM41 (cont)	#2303 (100 ha)	#2206 (10 ha)	#1202 (10 ha)
Cycle 1 (*n*)	Clumped (13)	Clumped (12)	Random (23)	Clumped (19)
R	0.62	0.52	0.88	0.50
z	-2.65	-3.17	-1.10	-4.19
Cycle 2 (*n*)	Clumped (38)	Clumped (18)	Random (9)	Random (43)
R	0.41	0.52	0.80	1.09
z	-6.93	-3.90	-1.14	1.13
Cycle 3 (*n*)	Clumped (39)	Clumped (71)	Clumped (47)	Random (14)
R	0.48	0.77	0.82	1.09
z	-6.26	-3.69	-2.37	0.61
Cycle 4 (*n*)	Clumped (16)	Clumped (50)	Clumped (21)	Random (36)
R	0.21	0.61	0.56	0.94
z	-6.07	-5.30	-3.84	-0.70
Cycle 5 (*n*)	Clumped (145)	Clumped (58)	Clumped (46)	Random (35)
R	0.20	0.48	0.83	0.88
z	-18.28	-7.59	-2.14	-1.34

Notes: The spatial distribution of (A) the location of the monkeys and (B) the distribution of feeding trees were classified using nearest neighbor analysis. Patterns were defined as random (R=1), clumped (R<1), or uniform (R>1). They deviated from a random pattern at the alpha level of 0.05 if z>1.96 or z<-1.96.

FIG. 19. Spatial patterns. The spatial distribution of the feeding trees and the bearded saki monkeys were categorized as (A) clumped, (B) random, or (C) uniform.

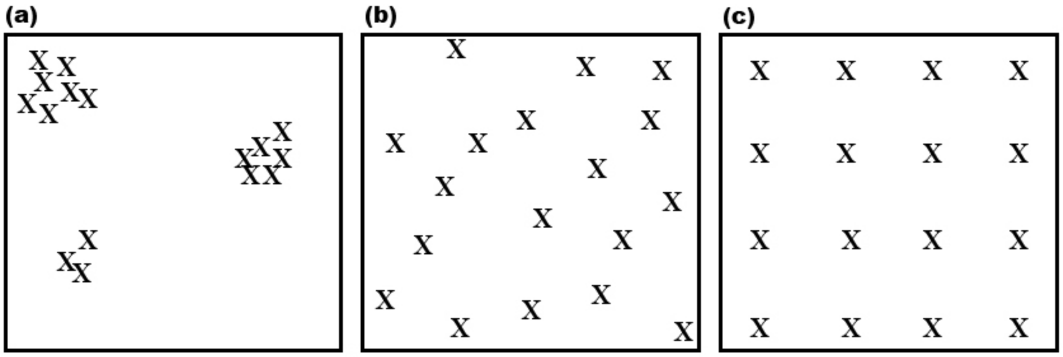

(a)
(b)
(c)

Fig. 20. Distance from start to finish. Distance between the first data point and the last data point of the day was used to characterize the daily travel path. By dividing the total distance between the start and finish points by the total distance traveled during that time period, it was possible to characterize the travel path on a continuum from a circle or polygon (value of zero) to a straight line (value of 1).

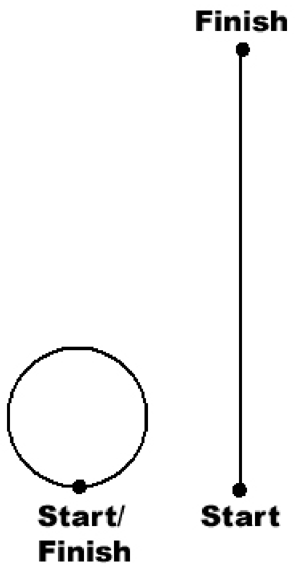

Finish
Start/
Finish
Start

Fig. 21. Daily area. (A) Bearded saki monkeys occupied a greater daily area in continuous forest than in 10-ha and 1-ha forest fragments ($F_{3,3}$=10.61, P=0.042). (B) Differences were even greater between forest size classes when contact time with the monkeys was taken into account ($F_{3,3}$=52.20, P=0.0043). Standard error bars are presented in the graphs.

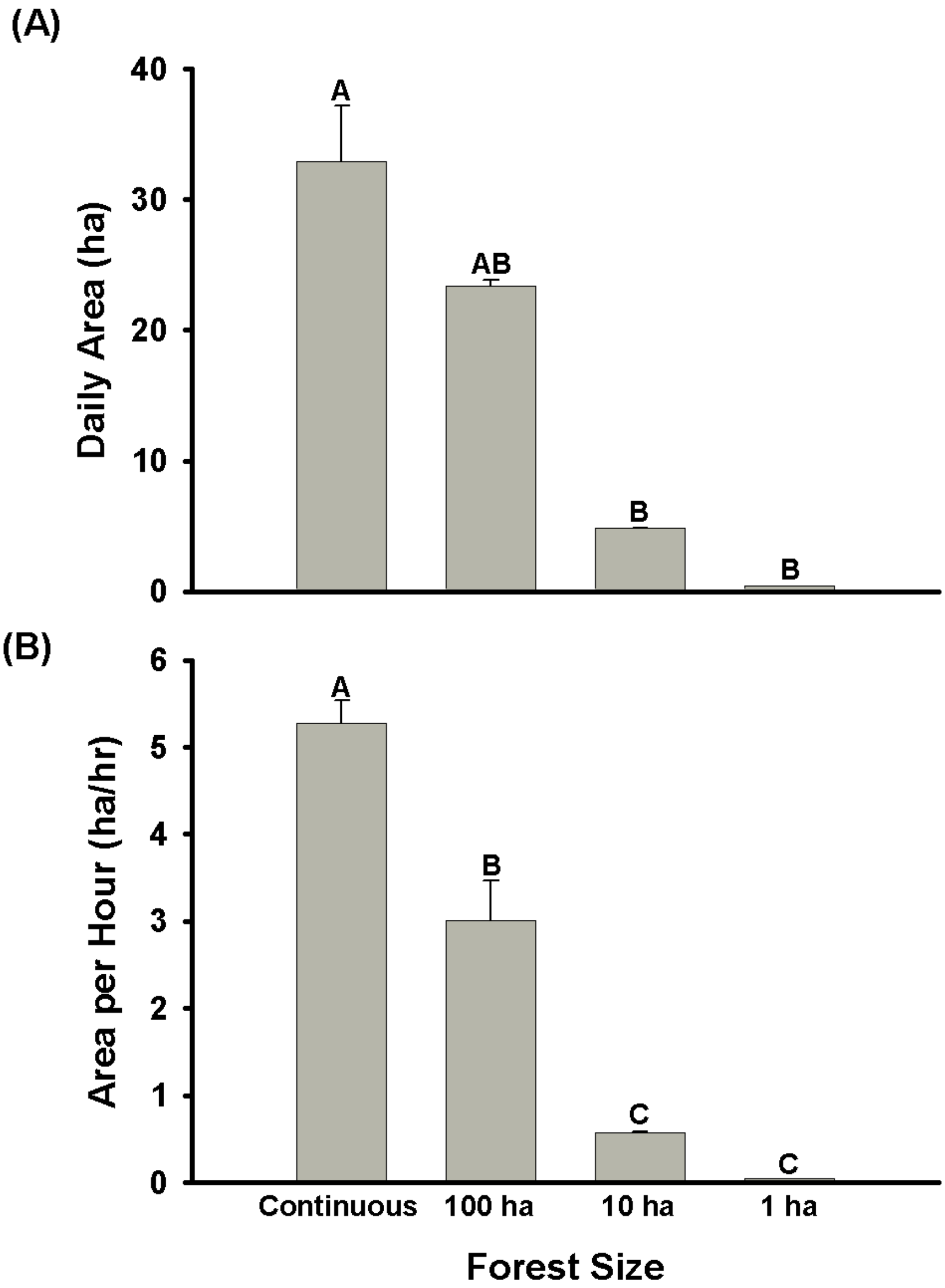

(A)
Daily Area (ha)
40
30
20
10
0
A
AB
B
B
(B)
Area per Hour (ha/hr)
6
5
4
3
2
1
0
A
B
C
C
Continuous
100 ha
10 ha
1 ha
Forest Size

FIG. 22. Area per hour across cycles. The area occupied by the bearded saki monkeys differed overall between cycles ($F_{1,1}$=356.31.20, P=0.0034); however, there was not much fluctuation between cycles in the 10-ha fragments. Standard error bars are presented for the 10-ha fragments. There are no error bars for the continuous forest and 100-ha sites because there was only one study site in each category that had data for all five cycles.

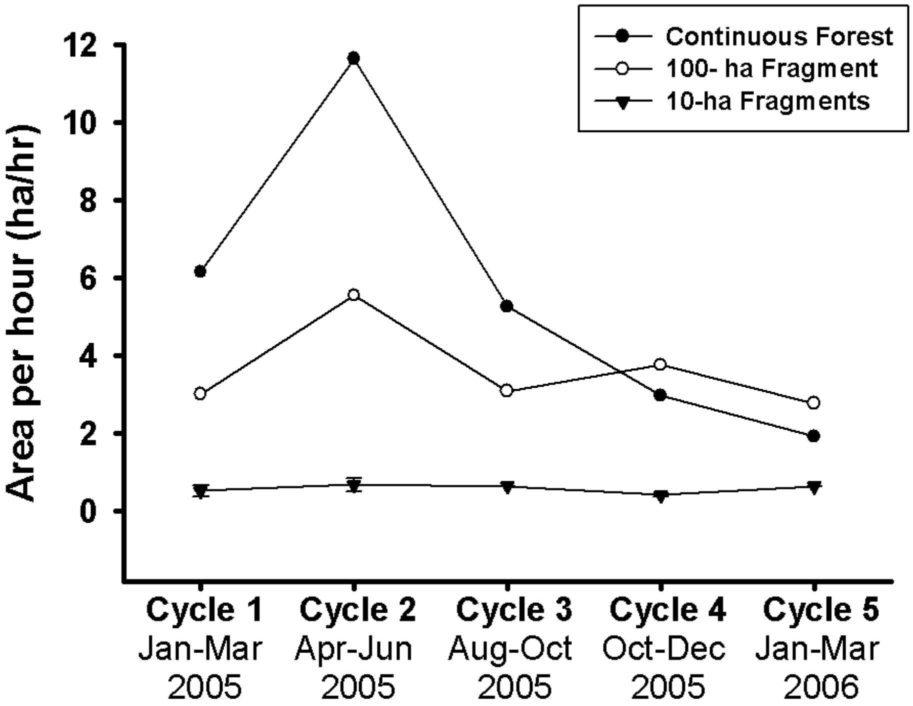
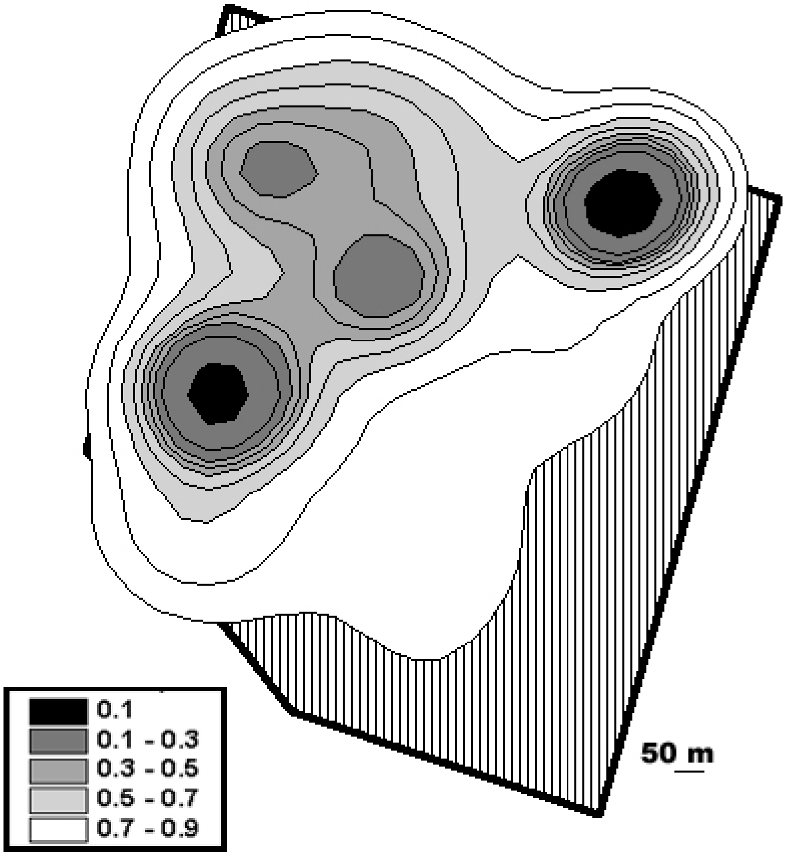
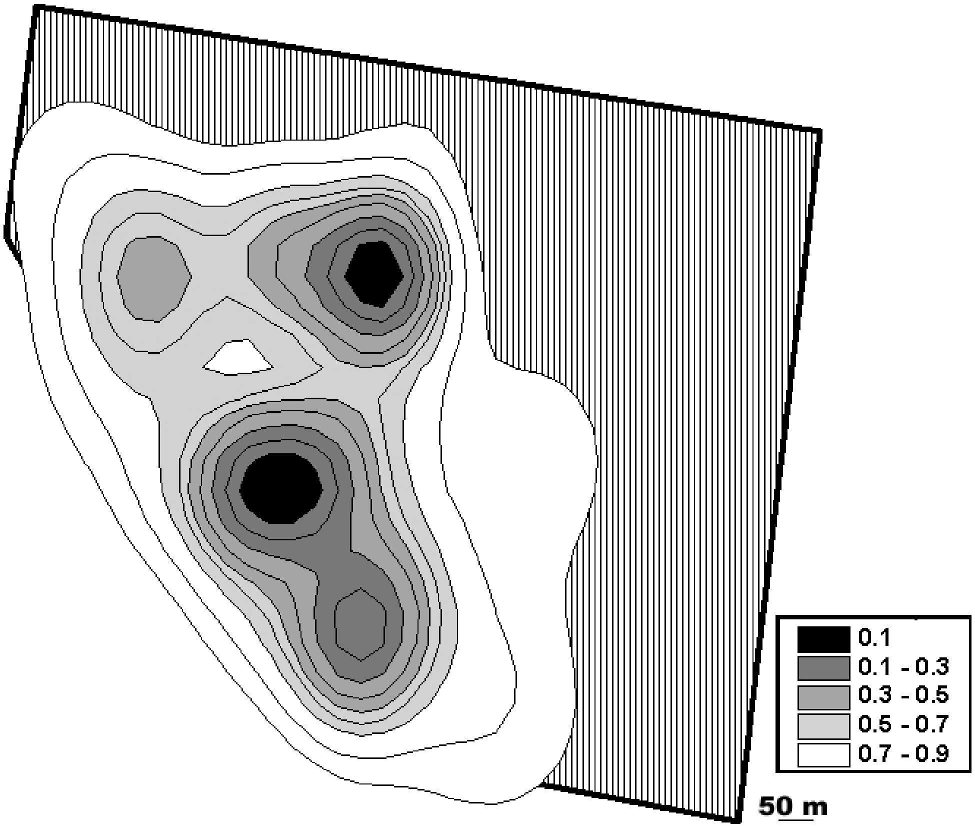

Continuous Forest
100- ha Fragment
10-ha Fragments
Area per hour (ha/hr)
12
10
8
6
4
2
0
Cycle 1
Jan-Mar
2005
Cycle 2
Apr-Jun
2005
Cycle 3
Aug-Oct
2005
Cycle 4
Oct-Dec
2005
Cycle 5
Jan-Mar
2006

FIG. 23. Spatial use of the forest fragments. Kernel density estimators show the probability of finding bearded saki monkeys within the area outlined by the contour lines. Dark areas represent the areas of greatest use by the monkeys. Bearded saki monkeys occupied (A) 83.46% of 100-ha fragment #2303; (B) 54.27% of 100-ha fragment #3304; (C) 100% of 10-ha fragment #1202; (D) 86.28% of 10-ha fragment #2206; and (E) 36.89% of 1-ha fragment #2107 in August 2003 (no bearded saki monkeys were found in the 1-ha fragments during 2005-2006). Figures B-E continue on the following pages.

