Introduction

Habitat fragmentation is an increasing global trend that impacts the sustainability of ecosystems worldwide (Lovejoy 2006). In the case of forest fragmentation, areas of contiguous forest are cleared, and a mosaic of patches surrounded by non-forested matrix remains. Forest fragmentation can affect local climate (Bierregaard Jr et al. 1992; Achard et al. 2002), habitat suitability (Gascon et al. 2000; Laurance et al. 2000), species richness (Bierregaard Jr et al. 1992; Malcolm 1997), seed dispersal (Chapman & Onderdonk 1998; Estrada et al. 1999), and predator–prey interactions (Asquith et al. 1997).

Primates vary in their diet composition and specializations for obtaining resources, and large-bodied primates that eat fruit usually require large home ranges (Clutton-Brock & Harvey 1977; Johns & Skorupa 1987; Onderdonk & Chapman 2000). Yet, studies relating degree of frugivory and species presence within forest fragments have yielded different results. Currently there is no consensus regarding the use of primate characteristics to predict the vulnerability of a species in fragmented habitat (Johns & Skorupa 1987; Estrada & Coates-Estrada 1996; Onderdonk & Chapman 2000; Marsh et al. 2003; Boyle & Smith 2010a). Therefore, further data are necessary to determine whether a general pattern exists between diet specialization and survival in fragmented habitats.

We focused our research on the northern bearded saki (Chiropotes satanas chiropotes). Bearded sakis (Chiropotes spp.) are specialized seed predators that derive approximately 90% of their diet from fruit (Ayres 1981; Peetz 2001). Although some studies have examined the genus Chiropotes in human-altered habitats (Ferrari et al. 1999; Peetz 2001; Port-Carvalho & Ferrari 2004; Veiga & Ferrari 2006), much of this research has focused on forested islands that were formed by the construction of and subsequent flooding by hydroelectric dams (Peetz 2001; Santos 2002; Veiga & Ferrari 2006).

Bearded sakis (Chiropotes spp.) typically live in large social groups that separate and rejoin throughout the day, have large home ranges, and travel long daily distances (Norconk 2011). Previous studies of bearded sakis have found that the species’ home range varies from 200 to 250 ha (Ayres 1981; van Roosmalen et al. 1981) in continuous forest. Research in Pará, Brazil (Silva 2003; Veiga 2006) and Venezuela (Peetz 2001) revealed that bearded sakis on human-created islands (see above) occupy areas of 16–250 ha. Thus, bearded saki home range size appears to be flexible.

The characteristic home-range size of bearded sakis in continuous forest is larger than any of the forest fragments in our study area. Therefore, our goals were to determine the minimal fragment size needed to sustain northern bearded saki populations, and also to determine how groups inhabiting fragmented forests differed behaviorally and ecologically from groups in undisturbed habitats. Here we present a review of our findings.

Methods

Study site

We conducted this research in the Biological Dynamics of Forest Fragments Project (BDFFP) reserve, located approximately 80 km north of Manaus, in the Brazilian state of Amazonas. BDFFP is facilitated by the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Smithsonian Tropical Research Institute (STRI). The project, initially called the Minimal Critical Size of Ecosystems project, began in 1979. Studies prior to and after fragmentation have provided a catalogue of changes in species distribution and loss (Lovejoy et al. 1984; Rylands & Keuroghlian 1988; Ferraz et al. 2003), forest composition and structure (Ferreira & Laurance 1997; Laurance et al. 1997; Nascimento et al. 2006) and microclimate (Kapos 1989; Murcia 1995).

The study site is tropical moist terra firme forest that receives 1900–3500 mm of rain annually with a dry season from June to October (Gascon & Bierregaard 2001; Laurance 2001). There are three fragment size classes (1 ha, 10 ha and 100 ha), as well as continuous primary forest that serves as a control for comparison (Gascon & Lovejoy 1998; Figure 24.1). The degree of isolation (i.e. distance to nearest forest patch, condition of the surrounding matrix) varies among the BDFFP fragments (Bierregaard & Stouffer 1997; Boyle & Smith...
and in 2006 there was more secondary growth forest in the matrix than in previous years (Boyle & Smith 2010a). In addition, there have been changes to the forest surrounding the study area, due to increased human pressures (Laurance & Luizão 2007; Boyle 2008a).