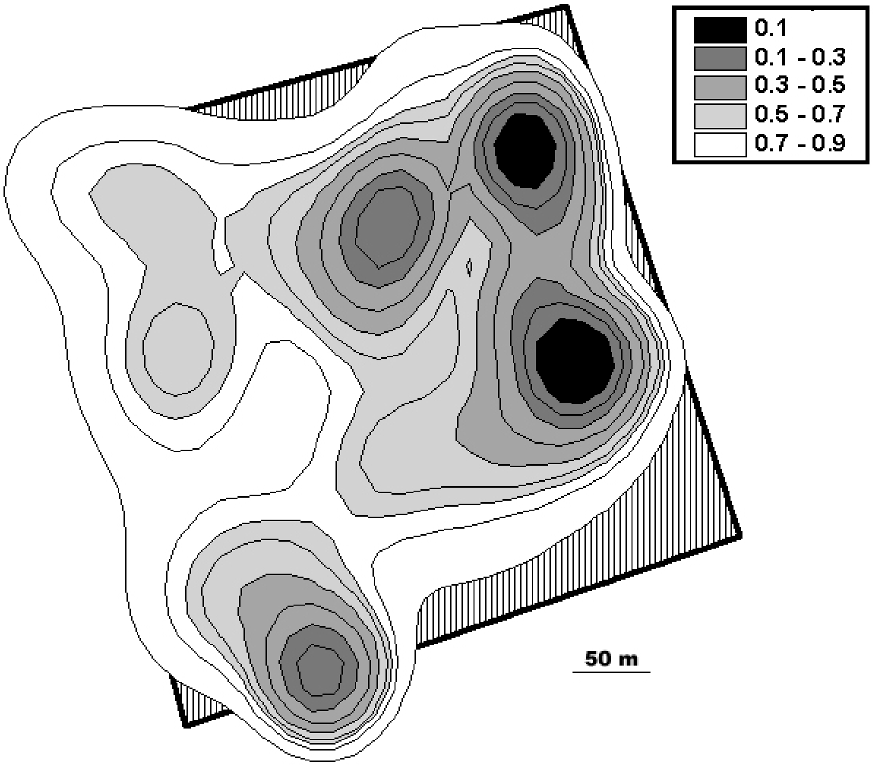
(A)



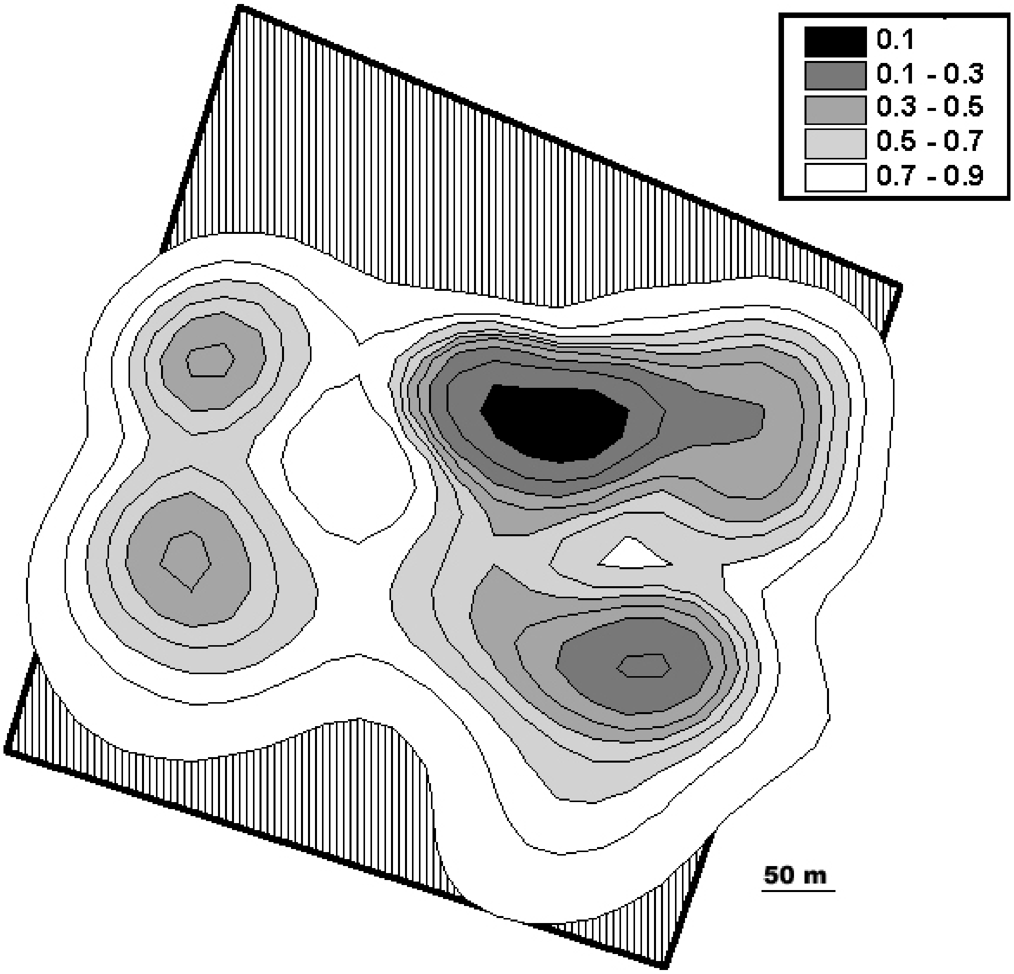
(B)



(C)



(D)



(E)

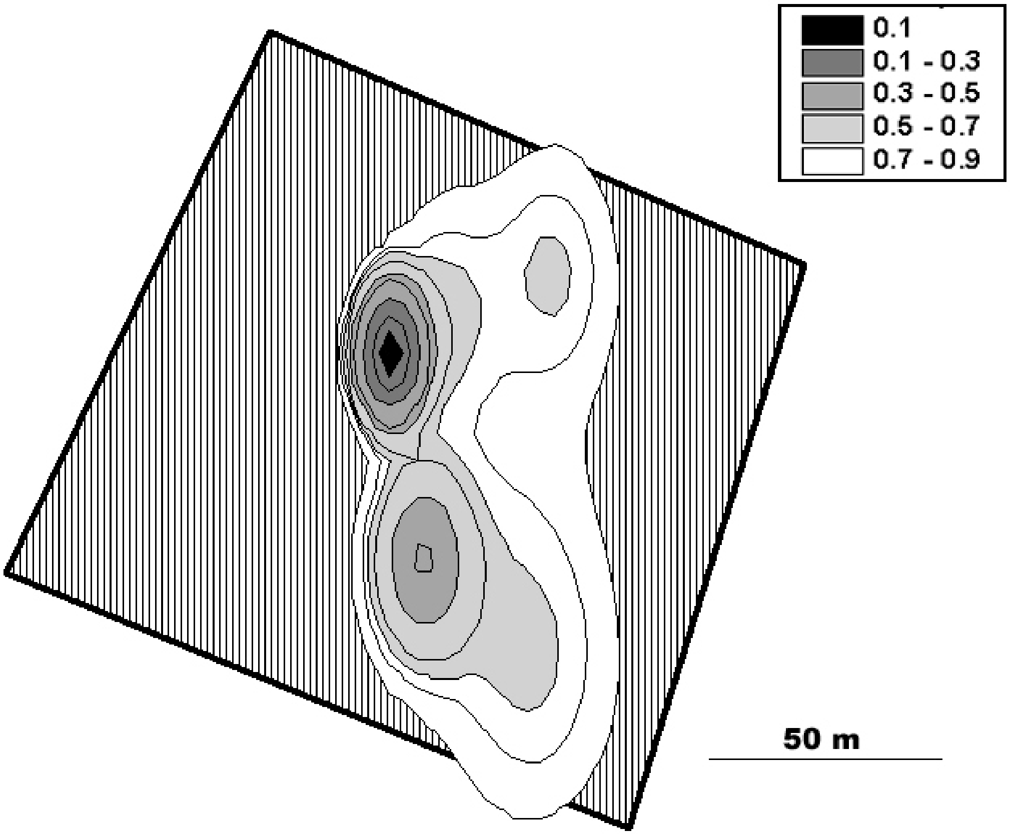


FIG. 24. Distance traveled. (A) Bearded saki monkeys traveled greater daily distances in continuous forest than in 10-ha and 1-ha forest fragments ($F_{3,3}$=58.97, P=0.0036). (B) Differences between the forest class sizes were even greater with comparisons between distances traveled per hour ($F_{3,3}$=155.13, P=0.0009). Standard error bars are presented in the graphs. (C) Distance traveled per ha was greater in the smaller fragments ($F_{3,3}$=431.78, P=0.0002).

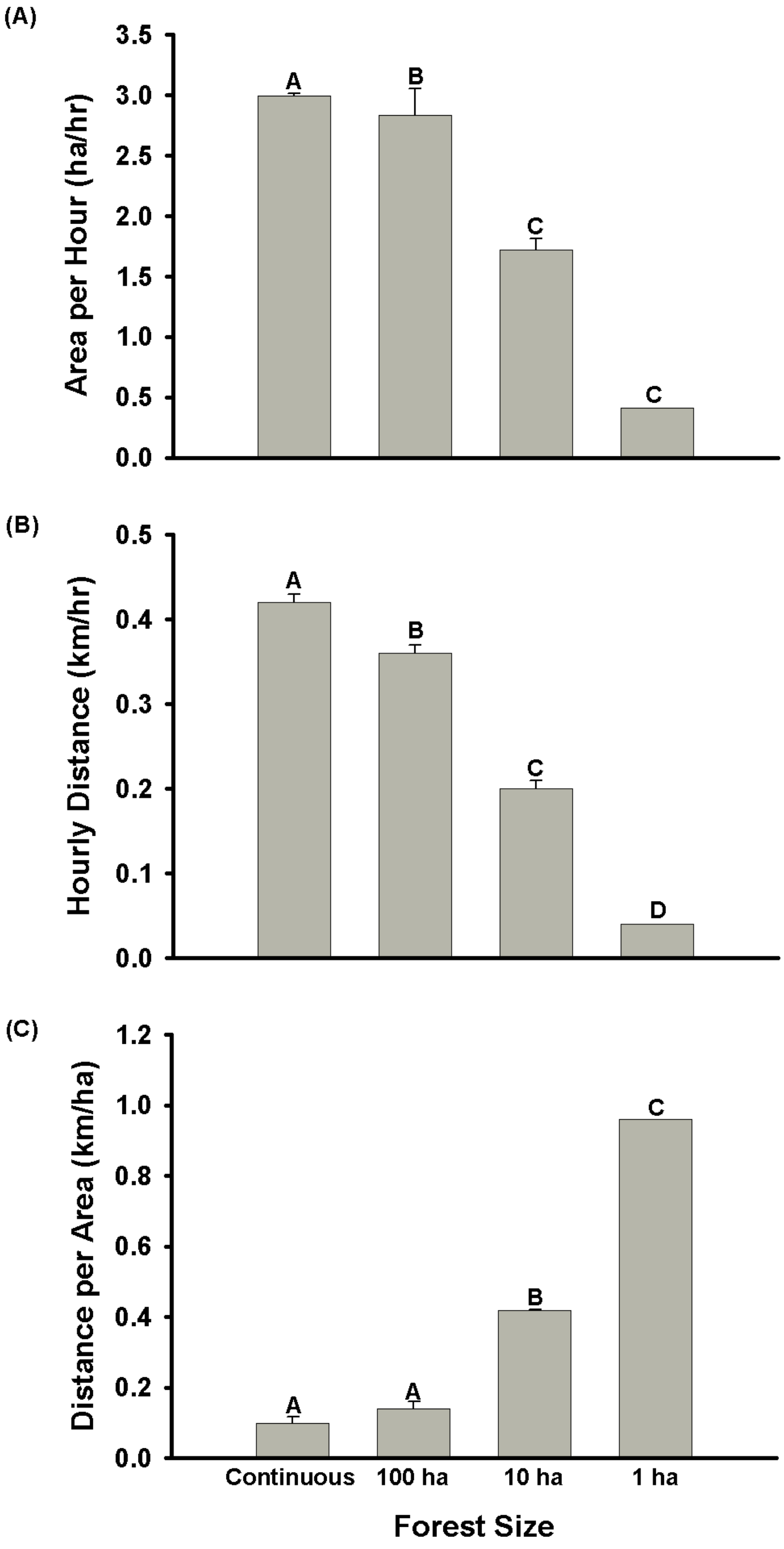

(A)
Area per Hour (ha/hr)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
A
B
C
C
(B)
Hourly Distance (km/hr)
0.5
0.4
0.3
0.2
0.1
0.0
A
B
C
D
(C)
Distance per Area (km/ha)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
A
A
B
C
Continuous
100 ha
10 ha
1 ha
Forest Size

FIG. 25. Travel patterns. Bearded saki monkey day travel routes in continuous forest (A, B) and a 10-ha forest fragment (C, D). Although the monkeys in continuous forest overall had greatest travel distances, straightest daily path, and smallest percentage of feeding trees revisited during a day, there daily variation existed. Distance traveled, the percentage of trees that were revisited for each mapped day, and overall study length were (A) 3.71 km, 0% revisited, 10 hr; (B) 4.07 km, 17% revisited, 11 hr; (C) 3.22 km, 33% revisited, 11 hr; and (D) 0.55 km, 0% revisited, 8 hr.

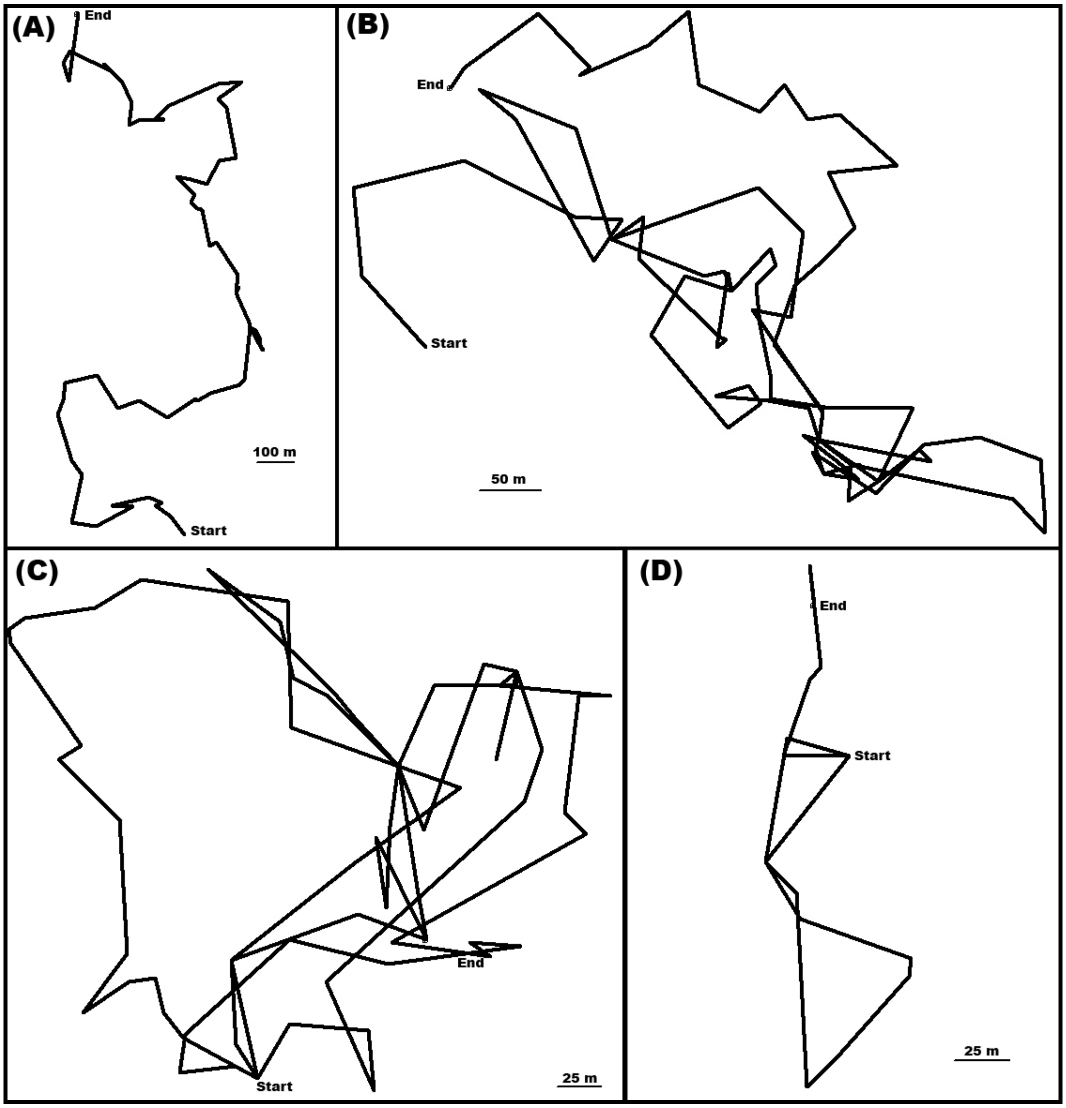

(A)
End
100 m
Start
(B)
End
Start
50 m
(C)
End
Start
25 m
(D)
End
Start
25 m

FIG. 26. Daily travel patterns. Bearded saki monkeys traveled in more circular routes in 10-ha and 100-ha fragments than did monkeys in continuous forest ($F_{3,3}$=9.58, P=0.048). Values close to 0 represent a circular route, and values close to 1 represent a straight-line route. Standard error bars are presented in the graph.

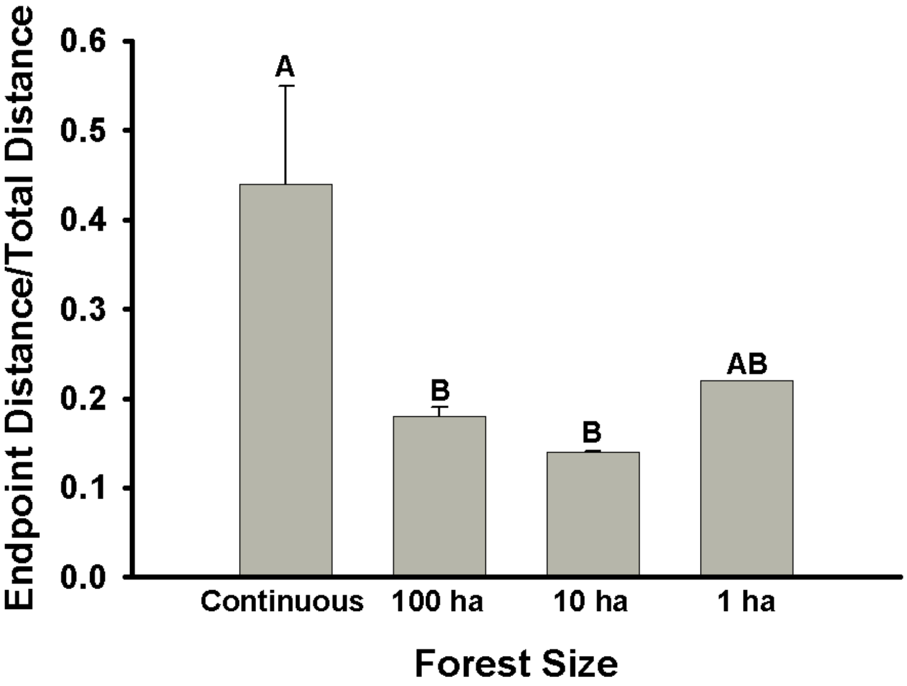
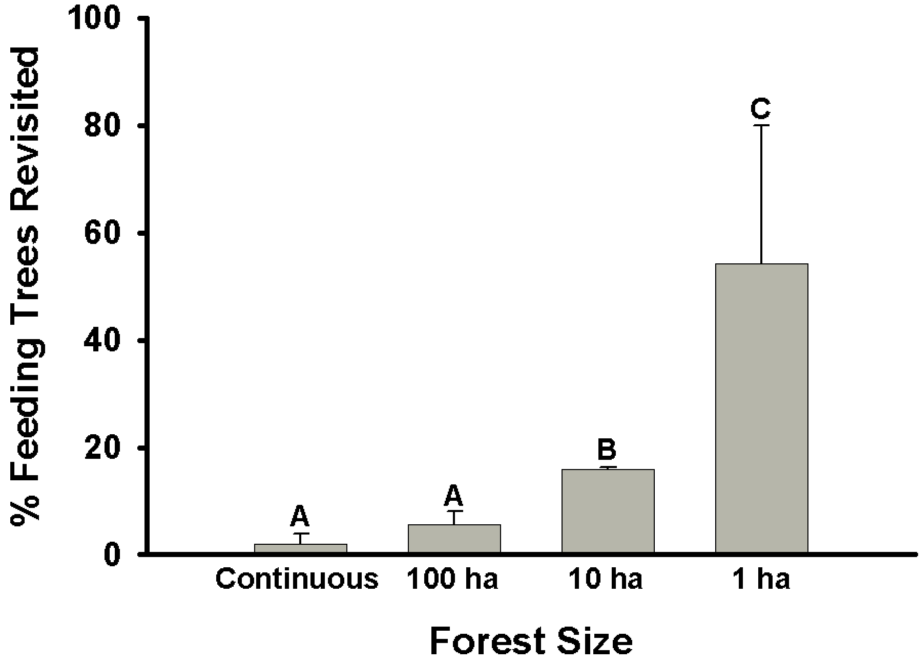

Endpoint Distance/Total Distance
0.0
0.1
0.2
0.3
0.4
0.5
0.6
A
B
B
AB
Continuous
100 ha
10 ha
1 ha
Forest Size

FIG. 27. Revisits to feeding trees. Bearded saki monkeys revisited a greater percentage of feeding trees daily in the smaller forest fragments than in the 100-ha fragments and continuous forest ($F_{3,3}$=103.34, P=0.0016). Standard error bars are presented in the graph.



100
80
60
40
20
0
% Feeding Trees Revisited
A
A
B
C
Continuous
100 ha
10 ha
1 ha
Forest Size

FIG. 28. Feeding trees' distance to fragment edge. The average distance of the bearded saki monkeys' feeding trees to the edge of the forest fragment was greater in 100-ha fragments (*n*=2) than in 10-ha fragments (*n*=2) and a 1-ha fragment (*n*=1); ($F_{2,2}$=37.65, P=0.026). Standard error bars are presented.

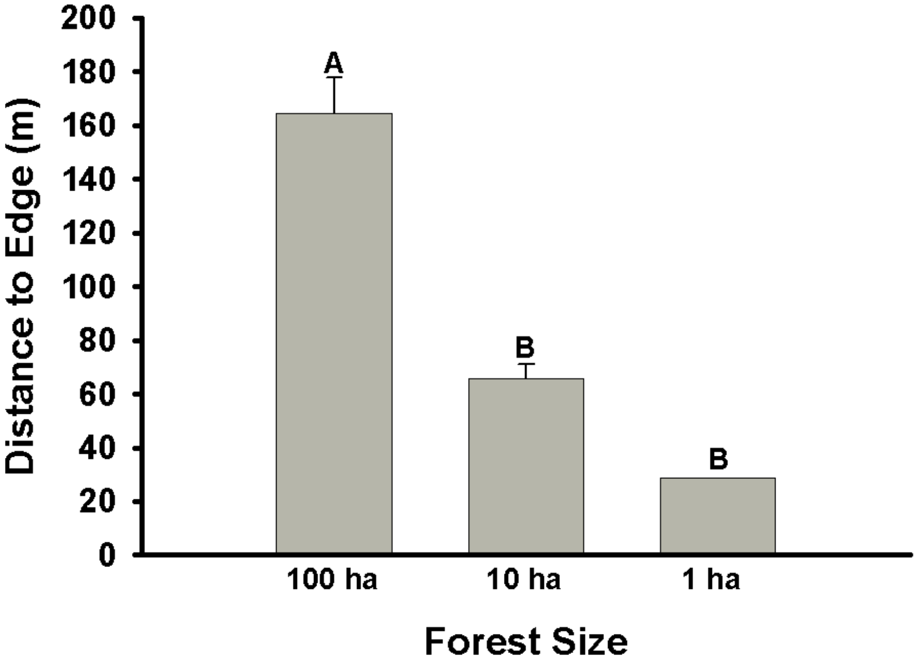

200
180
160
140
120
100
80
60
40
20
0
Distance to Edge (m)
A
B
B
100 ha
10 ha
1 ha
Forest Size

FIG. 29. Distribution of feeding trees. (A) Feeding trees located within 50 m of the border were present in all of the forest fragments, but there was a greater percentage of such trees in the smaller forest fragments ($F_{2,2}$=35.68, P=0.027). (B) The percent of a fragment's area occupied by the four categories varied by size class. (C) The observed distribution of the feeding trees differed from the expected distribution (based on area) in one 100-ha (χ^2=17.10, df=3, P<0.001) fragment, one 10-ha (χ^2=16.86, df=3, P<0.001) fragment, and one 1-ha (χ^2=9.55, df=3, P<0.025) fragment. There were fewer feeding trees within 50 m of the border than what was expected in all five forest fragments.

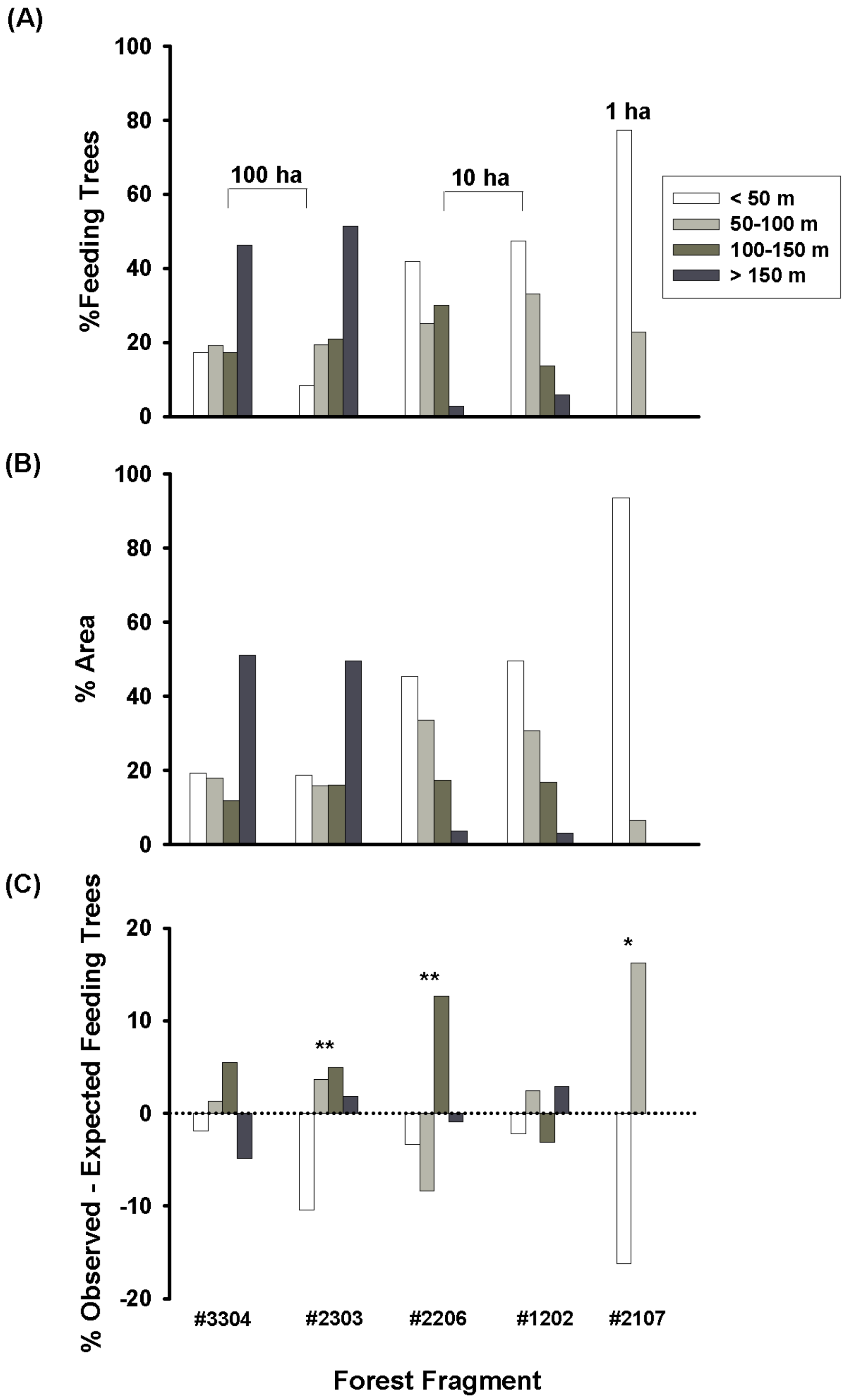
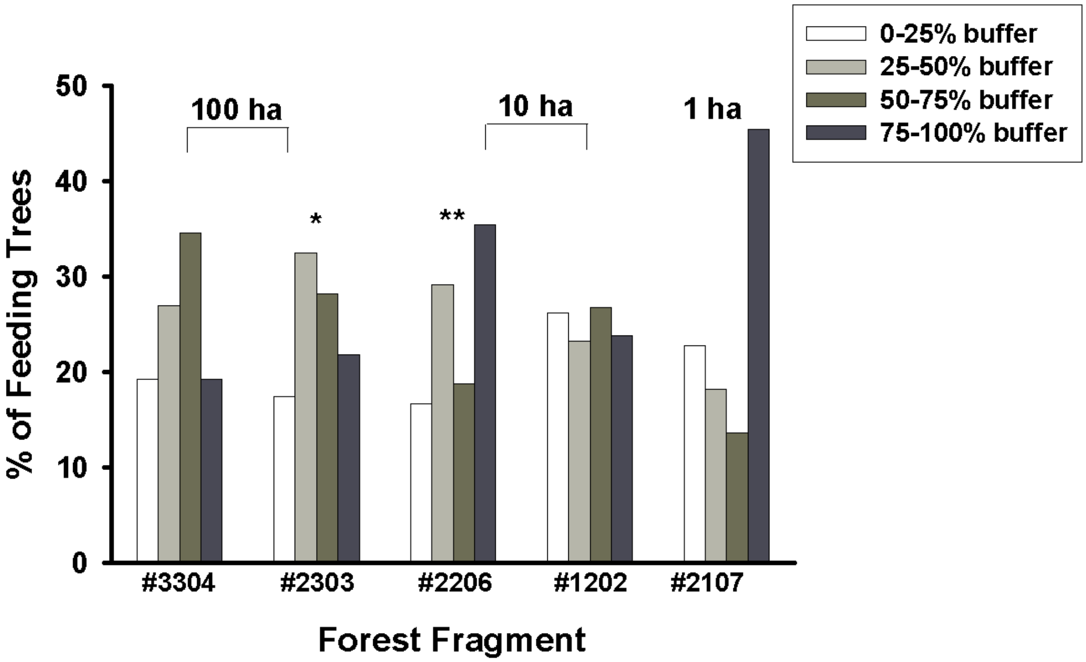

(A)
%Feeding Trees
100
80
60
40
20
0
100 ha
10 ha
1 ha
< 50 m
50-100 m
100-150 m
> 150 m
(B)
% Area
100
80
60
40
20
0
(C)
% Observed - Expected Feeding Trees
20
10
0
-10
-20
**
**
*
#3304
#2303
#2206
#1202
#2107
Forest Fragment

FIG. 30. Feeding trees' distance to fragment edge in relation to area. When the location of feeding trees to forest fragment edge were examined based on four buffer areas of equal size (<25% buffer being closest to the forest fragment's edge and >75% buffer being farthest from the edge), all forest fragments had 17-26% of their feeding trees within 25% of the forest edge, and there was no difference in the percentage of feeding trees found within the 25% buffer between forest size classes ($F_{2,2}$=0.49, P=0.67). Within each forest fragment, there was a difference between the observed and expected distributions of feeding trees in one 100-ha (χ^2=10.97 df=3, P<0.025) and one 10-ha (χ^2=13.50, df=3, P<0.005) fragment.


0-25% buffer
25-50% buffer
50-75% buffer
75-100% buffer
100 ha
10 ha
1 ha
*
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% of Feeding Trees
0
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#2107
Forest Fragment

CHAPTER 5

IMPLICATIONS FOR PRIMATE CONSERVATION IN CENTRAL AMAZONIA

Abstract. Deforestation in the Brazilian Amazon is a serious concern for primate conservation. This chapter presents both a summary of research findings and an update on the current status of six primate species (*Alouatta seniculus*, *Ateles paniscus*, *Cebus apella*, *Chiropotes sagulatus*, *Pithecia pithecia*, and *Saguinas midas*) at the Biological Dynamics of Forest Fragments Project (BDFFP) study area, located north of Manaus, Amazonas, Brazil. Although some of the primate species (e.g., *Alouatta*) have been persistently present in many of the forest fragments, other species (e.g., *Ateles*) have been virtually absent. Furthermore, often there are significant behavioral differences between monkeys living in forest fragments and those living in continuous forest. The primates at BDFFP are further threatened by a recent increase in human presence, as well as a federal colonization plan that would bring 180 families into the study area. Greater human density would likely increase deforestation and hunting pressure on the fauna, thereby threatening those plant and animal species that have not fared well in forest fragments. Furthermore, the colonization plan threatens future research at BDFFP and other research sites, as well as the Central Amazonian Conservation Corridor. Scientists and policymakers are working to develop alternative management plans in order to preserve this area of the Amazon that has ecological, educational, economical, and sociological importance.

INTRODUCTION

Deforestation and forest fragmentation are threats to species conservation worldwide (Gascon *et al.* 2001, Tabarelli and Gascon 2005). The world's largest rain forest, the Amazon, is one of the centers of deforestation (Fearnside 2005). Approximately 50% of the Amazon is located in Brazil (Skole and Tucker 1993), and although estimates vary, approximately 2.4 x 10^6 ha of forest are cleared per year in the Brazilian Amazon (Laurance *et al.* 2004).

Approximately 70% of the deforestation in the Brazilian Amazon can be attributed to medium-sized and large cattle ranches (Fearnside and Graça 2006, Fearnside 2007b). Additional clearing for soybean agriculture (Fearnside 2007b) and selective logging practices (Asner *et al.* 2005, Asner *et al.* 2006) further reduce the amount of intact forest. Deforestation activity is primarily concentrated in the "arc of deforestation," located in the southern and eastern areas of the Brazilian Amazon (Fearnside and Graça 2006), but new highway development plans (Fearnside 2007b) and colonization projects (Blumberg 2007, Laurance and Luizão 2007) threaten to increase deforestation across the Amazon.

Deforestation of the Brazilian Amazon forest for cattle ranches and soybean cultivation has been coupled with intense development of the transportation infrastructure. As roads are paved and more roads are built, areas that were once remote become easily accessible to humans. Often such developments result in an increase in logging and deforestation (Laurance *et al.* 2001a, Nepstad *et al.* 2001, Fearnside 2005, Asner *et al.* 2006, Kirby *et al.* 2006), as well as hunting (Laurance *et al.* 2000b, Peres and Lake 2003). In the Brazilian Amazon, two highways, the BR-163 (Santarém-Cuiabá) and BR-319 (Manaus-Porto Velho), are of particular concern (Fearnside 2005, 2007a).

The region surrounding a third highway, BR-174 (Manaus-Boa Vista), which leads to Venezuela, is the focal area for a controversial plan by the Brazilian federal agency Superintendência da Zona Franca de Manaus (SUFRAMA). The plan calls for at least six colonization projects that would bring 180 families into an area alongside the BR-174, as well as feeder roads such as ZF-3 (Blumberg 2007, Laurance and Luizão 2007). The colonization sites would be located approximately 80 km north of Manaus, a large city of approximately 1.6 million inhabitants (IBGE 2007). Such a project would threaten federally protected areas, a portion of the planned Central Amazonia Conservation Corridor, important research sites operated by the Instituto Nacional da Pesquisas de Amazônia (INPA) and Large Scale Biosphere-Atmosphere Experiment in Amazonia (LBA), and the existence of the Biological Dynamics of Forest Fragments Project (BDFFP), the longest-running study on forest fragmentation (Laurance and Luizão 2007).