Although research at BDFFP has been ongoing for more than three decades, research involving bearded sakis had been minimal, consisting of sporadic annual censuses in the forest fragments (Gilbert 2003), and behavioral research in the continuous forest (Frazão 1992). Our research is the first behavioral ecology study of bearded sakis that takes into account each of the nine fragments in addition to areas of continuous forest.

The presence of bearded sakis in the BDFFP fragments has been variable since the reserves were first isolated. Upon isolation, bearded sakis left the isolated reserve areas (Rylands & Keuroghlian 1988). Additional censuses found bearded sakis to be absent from the fragments until the mid 1990s when an adult male spent five months in one of the 10-ha fragments (#2206). In 1995, an adult male, adult female and infant were spotted in another 10-ha fragment (#1202) during a two-week period (Gilbert 1994; Gilbert & Setz 2001). An adult male bearded saki was present in one of the 10-ha BDFFP fragments (#1202) in 1997, and was joined by an adult female bearded saki by 2001. The third 10-ha fragment (#3206) has had no history of bearded saki inhabitants. The presence of bearded sakis in the two 100-ha BDFFP forest fragments (#2303 and #3303) was not noted until a census in 2000 (Gilbert 2003). Prior to 2003, bearded sakis had not been spotted in any of the four 1-ha BDFFP fragments.

Five other primate species (Alouatta macconnelli, Ateles paniscus, Cebus apella, Pithecia pithecia and Saguinus midas) reside in the BDFFP study area. Some species (e.g. Alouatta) frequently occupy forest fragments in all three size classes (1 ha, 10 ha and 100 ha), while other species (e.g. Ateles) are rarely present (Gilbert 2003; Boyle & Smith 2010a).

**Sampling methods**

We collected data during a preliminary study in July–August 2003, and then from January 2005 to June 2006. We surveyed nine forest fragments at the Dimona, Esteio and Porto Alegre ranches – four 1-ha, three 10-ha, and two 100-ha fragments – and two areas of continuous forest.

On the first day in each study area we conducted a primate census by walking line transects along already established trails, following the past methods used at BDFFP (Rylands & Keuroghlian 1988; Gilbert 2003). If bearded sakis were encountered during the primate census (Boyle & Smith 2010a), they were designated the focal group for that fragment’s data cycle, and subsequently relocated and followed for 3 consecutive days. One cycle through the nine fragments and two areas of continuous forest lasted approximately 56 days for a total of four cycles annually.

Upon locating a group of bearded sakis, we tracked the same group from the time they awoke in the morning until the time they settled down for the night (approximately 0530–1730), for a total of 604 behavioral contact hours. Due to the presence of researchers in the study area for nearly 30 years, the bearded sakis were habituated to human observers. Using group scan sampling techniques (Altmann 1974), we recorded the group’s GPS coordinates using a handheld GPS receiver every 5 min, as well as group size and composition, and the activity of each individual in sight. Activities included eating, foraging, resting, moving, traveling, social interactions and “other.” If individuals were eating fruit, flowers or leaves, we
marked the tree or liana with plastic flagging and assigned it a unique number. We returned later to each feeding location for floral identification. We noted the tree’s GPS coordinates, diameter at breast height (DBH), and the type of food (fruit, flower, leaf).

Later, we relocated the flagged trees, epiphytes and lianas using maps produced from the GPS data, and we collected plant material samples in order to identify food sources. Identifications were conducted both in the field and the INPA herbarium in Manaus, Brazil.

Spatial analyses
Based on the GPS data, we mapped the daily routes of the bearded saki groups and their feeding sites using ArcView 3.3. We determined daily distance traveled and home range (Boyle et al. 2009a) using the Home Range Extension (Rodgers & Carr 1998) for ArcView. We measured home-range size using both Minimum Convex Polygon (Odum & Kuenzler 1955) and Adaptive Kernel (Worton 1987) methods due to differences in home-range estimates when sample size was small (Boyle et al. 2009b).

Summary of findings
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 two of these groups were permanent residents during the study period (Table 24.1; Boyle & Smith 2010b). There were no bearded sakis in any of the four 1-ha fragments, with the exception of the presence of one subadult male in the 1-ha fragment (#2107) in July–August 2003. We do not know if this individual left the forest fragment or died.

Two of the 10-ha fragments (#1202 and #2206) had one bearded saki group each. These two groups were consistently present in the fragments in July–August 2003 and January 2005–June 2006. We never witnessed either group leaving the forest fragment. We never spotted bearded sakis in the 10-ha fragment (#3209) at Porto Alegre.