The BDFFP, operated by INPA and the Smithsonian Tropical Research Institute, began in 1979 and has resulted in approximately 600 publications, books, dissertations and theses by Brazilian and foreign scientists and students on the consequences of forest fragmentation (Laurance and Luizão 2007). Gascon and Bierregaard, Jr. (2001) and Gascon *et al.* (1999) provide a history of the project and a review of the research findings. The study site occupies 1,000 km^2, and is in the midst of the area slated by SUFRAMA for the colonization projects, even though sections of the BDFFP study area are national protected areas (Blumberg 2007, Laurance and Luizão 2007). Already there has been an influx of human inhabitants to the study area (Plate 3), and BDFFP has suffered from theft, intentional fires, hunting, and logging (Laurance and Luizão 2007).

Six primate species reside in the BDFFP study area: red howler monkey (*Alouatta seniculus*), black spider monkey (*Ateles paniscus*), brown capuchin monkey (*Cebus apella*), northern bearded saki (*Chiropotes sagulatus*), white-faced saki monkey (*Pithecia pithecia*), and golden-handed tamarin (*Saguinus midas*). Although research at BDFFP has been ongoing since 1979, primate research in the forest fragments has been sporadic, with in-depth behavioral and ecological research only on red howler monkeys (Neves 1985, Neves and Rylands 1991, Gilbert 1994, 1997, Santamaría and Rylands 2003, Gómez 2004), white-faced saki monkeys (Setz 1993, 1994, Setz *et al.* 1999), and bearded saki monkeys (Boyle *et al.* In press). These six primate species have not responded equally to forest fragmentation at BDFFP (Rylands and Keuroghlian 1988, Gilbert 2003) Therefore, there is still much to learn regarding the responses of the primates to forest fragmentation, and increased human pressure in the BDFFP study area could affect the conservation of all six species.

In this concluding chapter, I review the current status of the six primate species at the BDFFP, and I illustrate how recent development plans in the

Brazilian Amazon may affect the conservation of the nonhuman primates in the region both directly (i.e., deforestation, hunting) and indirectly (i.e., loss of scientific knowledge). Furthermore, I discuss current and proposed plans to improve conservation in the Amazon.

OVERVIEW OF FINDINGS

One consequence of deforestation is forest fragmentation. Forest fragments result when areas of contiguous forest are cleared, subsequently leaving a mosaic of patches surrounded by a non-forested matrix. As deforestation continues, the remaining forest becomes increasingly patchy, thereby leading to changes in species composition, distribution, and interactions, as well as local climate (Bierregaard Jr. *et al.* 1992, Malcolm 1997, Laurance *et al.* 2000a, Laurance *et al.* 2000b, Achard *et al.* 2002).

Although the effects of forest fragmentation on fauna, flora, climate, and ecological processes have been previously examined, to date there is no consensus as to which factors are primarily responsible for influencing a species' response to forest fragmentation (Harrison and Bruna 1999, Debinski and Holt 2000, Kattan and Murcia 2003). Furthermore, data are lacking for many taxa, including primates.

At the BDFFP study area, the presence of the six primate species in the forest fragments has been variable since the initial isolation of the fragments in the early 1980s (see Chapters 1 and 2). Red howler monkeys have been present in a greater number of forest fragments, and at a greater level of persistency, since the first isolation of the forest fragments in 1980. I found that this pattern continued in July-August 2003 and January 2005-June 2006. Aside from a couple sightings in one 10-ha fragment, black spider monkeys have been absent from the fragments for nearly 30 years. Brown capuchin monkeys have frequented the two 100-ha fragments, but have rarely been present in any of the smaller fragments. Northern bearded saki monkeys have re-colonized some of the forest fragments, and they consistently occupied two 10-ha fragments in 2005-2006, but these monkeys appeared to be less apt to travel between forested areas if the matrix did not consist of tall secondary growth. Other species, such as golden-handed tamarin monkeys and white-faced saki monkeys, also used many of the 10-ha and 100-ha fragments in 2005-2006, and both species appeared to travel across lower-growth matrix habitat.

Overall I found that the size of the forest fragment, its distance to the nearest forest patch larger than 0.50 ha, and the proportion of tall secondary growth forest in the matrix appeared to influence primate species richness of a forest fragment (Chapter 2). Therefore, larger forest fragments that were surrounded by a tall matrix and were located within close proximity to other forest patches had greater species richness. Unfortunately, due to the limited number of forest fragments at BDFFP, it was not possible to fully tease apart the variables, as the two largest forest fragments were also the closest to the other forest patches. However, the proportion of clear-cut area in the matrix, and the distance to continuous forest, were not found to affect primate species richness.

Therefore, it appears that forest patches as small as 0.50 ha and tall secondary growth forest may assist populations in the short-term, and should be considered in land management plans.

Primate characteristics (body size, degree of frugivory, home range size), on the other hand, were not predictive of the presence of a particular species in a fragment. One example of a species that did not follow the convention that highly frugivorous primates with large home ranges would not reside in forest fragments (Rylands and Keuroghlian 1988, Gilbert and Setz 2001) was the northern bearded saki monkey. This species was present in all three fragment size classes (1 ha, 10 ha, and 100 ha) in 2003, and in two 10-ha and the two 100-ha fragments in 2005-2006.

Although the northern bearded saki monkey resided in some of the BDFFP forest fragments, the monkeys living in the fragments had significantly different behavioral ecologies than the bearded saki monkeys that were living in the continuous forest (see Chapters 3 and 4). Northern bearded saki monkeys in the smaller forest fragments had smaller group sizes, smaller home ranges, and smaller daily distances traveled than their continuous forest counterparts. These monkeys also traveled in more circular daily paths, revisited feeding trees throughout the day, and traveled uniformly throughout the 10-ha fragments, even though their feeding trees were not distributed uniformly within the fragments. Furthermore, the monkeys in the small fragments spent less time traveling, more time resting, and less time engaged in social behaviors than the continuous forest monkeys. Lastly, there was little dietary species overlap among the bearded saki groups in the 10-ha (*n*=2) and 100-ha (*n*=2) fragments, and continuous forest (*n*=2). Monkeys living in the forest fragments were restricted to eating the particular plant species that remained in an area after the isolation of the forest fragment. In one of the 10-ha fragments, bearded saki monkeys regularly consumed plant species that were ignored in the other study sites, even though the species fruited during the study.

Therefore, while the presence of the bearded saki monkeys in some of the forest fragments could be considered as optimistic for the species' conservation status, as the monkeys appear to be flexible in their behavior, and can subsist in forest fragments that are a fraction of their characteristic home range size, the extreme behavioral differences between the bearded saki monkey groups, the lack of infants and juveniles in the small fragments, and the apparent isolation of the groups that were not crossing the matrix, indicate that the population may be at risk, particularly if human presence in the area increases.

DISCUSSION

Consequences of increased human impacts

SUFRAMA's colonization plan to bring in 180 families to the area has raised serious concern by scientists who foresee the plan having negative ecological, economical, and sociological consequences (Blumberg 2007, Laurance and Luizão 2007). Agricultural projects in the Amazon are often not profitable (Fearnside 2007b), due to the area's low soil fertility. Ranchers near the BDFFP's forest fragments have experienced this firsthand, and several ranches have been abandoned (Bierregaard Jr. and Gascon 2001). In fact, one of the main uses of forest in central Amazonia is burning it for charcoal (W. Laurance, pers. comm.). Therefore there is concern that the colonists would not benefit from the colonization plan (Blumberg 2007), and there would be increased rates of hunting, logging, and charcoal production. In addition, it is important to note that the plots of land in the SUFRAMA settlement areas would be sold to landowners, some for the purpose of weekend leisure; thus, the settlers are not currently homeless (R. Luizão, pers. comm.).

The possible demise of the BDFFP, a research site that spans three decades, would be a great scientific and educational loss. Approximately three decades of research have been conducted at the BDFFP, yet the BDFFP has also been a source of employment and educational opportunities (e.g., training in science and management) for local residents, for Brazilians from other areas of the country, and for the international community (Bierregaard Jr. *et al.* 2001, Laurance and Luizão 2007). Past and present BDFFP researchers have also partnered with other agencies to work with the rural population on agroforestry projects (e.g,. education, training, distribution of native seedlings), and to provide educational materials on how to make a living without disturbing the protected areas (R. Luizão, pers. comm.). Scientists also credit the cooperation between the local landowners and the BDFFP researchers for the success of the BDFFP project (Bierregaard Jr. and Gascon 2001). Therefore, increased human colonization of the study area threatens all aspects of the BDFFP, including the conservation of the primates in the area.

The BDFFP is a unique and valuable resource for the study of primates and forest fragmentation. Primate censuses were conducted prior to the isolation of the forest fragments, and subsequent censuses of the forest fragments have been intermittently conducted throughout the past three decades (Rylands and Keuroghlian 1988, Schwarzkopf and Rylands 1989, Gilbert and Setz 2001, Gilbert 2003). These data, combined with recent primate censuses, are imperative to determine the current status of the resident primate populations, to document any patterns of primate immigrations and extinctions that have arisen during the past 30 years, and to relate the presence or absence of the species to predictive variables (e.g., fragment size, distance to continuous forest, and condition of the matrix). In addition, the variations in fragment size (1-100 ha) and the configurations of fragments within the surrounding matrix (which varies from pasture to tall secondary growth forest) allow researchers to study the species within the fragments, as well as their use, or avoidance, of the surrounding landscape. Lastly, primates at BDFFP represent six species that vary in body size, diet, home range size, and social structure. Therefore, comparisons of the responses of the species to fragments of various sizes and surrounded by various compositional matrices, is a unique opportunity.

The findings to-date have shed light on the variability in responses of the six resident primate species to forest fragmentation. Understanding why some species are re-colonizing the forest fragments decades later, and how their use of the fragments' resources differ from those animals living in continuous forest, is critical for the conservation planning of the species.

Conservation implications

Overall there is a lack of knowledge of the Amazon's fauna and flora (Peres 2005), including the behavioral ecology of many free-ranging primates (Sussman 2007). If the SUFRAMA colonization plan is put into effect, it could disturb several major scientific research sites in the area, as well as the Central Amazonian Conservation Corridor. More importantly, an increase in colonists could result in the local demise of many plant and animal species, including many of the primates.

Primates are readily hunted in many parts of the tropics, and an influx of settlers to an area would likely bring extra hunting pressure. Human colonization in the eastern Brazilian Amazon has greatly affected the mammal community (Lopes and Ferrari 2000). All six primate species inhabiting the BDFFP region are hunted in some areas of the Amazon, though hunting pressure varies (Peres 1990, Alvard *et al.* 1997, de Souza-Mazurek *et al.* 2000, Peres 2001, de Thoisy *et al.* 2005, Cormier 2006).

To preserve biodiversity in areas experiencing human disturbance, it is important to understand how habitat modifications alter species survival over time. For example, primate presence has fluctuated at the BDFFP, thereby creating opportunities to study species that were not present in the forest fragments during the 1980s. Therefore, the continuation of primate research (e.g., censuses, behavioral studies, land cover classifications) at BDFFP is critical to understanding how (and to what extent) the primates use the forest fragments and the surrounding matrix.

There is serious conservation concern for the future of the BDFFP primates, in particular those that are virtually absent from the majority of the forest fragments (i.e., black spider monkeys, brown capuchin monkeys), those that appear to be severely isolated from other groups due to their hesitance to cross a young matrix (i.e., bearded saki monkeys), and those that may be currently under strong hunting pressure in the immediate areas surrounding the BDFFP reserves (i.e., black spider monkeys, red howler monkeys, and brown capuchin monkeys).

Possible solutions

There are conservation initiatives that are being proposed and implemented across the Amazon. In Manaus, researchers and environmental advocates have partnered with like-minded Brazilian agencies to urge SUFRAMA to 1) halt the colonization plan that would endanger the fauna, flora, and research at BDFPP and other sites, and also disrupt the Central Amazonia Conservation Corridor; 2) release the findings of its 2004 land-use report, which was developed by both SUFRAMA and scientists, as the colonization plan does not follow the recommendations for land use in the report; and 3) consult with scientific and research management organizations and government agencies, as well as the public, prior to commencing any forest-colonization plans (ATBC 2007, Blumberg

2007, Laurance and Luizão 2007). As a result of increased media attention regarding the colonization plan, both in Brazil and abroad (ATBC 2007, Blumberg 2007, Laurance and Luizão 2007, Leite 2007, Lopes 2007, Mongabay.com 2007), in February 2008 SUFRAMA temporarily suspended activities related to forest settlement near the BDFFP area (R. Luizão, pers. comm.). Furthermore, reports Luizão, the BDFFP has been invited to submit proposals for funding to develop a formal management plan for both the BDFFP and other regional protected areas.

The controversy surrounding the SUFRAMA colonization plan, and the recent increase in anthropogenic pressure (e.g., deforestation, hunting) in the BDFFP study area, are common conservation dilemmas found throughout the Amazon. Some federal agencies and institutions, non-government organizations, scientists, and other members of the public are heavily involved in developing, implementing, and enforcing conservation and management programs (Peres 2005, Azevedo-Ramos *et al.* 2006, Kirby *et al.* 2006); however, there has not always been agreement regarding land management and development plans among the various groups (Fearnside 2003). One conservation initiative, the Amazon Region Protected Areas (ARPA), would protect more than 10% of the Brazilian Amazon for a 10-year period, thereby increasing the amount of the Brazilian Amazon that is protected to 46% (Azevedo-Ramos *et al.* 2006). Other initiatives involve the conservation of land by indigenous groups (Zimmerman *et al.* 2001, Schwartzman and Zimmerman 2005, Nepstad *et al.* 2006). Therefore, although deforestation remains a major concern in the Brazilian Amazon, there are efforts being made to minimize additional forest loss.

Conclusion

Deforestation threatens the conservation of fauna and flora, as well as future research and understanding of little-studied taxa and processes. It also has economical and sociological consequences. This dissertation research has shown that primate species do not respond equally to habitat loss, and some species (i.e., northern bearded saki monkeys) that are capable of residing in forest fragments that are fractions of the species' characteristic home range size may not be able to survive in the long-term. Therefore, there is a need for the designation and monitoring of conservation areas and parks (Terborgh and van Schaik 2002, Peres 2005), as well as programs that encourage conservation by small landholders (Campos and Nepstad 2006) and people living near or within reserves (Nepstad *et al.* 2006). Increased knowledge and awareness of the habitat needs of the fauna and flora are necessary in order to design and implement successful conservation and management plans.

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PLATE 3. Human settlements. Settlers within the Biological Dynamics of Forest Fragments Project (BDFFP) study area have illegally cut native forest. Theft, hunting, and intentional fires have also posed problems to the BDFFP. This photograph depicts one settlement in July 2007. Photo courtesy of BDFFP/C. da Costa.

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LITERATURE CITED

Achard, F., H. D. Eva, H. J. Stibig, P. Mayaux, J. Gallego, T. Richards, and J. P. Malingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. Science **297**:999-1002.

Allan, B. F., F. Keesing, and R. Ostfeld. 2003. Effect of forest fragmentation on Lyme disease risk. Conservation Biology **17**:267-272.

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour **48**:227-265.

Alvard, M. S., J. G. Robinson, K. H. Redford, and H. Kaplan. 1997. The sustainability of subsistence hunting in the Neotropics. Conservation Biology **11**:977-982.

Anderson, J., J. M. Rowcliffe, and G. Colinshaw. 2007. Does the matrix matter? A forest primate in a complex agricultural landscape. Biological Conservation **135**:212-222.

Asner, G. P., E. N. Broadbent, P. J. C. Oliveira, M. Keller, D. E. Knapp, and J. N. M. Silva. 2006. Condition and fate of logged forests in the Brazilian Amazon. Proceedings of the National Academy of Sciences of the United States of America **103**:12947-12950.

Asner, G. P., D. E. Knapp, E. N. Broadbent, P. J. C. Oliveira, M. Keller, and J. N. Silva. 2005. Selective logging in the Brazilian Amazon. Science **310**:480-482.

Asquith, N. M., S. J. Wright, and M. J. Clauss. 1997. Does mammal community composition control recruitment in neotropical forests? Evidence from Panama. Ecology **78**:941-946.

ATBC. 2007. Resolution Supporting Conservation of Critical Ecosystems and Research Sites in Central Amazonia. Association for Tropical Biology and Conservation.

Attuquayefio, D. K., M. L. Gorman, and R. J. Wolton. 1986. Home range sizes in the wood mouse *Apodmus sylvaticus*: habitat, sex and seasonal differences. Journal of Zoology **210**:45-53.

Ayres, J. M. 1981. Observações sobre a ecologia e o comportamento dos cuxiús (*Chiropotes albinasus* e *Chiropotes satanas*, Cebidae: Primates). M.Sc. Thesis. Insituto Nacional de Pesquisas da Amazônia and Fundação Universidade do Amazonas, Manaus, Amazonas, Brazil.

Ayres, J. M. 1989. Comparative feeding ecology of the uakari and bearded saki, *Cacajao* and *Chiropotes*. Journal of Human Evolution **18**:697-716.

Azevedo-Ramos, C., B. D. do Amaral, D. C. Nepstad, S. B. Filho, and R. Nasi. 2006. Integrating ecosystem management, protected areas, and mammal conservation in the Brazilian Amazon. Ecology and Society **11**:17.

Bicca-Marques, J. C. 2003. How do howler monkeys cope with habitat fragmentation? Pages 283-303 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer Academic/Plenum Publishers, New York, New York, USA.

Bierregaard Jr., R. O., and C. Gascon. 2001. The Biological Dynamics of Forest Fragments Project: overview and history of a long-term conservation project. Pages 5-12 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Bierregaard Jr., R. O., W. F. Laurance, C. Gascon, J. Benitez-Malvido, P. M. Fearnside, C. R. Fonseca, G. Ganade, J. R. Malcolm, M. B. Martins, S. Mori, M. Oliveira, J. Rankin-De Merona, A. Scariot, W. Spironello, and B. Williamson. 2001. Principles of forest fragmentation and conservation in the Amazon. Pages 371-385 *in* R. O. Bierregaard Jr, C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Bierregaard Jr., R. O., T. E. Lovejoy, V. Kapos, A. A. Dossantos, and R. W. Hutchings. 1992. The Biological Dynamics of Tropical Rain-Forest Fragments. Bioscience **42**:859-866.

Bierregaard Jr., R. O., and P. C. Stouffer. 1997. Understory birds and dynamic habitat mosaics in Amazonian rainforests. Pages 138-155 *in* W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, Illinois, USA

Bingham, B. B., and B. R. Noon. 1997. Mitigation of habitat "take": application to habitat conservation planning. Conservation Biology **11**:127-139.

Bissonette, J. A., and I. Storch. 2002. Fragmentation: Is the message clear? Conservation Ecology (online) **6**:14.

Blumberg, J. 2007. Up in smoke. Smithsonian Magazine **38**:31.

Bonvicino, C. R., J. P. Boubli, I. B. Otazú, F. C. Almeida, F. F. Nascimento, J. R. Coura, and H. N. Seuánez. 2003. Morphologic, karyotypic, and molecular evidence of a new form of *Chiropotes* (Primates, Pitheciinae). American Journal of Primatology **61**:123-133.

Börger, L., N. Franconi, G. de Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006a. Effects of sampling regime on the mean and variance of home range size estimates. Journal of Animal Ecology **75**:1393-1405.

Börger, L., N. Franconi, F. Ferretti, F. Meschi, G. de Michele, A. Gantz, and T. Coulson. 2006b. An integrated approach to indentify spatiotemporal and individual-level determinants of animal home range size. The American Naturalist **168**:471-485.

Boyle, S. A., A. T. Smith, W. R. Spironello, and C. E. Zartman. In press. The behavioural ecology of northern bearded sakis (*Chiropotes sagulatus*) living in forest fragments of central Brazilian Amazonia. *in* A. Barnett, L. M. Viega, S. F. Ferrari, and M. A. Norconk, editors. Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, Cambridge, UK.

Brandon, K., G. A. B. da Fonseca, A. B. Rylands, and J. M. C. da Silva. 2005. Brazilian conservation: challenges and opportunities. Conservation Biology **19**:595-600.

Brotons, L., M. Mönkkönen, and J. L. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. The American Naturalist **162**:343-357.

Bull, E. L., and R. S. Holthausen. 1993. Habitat use and management of pileated woodpeckers in northeastern Oregon. Journal of Wildlife Management **57**:335-345.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy **24**:346-352.

Campos, M. T., and D. C. Nepstad. 2006. Smallholders, the Amazon's new conservationists. Conservation Biology **20**:1553-1556.

Cederlund, G. N., and H. Okarma. 1988. Home range and habitat use of adult female moose. Journal of Wildlife Management **52**:336-343.

Chapman, C. A. 1990. Ecological constraints on group size in three species of neotropical primates. Folia Primatologica **55**:1-9.

Chapman, C. A., and L. J. Chapman. 1990. Dietary variability in primate populations. Primates **31**:121-128.

Chapman, C. A., and L. J. Chapman. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. Journal of Tropical Ecology **12**:491-504.

Chapman, C. A., M. J. Lawes, L. Naughton-Treves, and T. Gillespie. 2003. Primate survival in community-owned forest fragments: Are metapopulation models useful amidst intensive use? Pages 63-76 *in* L. Marsh, editor. Primates in Fragments. Kluwer Academic, New York, New York, USA.

Chapman, C. A., L. Naughton-Treves, M. J. Lawes, M. D. Wasserman, and T. R. Gillespie. 2007. Population declines of colobus in western Uganda and conservation value of forest fragments. International Journal of Primatology **28**:513-528.

Chapman, C. A., and D. A. Onderdonk. 1998. Forests without primates: Primate/plant codependency. American Journal of Primatology **45**:127-141.

Cheptou, P.-O., and L. G. Avendaño V. 2006. Pollination processes and the Allee effect in highly fragmented populations: consequences for the mating system in urban environments. New Phytologist **172**:774-783.

Chew, S. C. 2001. World Ecological Degradation: Accumulation, Urbanization, and Deforestation 3000 B.C.-A.D. 2000. AltaMira Press, Walnut Creek, California, USA.

Chiarello, A. G. 1994. Diet of the brown howler monkey *Alouatta fusca* in a semi-deciduous forest fragment of southern Brazil. Primates **35**:25-34.

Ciofi, C., J. Puswati, D. Winana, M. E. de Boer, G. Chelazzi, and P. Sastrawan. 2007. Preliminary analysis of home range structure in the Komodo monitor, *Varanus komodoensis*. Coepia **2**:462-470.

Clarke, M. R., D. A. Collins, and E. L. Zucker. 2002. Responses to deforestation in a group of mantled howlers (*Alouatta palliata*) in Costa Rica. International Journal of Primatology **23**:365-381.

Clutton-Brock, T. H., and P. H. Harvey. 1977. Species differences in feeding and ranging behaviour in primates. Pages 557-584 *in* T. H. Clutton-Brock, editor. Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes. Academic Press, London, UK.

Cook, W. M., K. T. Lane, B. L. Foster, and R. D. Holt. 2002. Island theory, matrix effects and species richness patterns in habitat fragments. Ecology Letters **5**:619-623.

Cormier, L. 2006. A preliminary review of Neotropical primates in the subsistence and symbolism of indigenous lowland South American peoples. Ecological and Environmental Anthropology **2**:14-32.

Crockett, C. M. 1998. Conservation biology of the genus *Alouatta*. International Journal of Primatology **19**:549-578.

Crockett, C. M., and J. F. Eisenberg. 1987. Howlers: Variation in group size and demography. Pages 56-68 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, and T. T. Struhsaker, editors. Primate Societies. University of Chicago Press, Chicago, Illinois, USA.

Cruz, A. C. M. S., J. T. Borda, E. M. Patiño, L. Gómez, and G. E. Zunino. 2000. Habitat fragmentation and parasitism in howler monkeys (*Alouatta caraya*). Neotropical Primates **8**.

Curtis, J. T. 1956. The modification of mid-latitude grasslands and forests by man. Pages 721-736 *in* W. L. Thomas, editor. Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, Illinois, USA.

Dale, V. H., S. M. Pearson, H. L. Offerman, and R. V. Oneill. 1994. Relating patterns of land-use change to faunal biodiversity in the Central Amazon. Conservation Biology **8**:1027-1036.

Darby, H. C. 1956. The clearing of the woodland in Europe. Pages 183-216 *in* W. L. Thomas, editor. Man's Role in Changing the Face of the Earth. University of Chicago Press, Chicago, Illinois, USA.

Day, R. T., and R. W. Elwood. 1999. Sleeping site selection by the golden-handed tamarin *Saguinus midas midas*: The role of predation risk, proximity to feeding sites, and territorial defence. Ethology **105**:1035-1051.

de Oliveira, A. A., and S. A. Mori. 1999. A central Amazonian terra firme forest. I. High tree species richness on poor soils. Biodiversity and Conservation **7**:129-146.

de Souza-Mazurek, R. R., T. Pedrinho, X. Feliciano, W. Hilário, S. Gerôncio, and E. Marcelo. 2000. Subsistence hunting among the Waimiri Atroari Indians in central Amazonia, Brazil. Biodiversity and Conservation **9**:579-596.

de Thoisy, B., F. Renoux, and C. Julliot. 2005. Hunting in northern French Guiana and its impact on primate communities. Oryx **39**:149-157.

Debinski, D. M. 2006. Forest fragmentation and matrix effects: the matrix *does* matter. Journal of Biogeography **33**:1791-1792.

Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology **14**:342-355.

Defler, T. R. 1996. Aspects of the ranging pattern in a group of wild woolly monkeys (*Lagothrix lagotricha*). American Journal of Primatology **38**:289-302.

Di Fiore, A. 2003. Ranging behavior and foraging ecology of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in Yasuní National Park, Ecuador. American Journal of Primatology **59**:47-66.

Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. Biological Conservation **7**:129-146.

Didham, R. K., J. Ghazoul, N. E. Stork, and A. J. Davis. 1996. Insects in fragmented forests: A functional approach. Trends in Ecology and Evolution **11**:255-260.

Dietz, J. M., A. J. Baker, and J. D. Ballou. 2000. Demographic evidence of inbreeding depression in wild golden lion tamarins. Pages 203-211 *in* A. G. Young and G. M. Clarke, editors. Genetics, Demography and Viability of Fragmented Populations. Cambridge University Press, Cambridge, UK.

Dobson, A. P., and A. M. Lyles. 1989. The population dynamics and conservation of primate populations. Conservation Biology **3**:362-380.

Dumont, E. R. 2003. Bats and fruit: an ecomorphological approach. Pages 398-429 *in* T. H. Kunz and M. B. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago, Illinois, USA.

Dunbar, R. I. M. 1988. Primate Social Systems. Cornell University Press, Ithaca, New York, USA.

Emmons, L. H. 1999. Of mice and monkeys: Primates as predictors of mammal community richness. Pages 171-188 *in* J. G. Fleagle, C. Janson, and K. E. Reed, editors. Primate Communities. University of Cambridge Press, Cambridge, UK.

Estrada, A., A. Anzures, and R. Coates-Estrada. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. American Journal of Primatology **48**:253-262.

Estrada, A., and R. Coates-Estrada. 1988. Tropical rain-forest conversion and perspectives in the conservation of wild primates (*Alouatta* and *Ateles*) in Mexico. American Journal of Primatology **14**:315-327.

Estrada, A., and R. Coates-Estrada. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. International Journal of Primatology **17**:759-783.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**:50-59.

FAO. 2007. State of the World's Forests 2007. Food and Agricultural Organization of the United Nations, Rome, Italy.

Fearnside, P. M. 2003. Conservation policy in Brazilian Amazonia: understanding the dilemmas. World Development **31**:757-779.

Fearnside, P. M. 2005. Deforestation in Brazilian Amazonia: history, rates, and consequences. Conservation Biology **19**:680-688.

Fearnside, P. M. 2007a. Brazil's Cuiabá-Santarém (BR-163) Highway: The envirionmental cost of paving a soybean corridor through the Amazon. Environmental Management **39**:601-614.

Fearnside, P. M. 2007b. The fractured landscape. The American Prospect **18**:A11-A13.

Fearnside, P. M., and P. M. L. Graça. 2006. BR-319: Brazil's Manaus-Porto highway and the potential impact of linking the arc of deforestation to central Amazonia. Environmental Management **38**:705-716.

Fedigan, L. M., L. Fedigan, C. Chapman, and K. E. Glander. 1988. Spider monkey home ranges: a comparison of radio telemetry and direct observation. American Journal of Primatology **16**:19-29.

Ferrari, S. F., and V. H. Diego. 1995. Habitat fragmentation and primate conservation in the Atlantic Forest of eastern Minas Gerais, Brazil. Oryx **29**:192-196.

Ferrari, S. F., C. Emidio-Silva, M. A. Lopes, and U. L. Bobadilla. 1999. Bearded sakis in south-eastern Amazonia - back from the brink? Oryx **33**:346-351.

Ferrari, S. F., S. Iwanaga, A. L. Ravetta, F. C. Freitas, B. A. R. Sousa, L. L. Souza, C. G. Costa, and P. E. G. Coutinho. 2003. Dynamics of primate communities along the Santarém-Cuiabá highway in south-central Brazilian Amazonia. Pages 123-144 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer Academic, New York, New York, USA.

Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, and T. E. Lovejoy. 2003. Rates of species loss from Amazonian forest fragments. Proceedings of the National Academy of Sciences of the United States of America **100**:14069-14073.

Ferreira, L. V., and W. F. Laurance. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conservation Biology **11**:797-801.

Ford, S. M., and L. C. Davis. 1992. Systematics and body size: implications for feeding adaptation in New World monkeys. American Journal of Physical Anthropology **88**:415-468.

Frazão, E. 1991. Insectivory in free-ranging bearded sakis. Primates **32**:245-247.

Frazão, E. 1992. Dieta e estrategia de forragear de *Chiropotes satanas chiropotes* (Cebidae: Primates) na Amazônia central Brasileira. M.Sc. Thesis. Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.

Gascon, C., and R. O. Bierregaard Jr. 2001. The biological dynamics of forest fragments project: the study site, experimental design, and research activity. Pages 31-42 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Gascon, C., R. O. Bierregaard Jr., W. F. Laurance, and J. M. Rankin-De Mérona. 2001. Deforestation and forest fragmentation in the Amazon. Pages 22-30 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Gascon, C., W. F. Laurance, and T. E. Lovejoy. 2003. Forest fragmentation and biodiversity in central Amazonia. Pages 33-48 *in* G. A. Bradshaw and P. A. Marquet, editors. How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas. Springer-Verlag, Berlin, Germany.

Gascon, C., and T. E. Lovejoy. 1998. Ecological impacts of forest fragmentation in central Amazonia. Zoology-Analysis of Complex Systems **101**:273-280.

Gascon, C., T. E. Lovejoy, R. O. Bierregaard, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation **91**:223-229.

Gascon, C., G. B. Williamson, and G. A. B. da Fonseca. 2000. Ecology - Receding forest edges and vanishing reserves. Science **288**:1356-1358.

Gaulin, S. J. C., and C. K. Gaulin. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. International Journal of Primatology **3**:1-32.

Geosystems, L. 2005. ERDAS Field Guide^{TM}. Leica Geosystems Geospatial Imaging, LLC, Norcross, Georgia, USA.

Gese, E. M., J. R. Orrin, and W. R. Mytton. 1988. Home range and habitat use of coyotes in southeastern Colorado. Journal of Wildlife Management **52**:640-646.

Gilbert, K. A. 1994. Endoparasitic infection in red howling monkeys (*Alouatta seniculus*) in the central Amazonian basin. Ph.D. dissertation. Rutgers, New Brunswick, New Jersey, USA.

Gilbert, K. A. 1997. Red howling monkey use of specific defecation sites as a parasite avoidance strategy. Animal Behaviour **54**:451-455.

Gilbert, K. A. 2003. Primates and fragmentation of the Amazon forest. Pages 145-157 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer Academic, New York, New York, USA.

Gilbert, K. A., and E. A. Setz. 2001. Primates in a fragmented landscape: six species in Central Amazonia. Pages 262-270 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons From Amazonia: the Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Gómez, M. S. 2004. The effect of home range reduction on the ecology of red howler monkeys in central Amazonia. Ph.D. dissertation. University of Cambridge, Cambridge, UK.

Gonzalez-Kirchner, J. P. 1999. Habitat use, population density and subgrouping pattern of the Yucatan spider monkey (*Ateles geoffroyi yucatanensis*) in Quintana Roo, Mexico. Folia Primatologica **70**:55-60.

Goudie, A. 2001. The Human Impact on the Natural Environment. MIT Press, Cambridge, Massachusetts, USA.

Guillotin, M., and G. Dubost. 1994. Food choice and food competition among the three major primate species of French Guiana. Journal of Zoology **233**:551-579.

Haila, Y. 2002. A conceptual genealogy of fragmentation research: From island biogeography to landscape ecology. Ecological Applications **12**:321-334.

Hanski, I. 1994. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology and Evolution **9**:131-135.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

Hanski, I., and O. Ovaskainen. 2003. Metapopulation theory for fragmented landscapes. Theoretical Population Biology **64**:119-127.

Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trewhella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracing data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review **20**:97-123.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography **22**:225-232.

Harvey, P. H., and T. H. Clutton-Brock. 1981. Primate home-range size and metabolic needs. Behavioral Ecology and Sociobiology **8**:151-155.

Haskell, J. P., M. E. Ritchie, and H. Olff. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature **418**:527-530.

Hayne, D. W. 1949. Calculation of size of home range. Journal of Mammalogy **30**:1-18.

Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. MacDonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. Journal of Animal Ecology **74**:455-463.

Hershkovitz, P. 1985. A preliminary taxonomic review of the South American bearded saki monkeys genus *Chiropotes* (Cebidae, Platyrrhini), with the description of a new subspecies. Fieldiana **27**:1-46.

Heydon, M. J., and P. Bulloh. 1997. Mousedeer densities in a tropical rainforest: the impact of selective loggin. The Journal of Applied Ecology **34**:484-496.

Hombug, I. 1997. Ökologie and sozialverhalten einer gruppe von weißgesicht-sakis (*Pithecia pithecia pithecia* Linnaeus 1766) im Estado Bolívar, Venezuela. Ph.D. Dissertation. Universität Bielefeld, Bielefeld, Germany.

Hooge, P. N., and B. Eichenlaub. 1997. Animal Movement Extension to ArcView. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

Horwich, R. H. 1998. Effective solutions for howler conservation. International Journal of Primatology **19**:579-598.

IBGE. 2007. Contagem de População 2007. Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, Rio de Janeiro, Brazil.

Izawa, K. 1980. Social behavior of the wild black-capped capuchin (*Cebus apella*). Primates **21**:443-467.

Janzen, D. H. 1988. Management of habitat fragments in a tropical dry forest: growth. Annals of the Missouri Botanical Garden **75**:105-116.

Johns, A. D., and J. P. Skorupa. 1987. Responses of rain-forest primates to habitat disturbance - a review. International Journal of Primatology **8**:157-191.

Julliot, C. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical forest. American Journal of Primatology **40**:261-282.