Table 24.1 Northern bearded saki presence in nine forest fragments (2003–2006).

<table>
<thead>
<tr>
<th>Size</th>
<th>Present</th>
<th>Status</th>
<th>Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 ha</td>
<td>Dimona</td>
<td>(#2107)</td>
<td>Dimona</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2003 only</td>
<td>(#2108)</td>
</tr>
<tr>
<td></td>
<td>Esteio</td>
<td>(#1104)</td>
<td>Porto Alegre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(#3114)</td>
</tr>
<tr>
<td>10 ha</td>
<td>Dimona</td>
<td>(#2206)</td>
<td>Permanent</td>
</tr>
<tr>
<td></td>
<td>Esteio</td>
<td>(#1202)</td>
<td>Permanent</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Porto Alegre</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(#3209)</td>
</tr>
<tr>
<td>100 ha</td>
<td>Dimona</td>
<td>(#2303)</td>
<td>Nomadic</td>
</tr>
<tr>
<td></td>
<td>Porto Alegre</td>
<td>(#3304)</td>
<td>Nomadic</td>
</tr>
</tbody>
</table>

Each 100-ha fragment hosted one bearded saki group; however, these groups did not remain in their respective forest fragments (Boyle & Smith 2010b). These fragments were not fully isolated as forest “islands” (Boyle & Smith 2010a), and the bearded sakis used forested corridors to travel in and out of these fragments.

Group size
Bearded saki group size ranged from 1 to 35 individuals, and as forest patch size increased, so did group size (Boyle & Smith 2010b). Average group size (with standard error given in parentheses) was 1 individual in the 1-ha fragment, 3.79 (± 0.21) individuals in the 10-ha fragments, 12.15 (± 1.44) individuals in the 100-ha fragments and 22.89 (± 5.09) individuals in the continuous forest (Figure 24.2). Group size was constant at four individuals during the 2003 and 2005–2006 study periods for the group inhabiting a 10-ha fragment (#2206). Group size was four individuals for the group inhabiting another 10-ha fragment (#1202) until the disappearance of an adult female in October 2005. We do not know whether
the female left the fragment or died. During our study, no new individuals joined either of the bearded saki groups in the 10-ha fragments (Boyle & Smith 2010b).

Single offspring births occurred from mid October to early November 2005 in groups from the continuous forest, as well as groups that used the 100-ha fragments. Neither of the two 10-ha fragment bearded saki groups experienced births during the study period.

Diet
We tagged 993 trees, lianas and epiphytes that served as food for bearded sakis during our behavioral observations. These included 244 species in 115 genera in 14 different families (Table 24.2; Boyle 2008b; Boyle et al. 2012). We were unable to identify 19 of the 933 specimens.

The three families that were represented most often in the bearded saki diet were Sapotaceae (23%), Lecythidaceae (14%), and Chrysobalanaceae (8%). Overall, the most frequently used genera were Eschweileria (Lecythidaceae), Pouteria (Sapotaceae), and Licania (Chrysobalanaceae). The most prominent plant species were Micrandropsis scleroxylon (Euphorbiaceae), Eschweileria truncata (Lecythidaceae) and Ecclinusa guianensis (Sapotaceae). Lianas and epiphytes represented 17% of the overall bearded saki diet, and there was no difference in the proportion of lianas and epiphytes in the diet across forest sizes (Boyle 2008b; Boyle et al. 2012).

<table>
<thead>
<tr>
<th>Family</th>
<th>Total individuals</th>
<th># Genera</th>
<th># Species</th>
<th>Family</th>
<th>Total individuals</th>
<th># Genera</th>
<th># Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td>2 (0.22%)</td>
<td>1 (0.87%)</td>
<td>2 (0.82%)</td>
<td>Humiriaceae</td>
<td>10 (1.09%)</td>
<td>3 (2.61%)</td>
<td>3 (1.23%)</td>
</tr>
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<td>Anisophylloceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Icacinaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Annonaceae</td>
<td>41 (4.49%)</td>
<td>6 (5.22%)</td>
<td>11 (4.51%)</td>
<td>Lauraceae</td>
<td>3 (0.33%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>20 (2.19%)</td>
<td>4 (3.48%)</td>
<td>5 (2.05%)</td>
<td>Lecythidaceae</td>
<td>132 (14.44)</td>
<td>4 (3.48%)</td>
<td>16 (6.56%)</td>
</tr>
<tr>
<td>Araceae</td>
<td>2 (0.22%)</td>
<td>2 (1.74%)</td>
<td>2 (0.82%)</td>
<td>Leguminosae</td>
<td>55 (6.02%)</td>
<td>14 (12.17%)</td>
<td>24 (9.84%)</td>
</tr>
<tr>
<td>Arecaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Loganiaceae</td>
<td>6 (0.66%)</td>
<td>1 (0.87%)</td>
<td>3 (1.23%)</td>
</tr>
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<td>Bignoniaceae</td>
<td>13 (1.42%)</td>
<td>5 (4.35%)</td>
<td>8 (3.28%)</td>
<td>Malpighiaceae</td>
<td>7 (0.77%)</td>
<td>1 (0.87%)</td>
<td>2 (0.82%)</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td>5 (0.55%)</td>
<td>2 (1.74%)</td>
<td>3 (1.23%)</td>
<td>Maragaviaceae</td>
<td>2 (0.22%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>28 (3.06%)</td>
<td>1 (0.87%)</td>
<td>6 (2.46%)</td>
<td>Melastomataceae</td>
<td>18 (1.97%)</td>
<td>2 (1.74%)</td>
<td>2 (0.82%)</td>
</tr>
<tr>
<td>Caryocaraceae</td>
<td>5 (0.55%)</td>
<td>1 (0.87%)</td>
<td>3 (1.23%)</td>
<td>Memecylaceae</td>
<td>2 (0.22%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
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<td>Cecropiaceae</td>
<td>38 (4.16%)</td>
<td>1 (0.87%)</td>
<td>8 (3.28%)</td>
<td>Menispermaceae</td>
<td>13 (1.42%)</td>
<td>3 (2.61%)</td>
<td>6 (2.46%)</td>
</tr>
<tr>
<td>Celastraceae</td>
<td>2 (0.22%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Moraceae</td>
<td>39 (4.27%)</td>
<td>6 (5.22%)</td>
<td>12 (4.92%)</td>
</tr>
<tr>
<td>Chrysobalanaceae</td>
<td>71 (7.77%)</td>
<td>3 (2.61%)</td>
<td>18 (7.38%)</td>
<td>Myristicaceae</td>
<td>12 (1.31%)</td>
<td>2 (1.74%)</td>
<td>3 (1.23%)</td>
</tr>
<tr>
<td>Clusiaceae</td>
<td>15 (1.64%)</td>
<td>6 (5.22%)</td>
<td>8 (3.28%)</td>
<td>Myrtaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Combretaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Ocaceae</td>
<td>5 (0.55%)</td>
<td>3 (2.61%)</td>
<td>3 (1.23%)</td>
</tr>
<tr>
<td>Convulvulaceae</td>
<td>3 (0.33%)</td>
<td>1 (0.87%)</td>
<td>2 (0.82%)</td>
<td>Passifloraceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Cucurbitaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Polygalaceae</td>
<td>19 (2.08%)</td>
<td>2 (1.74%)</td>
<td>3 (1.23%)</td>
</tr>
<tr>
<td>Dilleniaceae</td>
<td>6 (0.66%)</td>
<td>3 (2.61%)</td>
<td>4 (1.64%)</td>
<td>Quinaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Duckeodendraceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Rubiaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
</tr>
<tr>
<td>Ebenaceae</td>
<td>2 (0.22%)</td>
<td>1 (0.87%)</td>
<td>2 (0.82%)</td>
<td>Sapotaceae</td>
<td>207 (22.65%)</td>
<td>7 (6.09%)</td>
<td>47 (19.26%)</td>
</tr>
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<td>Elaeocarpaceae</td>
<td>3 (0.33%)</td>
<td>1 (0.87%)</td>
<td>3 (1.23%)</td>
<td>Simaroubaceae</td>
<td>3 (0.33%)</td>
<td>2 (1.74%)</td>
<td>2 (0.82%)</td>
</tr>
<tr>
<td>Euphorbiaceae</td>
<td>68 (7.44%)</td>
<td>4 (3.48%)</td>
<td>5 (2.05%)</td>
<td>Violaceae</td>
<td>1 (0.11%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
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<tr>
<td>Flacourtiaceae</td>
<td>4 (0.44%)</td>
<td>1 (0.87%)</td>
<td>1 (0.41%)</td>
<td>Vochysiaceae</td>
<td>4 (0.44%)</td>
<td>3 (2.61%)</td>
<td>4 (1.64%)</td>
</tr>
<tr>
<td>Hippocrateaceae</td>
<td>39 (4.27%)</td>
<td>4 (3.48%)</td>
<td>8 (3.28%)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Average DBH of feeding trees was 37.9 cm (± 5.90). Of the 933 trees, epiphytes and lianas that were consumed by the bearded sakis, 94% served as a fruit resource for the monkeys, 5% as a flower resource and less than 1% as a leaf resource (Boyle 2008b).