Julliot, C., and D. Sabatier. 1993. Diet of the red howler monkeys (*Alouatta seniculus*) in French Guiana. International Journal of Primatology **14**:527-550.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. Journal of Tropical Ecology **5**:173-185.

Kar Gupta, K. 2007. Socioecology and conservation of the slender loris (*Loris tardigradus*) in southern India. Ph.D. dissertation. Arizona State University, Tempe, Arizona, USA.

Kattan, G. H., and C. Murcia. 2003. A review and synthesis of conceptual frameworks for the study of forest fragmentation. Pages 183-200 *in* G. A. Bradshaw and P. A. Marquet, editors. How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas. Springer-Verlag, Berlin, Germany.

Kessler, P. 1995. Preliminary field study of the red-handed tamarin, *Saguinus midas*, in French Guiana. Neotropical Primates **3**:184.

Kinzey, W. G. 1992. Dietary and dental adaptations in the Pitheciinae. American Journal of Physical Anthropology **88**:499-514.

Kinzey, W. G., and M. A. Norconk. 1990. Hardness as a basis of fruit choice in two sympatric primates. American Journal of Physical Anthropology **81**:5-15.

Kinzey, W. G., and M. A. Norconk. 1993. Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. International Journal of Primatology **14**:207-227.

Kirby, K. R., W. F. Laurance, A. K. Albernaz, G. Schroth, P. M. Fearnside, S. Bergen, E. M. Venticinque, and C. da Costa. 2006. The future of deforestation in the Brazilian Amazon. Futures **38**:432-453.

Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based proesses on forest fragmentation effects. Global Ecology and Biogeography **15**:8-20.

Kurosawa, R., and R. A. Askins. 2003. Effects of habitat fragmentation on birds in deciduous forests in Japan. Conservation Biology **17**:695-707.

Lara, A. C. P., and J. P. Jorgenson. 1998. Notes on the distribution and conservation status of spider and howler monkeys in the State of Quintana Roo, Mexico. Primate Conservation **18**:25-29.

Laurance, W. F. 1991a. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conservation Biology **5**:79-89.

Laurance, W. F. 1991b. Edge effects in tropical forest fragments - Application of a model for the design of nature reserves. Biological Conservation **57**:205-219.

Laurance, W. F. 2001. The hyper-diverse flora of the Central Amazon. Pages 47-53 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons From Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Laurance, W. F. 2002. Hyperdynamism in fragmented habitats. Journal of Vegetation Science **13**:595-602.

Laurance, W. F., M. A. Cochrane, S. Bergen, P. M. Fearnside, P. Delamônica, C. Barber, S. D'Angelo, and T. Fernandes. 2001a. The future of the Brazilian Amazon. Science **291**:438-439.

Laurance, W. F., P. Delamonica, S. G. Laurance, H. L. Vasconcelos, and T. E. Lovejoy. 2000a. Conservation - Rainforest fragmentation kills big trees. Nature **404**:836-836.

Laurance, W. F., L. V. Ferreira, J. M. Rankin-De Merona, and S. G. Laurance. 1998. Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology **79**:2032-2040.

Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. R. D. Merona, C. Gascon, and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments. Science **278**:1117-1118.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conservation Biology **16**:605-618.

Laurance, W. F., and R. Luizão. 2007. Driving a wedge into the Amazon. Nature **448**:409-410.

Laurance, W. F., J. M. R. D. Merona, A. Andrade, S. G. Laurance, S. D'Angelo, T. E. Lovejoy, and H. L. Vasconcelos. 2003. Rain-forest fragmentation and the phenology of Amazonian tree communities. Journal of Tropical Ecology **19**:343-347.

Laurance, W. F., R. Mesquita, R. Luizão, and F. Pinto. 2004. The Biological Dynamics of Forest Fragments Project: 25 years of research in the Brazilian Amazon. Tropinet **15**:1-3.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. Andrade, J. E. L. Ribeiro, J. P. Giraldo, T. E. Lovejoy, R. Condit, J. Chave, K. E. Harms, and S. D'Angelo. 2006a. Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences of the United States of America **103**:19010-19014.

Laurance, W. F., H. E. M. Nascimento, S. G. Laurance, A. C. Andrade, P. M. Fearnside, J. E. L. Ribeiro, and R. L. Capretz. 2006b. Rain forest fragmentation and the proliferation of successional trees. Ecology **87**:469-482.

Laurance, W. F., D. Pérez-Salicrup, P. Delamônica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001b. Rain forest fragmentation and the structure of Amazonian liana communities. Ecology **82**:105-116.

Laurance, W. F., H. L. Vasconcelos, and T. E. Lovejoy. 2000b. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. Oryx **34**:39-45.

Lee, J., and D. W. S. Wong. 2001. Statistical Analysis with ArcView GIS. John Wiley and Sons, New York, New York, USA.

Lehman, S. M., W. Prince, and M. Mayor. 2001. Variations in group size in white-faced sakis (*Pithecia pithecia*): Evidence for monogamy or seasonal congregations? Neotropical Primates **9**:96-101.

Lehman, S. M., R. W. Sussman, J. Phillips-Conroy, and W. Prince. 2006. Ecological biogeography of primates in Guyana. Pages 105-130 *in* S. M. Lehman and J. G. Fleagle, editors. Primate Biogeography. Springer, New York, New York, USA.

Leite, M. 2007. O gringo, a floresta e a escória. Folha do Meio Ambiente (Online). folhadomeio.com.br/publix/fma/folha/2007/08/gringo180.html.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237-240.

Lewinsohn, T. M., and P. I. Prado. 2005. How many species are there in Brazil? Conservation Biology **19**:619-624.

Li, B., C. Chen, W. Ji, and B. Ren. 2000. Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. Folia Primatologica **71**:375-386.

Linnell, J. D. C., R. Andersen, T. Kvam, H. Andrén, O. Liberg, P. Odden, and P. F. Moa. 2001. Home range size and choice of management strategy for lynx in Scandinavia. Environmental Management **27**:869-879.

Lopes, M. 2007. Pesquisadores contra assentamento da Suframa. Folha do Meio Ambiente (Online). folhadomeio.com.br/publix/fma/folha/2007/08/gringo180.html.

Lopes, M. A., and S. F. Ferrari. 2000. Effects of human colonization on the abundance and diversity of mammals in eastern Brazilian Amazonia. Conservation Biology **14**:1658-1665.

Lovejoy, T. E. 2006. Protected areas: a prism for a changing world. Trends in Ecology & Evolution **21**:329-333.

Lovejoy, T. E., R. O. Bierregaard, A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, K. S. Brown, A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 *in* M. E. Soule, editor. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, Massachusetts, USA.

Lovejoy, T. E., and D. C. Oren. 1981. The minimum critical size of ecosystems. Pages 7-12 *in* R. L. Burgess and D. M. Sharp, editors. Forest Island Dynamics in Man-dominated Landscapes. Springer-Verlag, New York, New York, USA.

Lu, D., P. Mausel, E. Brondizio, and E. Moran. 2002. Assessment of atmospheric correction methods for Landsat TM data applicable to Amazon basin LBA research. International Journal of Remote Sensing **23**:2651-2671.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17**:373-387.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Mace, G. M., and P. H. Harvey. 1983. Energetic constraints on home-range size. The American Naturalist **121**:120-132.

Malcolm, J. R. 1991. The small mammals of Amazonian forest fragments: Pattern and process. . Ph.D. dissertation. University of Florida, Gainesville, Florida, USA.

Malcolm, J. R. 1995. Forest structure and the abundance and diversity of Neotropical small mammals. Pages 624 *in* M. D. Lowman and N. M. Nadkarni, editors. Forest Canopies. Academic Press, San Diego, California, USA.

Malcolm, J. R. 1997. Biomass and diversity of small mammals in Amazonian forest fragments. Pages 207-221 *in* W. F. Laurance and R. O. Bierregaard Jr, editors. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, Illinois, USA.

Mandujano, S., L. A. Escobedo-Morales, R. Palacios-Silva, V. Arroyo-Rodríguez, and E. M. Rodriguez-Toledo. 2005. A metapopulation approach to conserving the howler monkey in a highly fragmented landscape in Los Tuxtlas, Mexico. Pages 513-538 *in* A. Estrada, P. A. Garber, M. S. M. Pavelka, and L. Luecke, editors. New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation. Springer, New York, New York, USA.

Marsh, L. K., C. A. Chapman, M. A. Norconk, S. F. Ferrari, K. A. Gilbert, J. C. Bicca-Marques, and J. Wallis. 2003. Fragmentation: specter of the future or the spirit of conservation? Pages 381-398 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer Academic, New York, New York, USA.

Martin, L. B., A. J. Olenjniczak, and M. C. Maas. 2003. Enamel thickness and microstructure in pitheciin primates, with comments on dietary adaptations of the middle Miocene hominoid *Kenyapithecus*. Journal of Human Evolution **45**:351-367.

McGarigal, K., and S. A. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications **12**:335-345.

McIntyre, S., and R. Hobbs. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conservation Biology **13**:1282-1292.

Milton, K., and M. L. May. 1976. Body weight, diet and home range area in primates. Nature **259**:459-462.

Mittermeier, R. A., and M. G. M. van Roosmalen. 1981. Preliminary observations on habitat utilization and diet in eight Surinam monkeys. Folia Primatologica **36**:1-39.

Mondet, B., P. F. C. Vasconcelos, A. P. A. Travassos da Rosa, E. S. Travassos da Rosa, S. G. Rodrigues, J. F. S. Travassos da Rosa, and D. J. Bicout. 2002. Isolation of yellow fever virus from nulliparous *Haemagogus* (*Haemagogus*) *janthinomys* in Eastern Amazonia. Vector Borne and Zoonotic Diseases **2**:47-50.

Mongabay.com. 2007. Scientists demand Brazil suspend Amazon colonization project. Mongabay.com. news.mongabay.com/2007/0827-atbc.html.

Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends in Ecology and Evolution **10**:58-62.

Napier, J. R., and P. H. Napier. 1967. A Handbook of Living Primates: Morphology, Ecology and Behaviour of Nonhuman Primates. Academic Press, New York, New York, USA.

Nascimento, H. E. M., A. C. S. Andrade, J. L. C. Camargo, W. F. Laurance, S. G. Laurance, and J. E. L. Ribeiro. 2006. Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. Conservation Biology **20**:853-860.

Nepstad, D., G. Carvalho, A. C. Barros, A. Alencar, J. P. Capobianco, J. Bishop, P. Moutinho, P. Lefebvre, J. Silva, U. L., and E. Prins. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecology and Management **154**:395-407.

Nepstad, D., S. Schwartzman, B. Bamberger, M. Santilli, D. Ray, P. Schlesinger, P. Lefebvre, A. Alencar, E. Prinz, G. Fiske, and R. Alicia. 2006. Inhibition of Amazon deforestation and fire by parks and indigenous lands. Conservation Biology **20**:65-73.

Neves, A. M. S. 1985. Alguns aspectos da ecologia de *Alouatta seniculus* em reserva isolada na Amazônia Central. B.S. Monograph. Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil.

Neves, A. M. S., and A. B. Rylands. 1991. Diet of a group of howling monkeys, *Alouatta seniculus*, in an isolated forest patch in central Amazonia. Pages 263-274 *in* A. B. Rylands and A. T. Bernades, editors. A Primatologia no Brasil, Volume 3. Sociedade Brasileira de Primatologia, Belo Horizonte, Minas Gerais, Brazil.

Nilsen, E. B., S. Pederson, and J. D. C. Linnell. 2007. Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecological Research **Online first**.

Norconk, M. A. 1996. Seasonal variation in the diets of white-faced and bearded sakis (*Pithecia pithecia* and *Chiropotes satanas*) in Guri Lake, Venezuela. Pages 403-423 *in* M. A. Norconk, A. L. Rosenberger, and P. A. Garber, editors. Adaptive Radiations of Neotropical Primates. Plenum Press, New York, New York, USA.

Norconk, M. A. 2006. Long-term study of group dynamics and female reproduction in Venezuelan *Pithecia pithecia*. International Journal of Primatology **27**:653-674.

Norconk, M. A. 2007. Sakis, uakaris, and titi monkeys: behavioral diversity in a radiation of primate seed predators. Pages 123-138 *in* C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder, editors. Primates in Perspective. Oxford University Press, New York, New York, USA.

Norconk, M. A., B. W. Grafton, and N. L. Conklin-Brittain. 1998. Seed dispersal by neotropical seed predators. American Journal of Primatology **45**:103-126.

Norconk, M. A., and W. G. Kinzey. 1994. Challenge of neotropical frugivory: travel patterns of spider monkeys and bearded sakis. American Journal of Primatology **34**:171-133.

Norconk, M. A., M. A. Raghanti, S. K. Martin, B. W. Grafton, L. T. Gregory, and B. P. E. De Dijn. 2003. Primates of Brownsberg Natuurpark, Suriname, with particular attention to the pitheciins. Neotropical Primates **11**:94-100.

Nupp, T. E., and R. K. Swihart. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy **81**:512-526.

Odum, E. P., and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk **72**:128-137.

Oliveira, A. C. M., and S. F. Ferrari. 2000. Seed dispersal by black-handed tamarins, *Saguinus midas niger* (Callitrichinae, Primates): implications for the regeneration of degraded forest habitats in eastern Amazonia. Journal of Tropical Ecology **16**:709-716.

Oliveira, J. M. S., M. C. Lima, C. Bonvincino, J. M. Ayres, and J. G. Fleagle. 1985. Preliminary notes on the ecology and behavior of the Guianan saki (*Pithecia pithecia*, Linnaeus 1766; Cebidae, Primate). Acta Amazônica **15**:249-263.

Onderdonk, D. A., and C. A. Chapman. 2000. Coping with forest fragmentation: the primates of Kibale National Park, Uganda. International Journal of Primatology **21**:587-611.

Palacios, E., and A. Rodriguez. 2001. Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest. American Journal of Primatology **55**:233-251.

Peetz, A. 2001. Ecology and social organization of the bearded saki *Chiropotes satanas chiropotes* (Primates: Pithecinae) in Venezuela. Ecotropical Monographs **1**:1-170.

Peres, C. A. 1990. Effects of hunting on western Amazonian primate communities. Biological Conservation **54**:47-59.

Peres, C. A. 1993. Structure and spatial organization of an Amazonian terra firme forest primate community. Journal of Tropical Ecology **9**:259-276.

Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conservation Biology **15**:1490-1505.

Peres, C. A. 2005. Why we need megareserves in Amazonia. Conservation Biology **19**:728-733.

Peres, C. A., and I. R. Lake. 2003. Extent of nontimber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon Basin. Conservation Biology **17**:521-535.

Pimley, E. R., S. K. Bearder, and A. F. Dixson. 2005. Home range analysis of *Perodicticus potto edwardsi* and *Sciurocheirus cameronensis*. International Journal of Primatology **26**:191-205.

Pope, T. R. 1996. Socioecology, population fragmentation, and patterns of genetic loss in endangered primates. Pages 119-159 *in* J. Avise and J. Hamrick, editors. Conservation Genetics: Case Histories from Nature. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Port-Carvalho, M., and S. F. Ferrari. 2004. Occurrence and diet of the black bearded saki (*Chiropotes satanas satanas*) in the fragmented landscape of western Maranhao, Brazil. Neotropical Primates **12**:17-21.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 *in* L. Boitani and T. K. Fuller, editors. Research Techniques in Animal Ecology: Controversies and Consequences. Columbia University Press, New York, New York, USA.

Ramos-Fernández, G., and B. Ayala-Orozco. 2003. Population size and habitat use of spider monkeys in Punta Laguna, Mexico. Pages 191-209 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer/Plenum Press, New York, New York, USA.

Rodgers, A. R., and A. P. Carr. 2002. HRE: The home range extension for ArcView. Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources, Ontario, Canada.

Row, J. R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia **4**:797-802.

Rylands, A. B., and A. Keuroghlian. 1988. Primate populations in continuous forest and forest fragments in central Amazonia. Acta Amazônica **18**:291-307.

Sallis, E. S., V. L. de Barros, S. L. Garmatz, R. A. Fighera, and D. L. Graça. 2003. A case of yellow fever in a brown howler (*Alouatta fusca*) in southern Brazil. Journal of Veterinary Diagnostic Investigation **15**:574-576.

Santamaría, M., and A. B. Rylands. 2003. Ecología básica de un grupo de *Alouatta seniculus* durante una estación seca en la Amazonía central brasilera. Pages 96-111 *in* V. Pereira-Benoga, F. N. Montoya, and A. Savage, editors. Primatología del Nuevo Mundo: Biología, Medicína, Manejo y Conservación. Centro de Primatologia Araguiatos Ltda, Bogotá, Colombia.

Santos, R. R. 2002. Ecologia de cuxiús (*Chiropotes satanas*) na Amazônia Oriental: perspectivas para a conservação de populaces fragmentadas. M.Sc. Universidade Federal do Pará, Belém, Pará, Brazil.

Schwartzman, S., and B. Zimmerman. 2005. Conservation alliances with indigenous peoples of the Amazon. Conservation Biology **19**:721-727.

Schwarzkopf, L., and A. B. Rylands. 1989. Primate species richness in relation to habitat structure in Amazonian rainforest fragments. Biological Conservation **48**:1-12.

Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77**:2075-2085.

Sekulic, R. 1982. Daily and seasonal patterns of roaring and spacing in four red howler *Alouatta seniculus* troops. Folia Primatologica **39**:22-48.

Setz, E. F. Z. 1993. Ecologia alimentar de um grupo de parauacus (*Pithecia pithecia chrysocephala*) em um fragmento florestal na Amazônia Central. Ph.D. dissertation. Universidade Estadual de Campinas, São Paulo, São Paulo, Brazil.