There was little dietary species overlap across all six inhabited sites (four forest fragments and two areas of continuous forest) in 2005–2006. Bearded sakis consumed only four species: *Eccinas guianensis*, *Eschweilera truncata*, *Hevea guianensis* and *Micropholis guianensis* (1.5 percent of the pooled flora) in all six study areas.

**Travel patterns**

Home-range size varied from 12 ha in a 10-ha fragment (actual fragment size was 13 ha) to 559 ha in the continuous forest (Boyle et al. 2009a). Bearded saki monkeys travelled greater daily distances in the continuous forest and 100-ha fragments than in the smaller fragments (Figure 24.3; Boyle et al. 2009a). Average daily distance was 2.99 km (± 0.02) in the continuous forest, 2.83 km (± 0.22) in the 100-ha fragments, 1.72 km (± 0.09) in the 10-ha fragments and 0.41 km in the 1-ha fragment. Bearded sakis living in the smaller fragments travelled in more circular patterns, and they revisited feeding trees more often throughout a day than did monkeys living in the larger forested areas (Boyle et al. 2009a). Furthermore, the monkeys did not concentrate their efforts in low-lying, riparian areas, yet they did travel through these areas to reach other areas of the forest.

**Discussion**

Northern bearded sakis show extreme flexibility in their behavioral ecology, as individuals in fragmented areas were found to have smaller group sizes, shorter daily distances traveled and smaller home ranges than individuals in continuous forest. Additionally, northern bearded sakis were found to exhibit variability in their diets across fragments. However, it is unclear whether this behavioral flexibility is sufficient for the long-term viability of this species in fragmented habitats.

We found northern bearded saki groups permanently inhabiting forest fragments as small as 2–3% the size of their home range in continuous forest. It may seem counterintuitive that “permanent” groups existed in two of the 10-ha fragments, while the groups in the 100-ha fragments left and re-entered the fragments frequently. We would have expected that the monkeys would have moved in and out of the smaller fragments more often than the larger fragments; however, one possible explanation for these results is that neither 100-ha fragment was completely isolated, but both 10-ha fragments were isolated. Northern bearded sakis in the 100-ha fragments nevertheless comprised smaller groups and traveled shorter daily distances than individuals in the continuous forest.

Flexibility was also evident in the species eaten by the northern bearded sakis, as less than half of consumed plant species were eaten at more than one study area. These results indicate that northern bearded sakis are capable of consuming a variety of plant species. When the plant species were separated by type (fruit, flower, leaf), we found that the northern bearded sakis consistently ate fruit (primarily seeds).

Although northern bearded sakis were present in forest fragments that were fractions of their characteristic home range in continuous forest, we found substantial differences in the behavioral ecology of northern bearded sakis in forest fragments and those in continuous forest. Two 10-ha fragments in this study contained northern bearded saki groups, but it is unknown how long these groups of three and four individuals can remain in an area as small as 10 ha, especially as there was no noted travel in and out of these fragments, and the monkeys in the 10-ha fragments failed to breed through the duration of the study. Copulations were witnessed in June and August 2005 in a 100-ha fragment and continuous forest site, and infants were seen in both 100-ha groups and both continuous forest groups in November and December 2005 (the early wet season). Bearded saki monkeys (*Chiropotes* spp.) reach sexual maturity at approximately 36 months, and interbirth interval is greater than 24 months (Peetz 2001). There have been no young juveniles in the 10-ha fragments since this study began in 2003; therefore, it is possible to infer that there had not been a successful birth in either group residing in the 10-ha fragments for at least 3.5 years (November 2002–June 2006). Therefore, we suggest continued monitoring of the forest fragments to document patterns of use and movement between forest areas, as well as changes in group composition.

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