Setz, E. F. Z. 1994. Feeding ecology of golden-faced sakis. Neotropical Primates **2**:13-14.

Setz, E. Z. F., J. Enzweiler, V. N. Solferini, M. P. Amêndola, and R. S. Berton. 1999. Geophagy in the golden-faced saki monkey (*Pithecia pithecia chrysocephala*) in the Central Amazon. Journal of Zoology **247**:91-103.

Shannon, C. E. 1948. A mathematical theory of communication. Bell System Technical Journal **27**:379-423, 623-656.

Sierra, R. 2000. Dynamics and patterns of deforestation in the western Amazon: the Nape deforestation front, 1986-1996. Applied Geography **20**:1-16.

Silva-López, G., J. Motta-Gill, and A. I. Sánchez-Hernández. 1988. Distribution and status of the primates of Guatemala. Primate Conservation **18**:30-41.

Silva, J., J. S., and W. M. B. Figueiredo. 2002. Revisão sistemática dos cuxiús, gênero *Chiropotes* Lesson, 1840 (Primates, Pithecidae). Pages 21 *in* Livro de Resumos: Xth Congresso Brasileira de Primatologia: Amazônia - A Última Fronteira. Sociedade Brasileira de Primatologia, Belém, Pará, Brazil.

Silva, S. S. B. 2003. Comportamento alimentar do cuxiú-preto (*Chiropotes satanas*) na área de influência do resrvatório da usina hidreléctric de Tucuruí-Pará. Masters Thesis. Museu Paraenses Emílio Goeldi and Universidade Federal do Pará, Belém, Pará, Brazil.

Silver, S. C., and L. K. Marsh. 2003. Dietary flexibility, behavioral plasticity, and survival in fragments: lessons from translocated howlers. Pages 251-265 *in* L. K. Marsh, editor. Primates in Fragments: Ecology and Conservation. Kluwer Academic, New York, New York, USA.

Simberloff, D., and L. G. Abele. 1976. Island biogeograhy theory and conservation practice. Science **191**:285-286.

Simmen, B. 1992. Competitive utilization of Bagassa fruits by sympatric howler and spider monkeys. Folia Primatologica **58**:155-161.

Simmen, B., and D. Sabatier. 1996. Diets of some French Guianan primates: food composition and food choices. International Journal of Primatology **17**:661-693.

Sizer, N. 1992. The impact of edge formation on regeneration and litterfall in a tropical rain forest fragment in Amazonia. Ph.D. Dissertation. Cambridge University, Cambridge, UK.

Skole, D., and C. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon - satellite data from 1978 to 1988. Science **260**:1905-1910.

Skorupa, J. P. 1986. Responses of rainforest primates to selective logging in Kibale Forest, Uganda: a summary report. Pages 57-70 *in* K. Benirschke, editor. Primates: The Road to Self-Sustaining Populations. Springer-Verlag, New York, New York, USA.

Spironello, W. R. 2001. The brown capuchin monkey (*Cebus apella*): ecology and home range requirements in Central Amazonia. Pages 271-283 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA.

Stouffer, P. C., and S. H. Borges. 2001. Conservation recommendations for understory birds in Amazonian forest fragments and second-growth areas. Pages 248-261 *in* R. O. Bierregaard Jr., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. Lessons from Amazonia: The Ecology and Conservation of a Fragmented Forest. Yale University Press, New Haven, Connecticut, USA

Strier, K. B. 2003. Primate Behavioral Ecology. Allyn and Bacon, Boston, Massachusetts, USA.

Sussman, R. W. 1999. Primate Ecology and Social Structure, Volume 2: New World Monkeys. Pearson Custom Publishing, Needham Heights, Massachusetts, USA.

Sussman, R. W. 2007. A brief history of primate field studies. Pages 6-10 *in* C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, and S. K. Bearder, editors. Primates in Perspective. Oxford University Press, New York, New York, USA.

Swart, J., and M. J. Lawes. 1996. The effect of habitat patch connectivity on samango monkey (*Cercopithecus mitis*) metapopulation persistence. Ecological Modelling **93**:57-74.

Symington, M. M. 1988. Black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. American Journal of Primatology **1**:45-67.

Tabarelli, M., and C. Gascon. 2005. Lessons from fragmentation research: improving management and policy guidelines for biodiversity conservation. Conservation Biology **19**:734-739.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330-344 *in* M. E. Soulé, editor. The Science of Scarcity and Diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. Science **294**:1923-1926.

Terborgh, J., and C. van Schaik. 2002. Why the world needs parks. Pages 3-14 *in* J. Terborgh, C. van Schaik, L. Davenport, and M. Rao, editors. Making Parks Work. Island Press, Washington, D.C., USA.

Trolle, M. 2003. Mammal survey in the Rio Jauaperí region, Rio Negro Basin, the Amazon, Brazil. Mammalia **67**:75-83.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecological Applications **12**:354-363.

Tufto, J., R. Andersen, and J. Linnell. 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology **65**:715-724.

Tutin, C. E. G. 1999. Fragmented living: behavioural ecology of primates in a forest fragment in the Lopé Reserve, Gabon. Primates **40**:249-265.

van Roosmalen, M. G. M. 1985. Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. Acta Amazônica **15**:1-238.

van Roosmalen, M. G. M., R. A. Mittermeier, and J. G. Fleagle. 1988. Diet of the northern bearded saki (*Chiropotes satanas chiropotes*): A neotropical seed predator. American Journal of Primatology **14**:11-35.

van Roosmalen, M. G. M., R. A. Mittermeier, and K. Milton. 1981. The bearded sakis, genus Chiropotes. Pages 419-442 *in* A. F. Coimbra-Filho and R. A. Mittermeier, editors. Ecology and Behavior of Neotropical Primates. Academia Brasileira de Ciências, Rio de Janeiro, Rio de Janeiro, Brazil.

Veiga, L. M. 2006. A ecologia e o comportamento do cuxiú-preto (*Chiropotes satanas*) na paisagem fragmentada da Amazônia Oriental. Ph.D. Dissertation. Universidade Federal do Pará, Belém, Pará, Brazil.

Veiga, L. M., and S. F. Ferrari. 2006. Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in eastern Brazilian Amazonia. American Journal of Primatology **68**:209-215.

Vié, J.-C., C. Richard-Hansen, and C. Fournier-Chambrillon. 2001. Abundance, use of space, and activity patterns of white-faced sakis (*Pithecia pithecia*) in French Guiana. American Journal of Primatology **55**:203-221.

Viega, L. M. 2006. A ecologia e o comportamento do cuxiú-preto (*Chiropotes satanas*) na paisagem fragmentada da Amazônia Oriental. Ph.D. Dissertation. Universidade Federal do Pará, Belem.

Vieira, T. 2005. Aspectos da ecologia do cuxiú de Uta Hick, *Chiropotes utahickae* (Hershkovitz, 1985), com ênfase na exploração alimentar de espécies arbóreas da ilha de Germoplasma, Tucuruí-PA. M.Sc. Thesis. Museu Paraense Emílio Goéldi e Universidade Federal do Pará, Belém, Pará, Brazil.

Wiktander, U., O. Olsson, and S. G. Nilsson. 2001. Seasonal variation in home-range size, and habitat area requirement of the lesser spotted woodpecker (*Dendrocopos minor*) in southern Sweden. Biological Conservation **100**:387-395.

Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist **125**:879-887.

Worton, B. J. 1987. A review of models of home range for animal movement. Ecological Modelling **38**:277-298.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology **70**:164-168.

WRI. 1990. World Resources 1990-1991. Oxford University Press, Oxford, UK.

Zamora, A. G., and S. Mandujano. 2003. Uso de fragmentos por *Ateles geoffroyi* en el sureste de México. Neotropical Primates **11**:172-175.

Zar, J. H. 1999. Biostatistical Analysis: Fourth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zhang, S.-Y. 1995. Activity and ranging patterns in relation to fruit utilization by brown capuchins (*Cebus apella*) in French Guiana. International Journal of Primatology **16**:489-507.

Zimmerman, B., C. A. Peres, J. R. Malcolm, and T. Turner. 2001. Conservation and development alliances with the Kayapó of south-eastern Amazonia, a tropical forest indigenous people. Environmental Conservation **28**:10-22.

APPENDIX A

PLANT SPECIES CONSUMED BY THE NORTHERN BEARDED SAKI MONKEY

Bearded sakis consumed seeds (S), fruits (F), flowers (W), and leaves (L) from 933 trees, lianas, and hemiepiphytes during behavioral scans in 2005-2006. Overall, there were 47 families, 115 genera, and 244 species consumed. Nineteen plant specimens were not successfully identified. Unique species, defined as species that were consumed by only one of the six bearded saki groups, are indicated by *. Unique dietary species that were both present and producing fruit in at least one other study site, but were not eaten by bearded saki monkeys in at least one of the study sites, are indicated by †. If the fruit or seeds of the plant species were eaten, the condition of the fruit was indicated as ripe (R) or unripe (U).

Taxon		Item	Fruit	%
Anacardiaceae	*Anacardium parvifolium**	F	R	0.11
	*Anacardium spruceanum**	F	R	0.11
Anisophylleaceae	*Anisophyllea manausensis**†	S	U	0.11
Annonaceae	*Anaxogorea phaeocarpa**	S	R	0.11
	*Bocageopsis multiflora**†	S	U	0.11
	Dugetia chrysea	S	R,U	0.76
	*Dugetia pycnastera**	S	R	0.11
	Dugetia stelechantha	F,S	R	0.54
	*Guatteria discolor**	S	R	0.11
	Unonopsis duckei	S,W	U	0.33
	*Xylopia benthamii**	S	U	0.11
	Xylopia calophylla	F,S	R,U	1.09
	*Xylopia cf. nitida**	F,S	U	0.11
	Xylopia polyantha	S	R,U	1.09
Apocynaceae	*Couma guianensis**	F,S	R	0.11
	*Geissospermum argenteum**	S	R,U	0.22
	Mandevilla sp.*	S	R	0.11
	Odontadenia puncticulosa	F,S	R,U	0.98
	Odontadenia sp.	S	R,U	0.87
Araceae	*Heteropsis flexuosa**	S	U	0.11
	*Philodendron goeldii**	S	U	0.11
Arecaceae	*Mauritia flexuosa**	F	R	0.11
Bignoniaceae	*Arrabideaea nigrescens**	S	U	0.11
	*Arrabideaea triplinervia**	S	U	0.11
	Arrabideaea sp.	S	U	0.22
	*Lundia densiflora**	W		0.11
	*Mansoa alliacea**	F,W	R	0.22
	Mansoa sp.	W		0.11
	*Memora longilinea**	S,W	U	0.11
	*Tynnanthus panurensis**	S	U	0.11
Bombacaceae	*Castostemma albuquerquei**	F,S	R	0.22
	*Castostemma milanezii**	S	U	0.11
	*Scleronema micranthum**†	S,W	R	0.22
Burseraceae	*Protium altsonii*	S	U	0.76
	Protium apiculatum	S	U	0.33
	*Protium decandrum**	S	U	0.11
	Protium hebetatum	S	R,U	1.20
	*Protium nitidifolium**†	S	U	0.22
	*Protium tenuifolium**	S	R	0.11
	Protium sp.	S	R	0.33
Caryocaraceae	*Caryocar glabrum*	S	R	0.22
	*Caryocar pallidum**	F	R	0.11
	*Caryocar villosum**	F	R	0.22

Taxon		Item	Fruit	%
Cecropiaceae	*Pourouma bicolor*	F,S	R,U	0.98
	*Pourouma cecropiifolia**	F	R	0.11
	*Pourouma cucura**	S	U	0.11
	*Pourouma guianensis**	F	R	0.22
	*Pourouma ovata**	S	U	0.22
	Pourouma tomentosa	F,S	R,U	1.30
	*Pourouma villosa**	F	R	0.76
	Pourouma velutina	S	U	0.11
	Pourouma sp.	S	U	0.33
Celastraceae	*Goupia glabra**	S	R,U	0.22
Chrysobalanaceae	*Couepia longipendula*	S	R,U	0.98
	*Couepia obovata**	S	R	0.11
	Couepia sp.	S	U	0.11
	*Hirtella bicornis**	S	U	0.11
	*Hirtella rodriguiseii**	S	R	0.11
	*Licania apetala**	S	U	0.11
	Licania bracteata	S	R,U	0.22
	*Licania canescens**	S	R	0.11
	Licania heteromorpha	F,S	R,U	2.50
	Licania impressa	S	R,U	0.43
	*Licania lata**	S	R,U	0.33
	Licania longistyla	S	U	0.22
	Licania micrantha	S	R,U	0.76
	*Licania niloi**	S	U	0.11
Chrysobalanaceae	*Licania oblongifolia**	S	R	0.11
	*Licania sandwithii**	S	U	0.11
	Licania sothersae	S	R,U	0.22
	*Licania unguiculata**	W		0.11
	Licania sp.	S	R,U	0.54
Clusiaceae	*Clusia grandiflora*	F,S	R	0.33
	*Clusia insignis**	S	U	0.22
	*Clusia panapanari**	F,S	R	0.22
	*Clusiella axillaris**	L		0.11
	Monronobea coccinea	S	R	0.22
	*Oedematopus cf. octandrus**	W		0.11
	*Tomovita cf. martiana**	S	U	0.11
	Vismia sp.*†	S	U	0.11
Combretaceae	*Buchenavia congesta**†	F	R	0.11
Convolvulaceae	*Dicranostyles integra*	S	R	0.22
Convolvulaceae	*Dicranostyles scandens**	S	R	0.11
Cucurbitaceae	*Gurania huebneri**	S	U	0.11

Taxon		Item	Fruit	%
Dilleniaceae	*Davilla kunthii**	S	R	0.11
	*Pinzona coriacea**[†]	S	R	0.11
	Tetracera amazonica	S	U	0.22
	*Tetracera willdenowiana**	S	R	0.11
Duckeodendraceae	*Duckeodendron cestroides**	F	U	0.11
Ebenaceae	*Diospyros cavalcantei**	S	U	0.11
	*Diospyros pseudoxylopia**	S	U	0.11
Elaeocarpaceae	*Sloanea brachytepala**	S	R,U	0.11
	*Sloanea floribunda**	S	R	0.11
	Sloanea sp.	S	U	0.11
Euphorbiaceae	*Croton lanjouwensis**[†]	S	R,U	0.22
	Hevea guianensis	S,W	R,U	1.85
	*Mabea caudata**	S	U	0.11
	Mabea sp.*	S	U	0.11
	Micrandropsis scleroxylon	S	R,U	5.11
Flacourtiaceae	*Laetia procera**	S	R	0.33
	Laetia sp.	S	R	0.11
Hippocrateaceae	*Cheiloclinium cognatum**	S	U	0.43
	*Cheiloclinium diffusiflorum**	S	R	0.11
	Cheiloclinium hippocrateoides	F,S	R,U	1.41
	Cheiloclinium sp.	S	R,U	0.98
	Peritassa sp.*	S	R	0.11
	*Salacia impressifolia**	S	U	0.22
	Salacia insignis	S	R,U	0.76
	*Tontelea fluminensis**	S	U	0.11
	Tontelea sp.	S	U	0.11
Humiriaceae	*Endopleura uchi*	F,W	R	0.43
	Sacoglottis mattogrossensis	F,S	R,U	0.43
	Vantanea macrocarpa	S	R,U	0.22
Icacinaceae	*Dendrobangia boliviana**	S	U	0.11
Lauraceae	*Ocotea ceanothifolia**[†]	S	U	0.11
Lecythidaceae	*Corythophora alta**[†]	S	R	0.22
	Corythophora rimosa	S	R	0.54
	Couratari stellata	S,W	R,U	0.43
	Eschweilera atropetiolata	S,W	U	0.33
	Eschweilera coriacea	S,W	U	0.76
	Eschweilera cyathiformis	S,W	R,U	1.41
	Eschweilera grandiflora	S,W	U	0.76
	Eschweilera micrantha	S	U	0.22
	Eschweilera pseudodecolorans	S,W	U	0.54
	Eschweilera romeu-cardosoi	S	R,U	0.33
	Eschweilera truncata	S	R,U	4.46
	Eschweilera wachenheimii	S,W	R,U	2.39
	*Lecythis gracieana**	S	U	0.11

Taxon		Item	Fruit	%
Lecythidaceae	*Lecythis parvifructa**	S,W	U	0.22
	*Lecythis poiteaui**	W		0.11
	*Lecythis prancei**	S	R,U	0.43
Leguminosae	*Abarema cochleata*	S	R,U	0.54
	*Bauhinia alata**	S	U	0.11
	*Derris amazonica**	S	R	0.54
	*Dipteryx magnifica**	S	U	0.11
	Eperua glabrifolia	S	R,U	0.43
	*Hymenaea parvifolia**	S	R	0.11
	*Inga alba**	S	U	0.11
	*Inga bicoloriflora**	S	U	0.33
	Inga huberi	S	R,U	0.33
	*Inga panurensis**	S	R	0.11
	*Inga paraensis**	S	U	0.22
	*Inga rubiginosa**	S	R	0.11
	*Inga splendens**	S	R	0.33
	Inga sp.	S	U	0.43
	*Machaerium aff. negrensis**	S	R	0.11
	*Machaerium ferox**	S	U	0.11
	*Machaerium multifoliolatum**	S	R	0.11
	*Machaerium quinata**	S	U	0.11
	Machaerium sp.	S	U	0.22
	*Macrolobium limbatum**†	S	U	0.22
	*Mimosa guilandinae**	S	U	0.11
	*Piptadenia minutiflora**	S	U	0.22
	*Pterocarpus officinalis**	S	U	0.11
	Stryphnodendron sp.*	S	U	0.11
	*Swartzia cuspidata**	S	U	0.11
	*Swartzia recurva**	S	U	0.11
Loganiaceae	*Strychnos aff. asperula**	S	R	0.22
	Strychnos cogens	S	R	0.33
	Strychnos sp.	S	U	0.11
Malpighiaceae	*Brysonima chrysophylla**	F	R	0.22
	Brysonima stipulacea	F,S	R,U	0.54
Marcgraviaceae	*Norantea guianensis**	S	R	0.22
Melastomataceae	*Bellucia dichotoma**†	F,S	R	0.65
	Miconia burchelli	F,S	R,U	1.30
Memecylaceae	*Mouriri collocarpa**	F	R	0.22
Menispermaceae	*Abuta imene**	F	R	0.11
	*Abuta rufescens**	F,S	R	0.11
	*Abuta sandwithiana**	S	R	0.11
	Abuta sp.	F,S	R,U	0.76
	*Anomospermum solimoesanum**	S	U	0.11
	*Telitoxicum minutiflorum**	S	R,U	0.11

Taxon		Item	Fruit	%
Menispermaceae	*Telitoxicum rodriguesii**	F,S	R	0.11
Moraceae	*Brosimum acutifolium*	F,S	R,U	0.22
	Brosimum parinarioides	F,S,W	R,U	0.76
	*Brosimum potabile**	S	U	0.11
	Brosimum rubescens	S	U	1.09
	Clarisia racemosa	F,S	R,U	0.43
	*Ficus mathewsii**	F,S	R	0.11
	Ficus sp.*	F,S	U	0.11
	Helicostylis scabra	F,S	R,U	0.54
	Helicostylis tomentosa	F,S	R,U	0.22
	*Helicostylis turbinata**	S	U	0.11
	*Naucleopsis caloneura**†	S	U	0.22
	Pseudolmedia laevis	S	U	0.33
Myristicaceae	*Iryanthera juruensis**	S	U	0.11
	*Iryanthera laevis**	S	U	0.11
	Osteophloeum platyspermum	S	R,U	1.09
Myrtaceae	*Myrcia* sp.*	F,S	R	0.11
Olacaceae	*Chaunochiton kappleri**	S	U	0.11
	*Dulacia guianensis**	S	U	0.11
	Minquartia guianensis	F,S	R,U	0.33
Passifloraceae	*Passiflora edulis**	S	U	0.11
Polygalaceae	*Moutabea aff.* sp.3*	S	U	0.22
	Moutabea guianensis	S	U	1.09
	Moutabea sp.	S	U	0.65
	*Securidaca cf. volubilis**	W		0.11
Quiinaceae	*Touroulia guianensis**	S	U	0.11
Rubiaceae	*Malanea* sp.*	F	R	0.11
Sapotaceae	*Chrysophyllum aff. argentium**	S	U	0.11
	Chrysophyllum amazonicum	S	U	0.33
	Chrysophyllum manaosense	S	R,U	0.54
	Chrysophyllum pomiferum	S,L	U	0.22
	Chrysophyllum prieurii	S	R,U	0.33
	Chrysophyllum sanguinolentum	S	R,U	0.87
	*Chrysophyllum sparsiflorum**	S	U	0.11
	Chrysophyllum wilsonii	S	R,U	0.33
	Ecclinusa guianensis	S	R,U	2.83
	*Ecclinusa lanceolata**	S	U	0.11
	Manilkara bidentata	F,S	R,U	1.63
	Manilkara calvalcantei	F,S	R,U	0.33
	Manilkara huberi	S	U	0.76
	*Micropholis cylindropcarpa**	S	U	0.11
	Micropholis guyanensis	S,W	R,U	1.20
	*Micropholis mensalis**	S	U	0.11
	*Micropholis splendens**	S	U	0.11

Taxon		Item	Fruit	%
Sapotaceae	*Pouteria aff. ambelaniifolia**	S	R,U	0.22
	*Pouteria aff. gardneri**	F,S	R	0.11
	Pouteria anomala	S	R,U	1.09
	*Pouteria campanulata**	F,S	R	0.11
	Pouteria cladantha	S	U	0.33
	*Pouteria cuspidata**	F,S	R	0.11
	Pouteria erythrochrysa	F,S	R	0.33
	*Pouteria eugeniifolia**	S	U	0.22
	Pouteria filipes	S	R,U	0.43
	*Pouteria fimbriata**	S	U	0.11
	*Pouteria flavilatex**	S	U	0.11
	Pouteria freitasii	F,S	R,U	0.43
	*Pouteria fulva**	S	U	0.11
	Pouteria guianensis	F,S	R,U	1.96
	Pouteria hispida	S	U	0.33
	*Pouteria laevigata**	S	U	0.11
	*Pouteria maxima**	S	R	0.11
	Pouteria minima	S	U	0.22
	Pouteria pallens	S	R,U	0.43
	*Pouteria peruviensis**	S	U	0.22
	Pouteria reticulata	F,S	R,U	0.98
	Pouteria sp.10*	S	U	0.11
	*Pouteria stipulifera**	S	R,U	0.33
	*Pouteria torta**	S	U	0.11
	*Pouteria venosa**	W		0.11
	Pouteria vernicosa	F,S	R,U	0.43
	*Pouteria virescens**	S	R	0.11
	*Pradosia cochlearia**	S	U	0.11
	*Pradosia decipiens**	S	U	0.11
	Sarcaulus brasiliensis	S	U	0.43
Simaroubaceae	*Simaba polyphylla**	S	U	0.22
	*Simarouba amara**	S	U	0.11
Violaceae	*Amphirrhox* sp.*[†]	S	U	0.11
Vochysiaceae	*Erisma bicolor**	S	R	0.11
	*Erisma bracteosum**	S	R	0.11
	*Qualea labouriauna**	S	U	0.11
	*Ruizterania albiflora**	F,S	R	0.11

APPENDIX B

ACCURACY OF HOME RANGE ANALYSIS WITH SMALL SAMPLE SIZES

Abstract. Accurate estimates of an individual's home range are important in order to understand an individual's use of space in its habitat. This paper examines the accuracy of two common methods, minimum convex polygon (MCP) and kernel density estimators (KDE). Field data were collected in July-August 2003 and January 2005-April 2006 on northern bearded saki monkeys (*Chiropotes sagulatus*) living in forest fragments and continuous forest areas in the Brazilian Amazon. The geographic location of the monkey group was recorded every five minutes during the field study using a handheld GPS unit. All locations were plotted in ArcView 3.3, and home range and day range were calculated using MCP and KDE in Home Range Extension (Rodgers and Carr 2002). KDE estimated areas larger than MCP in 94% (*n*=64) of the calculations. When the sample size was small (less than 79 data points), the average difference between MCP and KDE estimates was 121% of the area estimated by MCP. When sample size was larger (more than 191 data points), the average difference between the two methods was less than 6%. When estimates of the daily area used by monkeys in two small (13.67 ha and 13.96 ha) forest fragments were compared to the fragments' actual size, KDE calculated an area that was larger than the forest fragment 11% of the time. KDE also overestimated area in all 50 simulations of 120 random points within a forest fragment of known size. Therefore, MCP was more accurate in calculating home and day range than KDE.

INTRODUCTION

An individual’s home range is the area that it uses for its regular activities (Burt 1943). There are many means by which one may calculate home range size (Worton 1987, Powell 2000, Rodgers and Carr 2002). Often such methods provide different home range estimates, and it is debated which method is best (Seaman and Powell 1996, Powell 2000, Hemson *et al.* 2005, Pimley *et al.* 2005, Börger *et al.* 2006a, Row and Blouin-Demers 2006, Ciofi *et al.* 2007).

Here I investigate the accuracy of estimates for two common methods for determining home range size: minimum convex polygon (MCP) and kernel density estimators (KDE). MCP calculates home range size by drawing a convex polygon around the location points of the individuals (Hayne 1949). Although MCP has limitations (Worton 1987, Powell 2000, Börger *et al.* 2006a, Nilsen *et al.* 2007), it is still one of the most widely used methods for calculating home range today (Powell 2000, Row and Blouin-Demers 2006). KDE uses nonparametric statistics to calculate the probability of finding an individual in a particular location (Worton 1989). Although KDE has been touted as being more accurate than MCP (Powell 2000, Pimley *et al.* 2005, Börger *et al.* 2006a), not everyone agrees that it is the best method for determining home range size (Hemson *et al.* 2005, Row and Blouin-Demers 2006).

METHODS

This study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP) reserves, located approximately 80 km north of Manaus, Brazil.

The BDFFP is the longest-running study on forest fragmentation. Forest fragments range in size from 1ha to 100 ha, and Chapter 1 provides an overview of the BDFFP history and research.

Geographic data were collected on the location of bearded saki monkeys (*Chiropotes sagulatus*) in July-August 2003 and January 2005-March 2006 in nine forest fragments—four 1-ha (#1104, #2107, #2108, and #3114), three 10-ha (#1202, #2206, and #3209), and two 100-ha fragments (#2303 and #3304)—and two areas of continuous forest (Km41 and Cabo Frio). Each forest fragment and continuous forest area were surveyed for bearded saki monkeys during a data collection cycle. It took approximately 2.5 months to complete each cycle. I conducted one census cycle in July-August 2003, four cycles in 2005, and one cycle in 2006. The durations of the cycles were as follows: July-August 2003 (Cycle 2003), January-March 2005 (Cycle 1), April-June 2005 (Cycle 2), August-October 2005 (Cycle 3), October-December 2005 (Cycle 4), January-March 2006 (Cycle 5). Additional data were collected in April 2006 for a sixth cycle of the 10-ha fragment #1202 because this fragment's study group was the best documented, and provided opportunity for additional seasonal analyses for another area of the overall research.

On the first day in each of the forest fragments and continuous forest locations, a primate census was conducted along the established trails. Chapters 2, 3, and 4 provide additional details regarding the censuses. If bearded saki monkeys were present in the study area, they were followed for three consecutive days, from dawn until dusk. The geographic location of the study animals was noted every five minutes using a handheld Garmin V GPS receiver.

I mapped the travel routes of each of the six groups in ArcView 3.3, and determined their daily distance traveled, daily area of space used, and home range size for each of the monkey groups using the Home Range Extension (Rodgers and Carr 2002) in ArcView 3.3. I determined daily area used and home range size using both MCP and KDE. Comparisons were made between MCP and KDE.

Next I compared the MCP and KDE estimates for two bearded saki groups that occupied two of the study's forest fragments. One group inhabited a 13.67 ha forest fragment (#1202) and the other group inhabited a 13.96 ha forest fragment (#2206). Estimates of the daily area used by the groups were compared against the actual size of the two forest fragments. Because the animals never left these two forest fragments during the study, the size of the fragment provided an upper limit of the size of the area used by the monkeys.

Although the day ranges of the bearded saki monkeys provided a means by which to compare MCP and KDE methods, it was likely that overestimates were not being detected. Bearded saki monkeys used, on average, less than 5 ha during a day in fragments #1202 and #2206. Furthermore, the monkeys that lived in fragment #2206 only used 86% of the forest fragment during the entire study period. Therefore, the frequency that MCP and KDE overestimated the size of the area occupied by the bearded saki monkeys was likely greater than detected, since the estimates were compared against the actual size of the fragments.

In order to address this problem, I randomly selected 120 points (of the 1944 possible points) within forest fragment #1202 using the random selection function in the ArcView extension Animal Movement (Hooge and Eichenlaub 1997), and calculated the area using both MCP and KDE methods with Home Range Extension (Rodgers and Carr 2002). I selected 120 points because this sample size accounted for 10 hours of data during one day. I repeated the process 50 times, with a different selection of random points each time. Estimates were then compared against the actual forest size.

RESULTS

Estimates for home range and day range differed between MCP and KDE (Table 17). Overall, the average difference between the two methods was 78% (range 1.5%-427.9%). The KDE estimate was larger than the MCP estimate in 94% of the cases (n=69). When the data were split in groups according to sample size, the average difference in area between MCP and KDE estimates (±standard error) was greatest (120.99% ±14.64) when less than 79 points were used, and smallest (5.57% ±1.69) when more than 191 points were used. Overall KDE provided the largest estimate of home range size in 100% (*n*=25) of the cases when there were less than 79 points, but when there were more than 191 points, this was the case only 57% (*n*=7) of the time.

In the estimates of daily area used by the monkeys in the two forest fragments of 13.67 ha and 13.96 ha, KDE calculated areas that were larger than the actual size of the forest fragment in 11.11% (*n*=4) of the cases. MCP never calculated an area that was greater than the forest fragment's actual size (Table 18). Overall overestimation by KDE averaged 2.67 (± 0.75) ha, which ranged from 1.98% to 40.01% of the forest fragment's actual size.

When 120 random points were selected 50 times within fragment #1202, KDE estimated an area that was larger than the actual size of the forest fragment 100% of the time. The estimates were on average 1.95 (±0.12) ha larger than the forest fragment. MCP never estimated an area that was greater than the actual size of the forest fragment. Comparisons between MCP and KDE showed the average difference between estimates to be 4.66 (±0.10) ha, and KDE had a larger estimate in 100% of the simulations.

DISCUSSION

Methods for estimating home range size are not equal. I found that when sample size was large (192 data points or more), estimates using MCP and KDE were relatively similar, with an average difference between the two methods being less than 6% of the calculated MCP size. As sample size decreased, the difference between MCP and KDE estimates increased.

When comparisons were made between estimates of daily area used by the bearded saki monkeys and the possible upper limit of these estimates, defined as the actual size of the forest fragment, KDE overestimated daily area used in

22% of the cases. The estimate was, on average, 20% larger than the actual area of the fragment. At times this estimate was 40% larger than the actual size of the forest available to the monkeys.

When 50 sets of 120 points were randomly selected from the pool of 1944 points associated with fragment #1202, KDE provided area estimates that were greater than the actual size of the forest fragment in 100% of the simulations. MCP never overestimated the area. The average differences between the two methods represented 35% of the fragment’s total area.

Although KDE is a popular method in estimating home range, Row and Blouin-Demers (2006) also found that KDE was not as accurate as MCP in estimating the home range size of herpetofauna. They suggested the use of MCP for estimating home range size, and the use of KDE for analyzing the particular spatial use of the home range, with the smoothing factor adjusted so that the 95% kernel estimation equals the MCP home range calculation.

Other primate studies, however, found that KDE was more accurate, as MCP overestimated the area used (Pimley et al. 2005, Kar Gupta 2007). In both studies, home range size was calculated on small, nocturnal primates with small home ranges, and the species concentrated their time in parts of their range. In contrast, bearded saki monkeys are diurnal, medium-bodied primates with large home ranges. Therefore, the accuracy of MCP and KDE may depend on the behavioral ecology of the study species. Although home range estimates of the bearded saki monkeys in continuous forest were similar with MCP and KDE, day range estimates in continuous forest were consistently higher with KDE. Therefore, it appears that sample size is a concern for estimating day range of animals that have an average daily range of 33 ha (see Chapter 4).

When bearded saki monkeys were restricted to small forest fragments, KDE again provided larger estimates. One possible explanation for the discrepancy in estimates between MCP and KDE in forest fragments is that each of the monkey groups ranged over most of its fragment, including the fragment’s edges; however, these groups did not travel out of the fragment. KDE often produced contour lines that exceeded the fragment’s borders, thereby overestimating the area used. Therefore, MCP may be appropriate for fragmentation studies, as well research of territorial species, as activity along the perimeter of the territory may lead to higher KDE estimates.

The findings from this study emphasize the importance of choosing the appropriate method for calculating the size of an area used by individuals. Attention should be paid to sample size, as well as the study species’ behavioral ecology.

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TABLE 17. Comparisons of home range and day range estimates.

	Difference in area	Larger estimate
Average	77.61%	KDE (94%, n=69)
Range	1.5 - 427.9%	
192≤ x≥1944 points	5.57% (±1.69)	KDE (57%, n=7)
80≤x≥134 points	61.93% (±3.86)	KDE (97%, n=37)
38≤x≥78 points	120.99% (±14.64)	KDE (100%, n=25)

Notes: Home range and day range estimates by minimum convex polygon (MCP) and kernel density estimators (KDE) methods varied. Average difference in area (±standard error) is based on the MCP estimated area, since it was consistently smaller than the KDE estimate.

TABLE 18. Overestimations of range.

	Fragment #1202	Fragment #2206
Actual size	13.67 ha	13.96 ha
MCP overestimation frequency	0.00	0.00
KDE overestimation frequency	0.20	0.25
Range	0.27-5.47 ha	1.15-4.12 ha
Mean	2.95 (±1.24) ha	1.98 (±0.72) ha

Notes: Comparisons between day range and the actual area available to the bearded saki monkeys (defined as the size of the forest fragment) found that kernel density estimators (KDE) provided an estimate of area that was greater than the actual size of the forest fragment. Minimum convex polygon (MCP) did not. Standard error is provided.

APPENDIX C

PUBLICATIONS

Portions of Chapter 3 and Chapter 5 have been previously published (or are currently in press). All coauthors have provided consent to reproduce published works within this dissertation.

Chapter 3:

Boyle, S. A., A. T. Smith, W. R. Spironello, and C. E. Zartman. In press. The Behavioural Ecology of Northern Bearded Sakis (*Chiropotes sagulatus*) Living in Forest Fragments of Central Brazilian Amazonia *in* A. Barnett, L. M. Viega, S. F. Ferrari, and M. A. Norconk, editors. Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, Cambridge, UK.

Chapter 5:

Boyle, S. A. 2008. Human impacts on primate conservation in central Amazonia. Tropical Conservation Science **1**:6-17.