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Habitat Selection and Use of Space by Bald-Faced Sakis (*Pithecia irrorata*) in Southwestern Amazonia: Lessons from a Multiyear, Multigroup Study

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Abstract Population density and distribution in tropical forest vertebrates are directly linked to patterns of use of space relative to habitat structure and composition. To examine how forest type may explain the ranging behavior and high variance in group density observed within the geographic range of bald-faced saki monkeys (*Pithecia irrorata*), we monitored habitat use of 5 neighboring focal groups of this species in southwestern Amazonia over 3 yr. To test whether sakis are unflooded (terra firme) forest specialists, we compared home range (HR) use to the corresponding availability of 4 main forest types and quantified HR size and activity budgets as a function of forest type. HR size varied from 16 to 60 ha, and saki population density at this scale (12.5±6.4 SD individuals/km^2) was more closely related to forest type than to group size. Although sakis were not obligate habitat specialists, groups clearly avoided bamboo forest and preferred terra firme forest. Terra firme forests were associated with small HRs, intensive use, high HR overlap, and territorial defense, all of which suggest that saki densities will be higher in areas dominated by terra firme forest where large patches of bamboo (*Guadua* spp.) are absent. The increased desiccation and subsequent forest fires expected in this region from the combined impacts of climate change and human land use potentially threaten the long-term viability of old-growth terra firme forest specialists such as

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sakis. Regional-scale conservation efforts should ensure that extensive blocks of terra firme forest are protected in areas that remain relatively free of bamboo.

Keywords Amazon · Habitat selection · Home range · *Pithecia irrorata* · Saki monkey

Introduction

Patterns of movements and use of space in heterogeneous landscapes provide key insights into the resource and habitat requirements of animal populations (Hemson *et al.* 2005; Powell 2000). Specifically, the size and juxtapositioning of adjacent home ranges (HRs) with respect to habitat type, combined with the use of different habitats within a HR, help us identify habitat preferences that affect the density, ecological distribution, and ultimately the viability of a given population (Horner and Powell 1990; Powell 2000). Analysis of animals' ranging behavior relative to habitat type can be used to understand the determinants of density, and, consequently, to help explain fine-scale distribution patterns within their geographic ranges. There is general agreement among ecologists that preference is implied by greater use of a habitat type than would be expected by chance, given the availability of that habitat (Alldredge and Griswold 2006). Individuals of a species that consistently specialize on a particular habitat type should thus maintain some minimum portion of their HR areas in that habitat and use it preferentially (Buskirk and Millspaugh 2006). Similarly, smaller HRs and greater HR overlap within certain habitat types may indicate habitat preference (McLoughlin and Ferguson 2000); individuals would therefore be expected to maintain larger HRs where preferred habitat type(s) are more sparsely distributed (Carey *et al.* 1990; Wallace 2006). In addition, the propensity of individuals or group members to forage, rest, and interact agonistically with conspecifics within different habitats of their HRs can shed light on the relative value of habitat types to the species (Dietz *et al.* 1997; Porter *et al.* 2007). Conversely, the population density and patterns of use of space should be similar across habitat types for habitat generalists. Further, previous primate studies have shown a positive correlation between HR size and both group size (Grant *et al.* 1992; Milton and May 1976) and group metabolic requirements (Nunn and Barton 2000).

Saki monkeys (*Pithecia* spp.) are medium-sized, small-group-living forest primates distributed across the Amazon basin that specialize on immature fruits from a broad spectrum of plant species (Norconk and Conklin-Brittain 2004; Palminteri *et al.* in press; Peres 1993a). We would therefore expect them to occur at relatively consistent group densities across the vast tracts of unbroken forest within their geographic range. However, little is known about their use of space across different forest habitats; what little information is available suggests a preference for tall, unflooded (terra firme) forest but the trend is ambiguous. Some studies have suggested that sakis are terra firme forest specialists (de la Torre *et al.* 1995; Mittermeier and van Roosmalen 1981; Sheth *et al.* 2009), whereas others have found that they occur within multiple forest habitats (Haugaasen and Peres 2005; Oliveira *et al.* 1985; Peres 1993b), though typically at low densities (Christen and Geissmann 1994; Mittermeier and van Roosmalen 1981; Peres 1997) or at uneven rates of occupancy (Freese *et al.* 1982; Johns 1986; Palminteri *et al.* 2011). The sources of these apparent discrepancies could include differences in study methodology or spatial scale; although most of these studies relied on transect surveys, the primary technique used to estimate mammal abundance in areas with limited access. Nevertheless, none of the studies monitored *Pithecia* systematically, and the quiet nature of sakis and their evasive responses to human presence make them difficult to census accurately, pointing to the need for research that focuses specifically on their habitat selection and ranging behavior.

Here, we examine the patterns of habitat use, both overall and for individual activities, and habitat selection in bald-faced sakis (*Pithecia irrorata*) in the southeastern Peruvian Amazon. For 5 focal groups, we examine HR size and the intensity of use across 4 major forest types, with respect to their availability, within HR areas, core areas, and areas of HR overlap. Given the positive relationship between primate HR size and group size, we expect smaller groups to maintain smaller HRs than larger groups. Conversely, we expect HRs to be smaller where larger areas of preferred habitats are available (Struhsaker 1967). We therefore measured HR size and selection of forest habitats as a function of both group size and forest type. In particular, we investigate whether habitat preferences indicated specialization on terra firme forest and to what extent such preferences may explain the patchiness and variable group densities reported for this species across its range (Branch 1983; Christen and Geissmann 1994; Palminteri *et al.* 2011). We also quantified habitat selection with respect to major activity patterns, including intergroup interactions, which we expected to occur more frequently in preferred habitat types.

This is one of the few landscape-scale studies on patterns of habitat selection by a tropical forest primate based on multiple focal groups. The monitoring of several neighboring groups over a 3-yr period in a naturally heterogeneous landscape mosaic enabled intergroup comparisons of space use within a single primate population and contributed to our understanding of the value of multiple-group studies. It also helped to minimize several potential sources of bias, including variation in ecological constraints—such as intraspecific competition or predation threat—that restrict or otherwise modify an individual's access to habitat (Hobbs and Hanley 1990; Van Horne 1983) and the natural variation in habitat preference by group (Aebischer *et al.* 1993; Garshelis 2000; McClean *et al.* 1998), season, and year. Finally, our multigroup approach allowed us to measure HR overlap among 5 adjacent groups to test whether overlap is positively associated with HR size (Nunn and Barton 2000) or forest type, and thus whether overlap estimates can be used to refine primate density estimates.

Methods

Study Area

We conducted the study in the southwestern Amazon, between the Madre de Dios and Los Amigos rivers of the Madre de Dios region (MDD) in Peru. The 450-ha study area (12°34′07″S, 70°05′57″W) is located in structurally intact moist forest *ca.* 270 masl within the 145,000-ha privately managed Los Amigos Conservation Concession. Mean annual rainfall at the site between 2005 and 2007 was 2430 mm (http://atrium.andesamazon.org; BRIT 2009). We selected the study area on the basis of its habitat diversity to facilitate examination of the relative use of different forest types (Fig. 1). The study area was characterized by 2 major geomorphological formations: the contemporary floodplain of the Los Amigos and Madre de Dios rivers and a flat upland terrace (terra firme), *ca.* 70 m above the floodplain and separated from it by a steep forested embankment. The supra-annually inundated floodplain was primarily a 25–30 m tall, closed-canopy evergreen forest (190 ha), but included 2 small patches (8 and 12 ha) of monodominant stands of the palm *Mauritia flexuosa* (palm swamp).

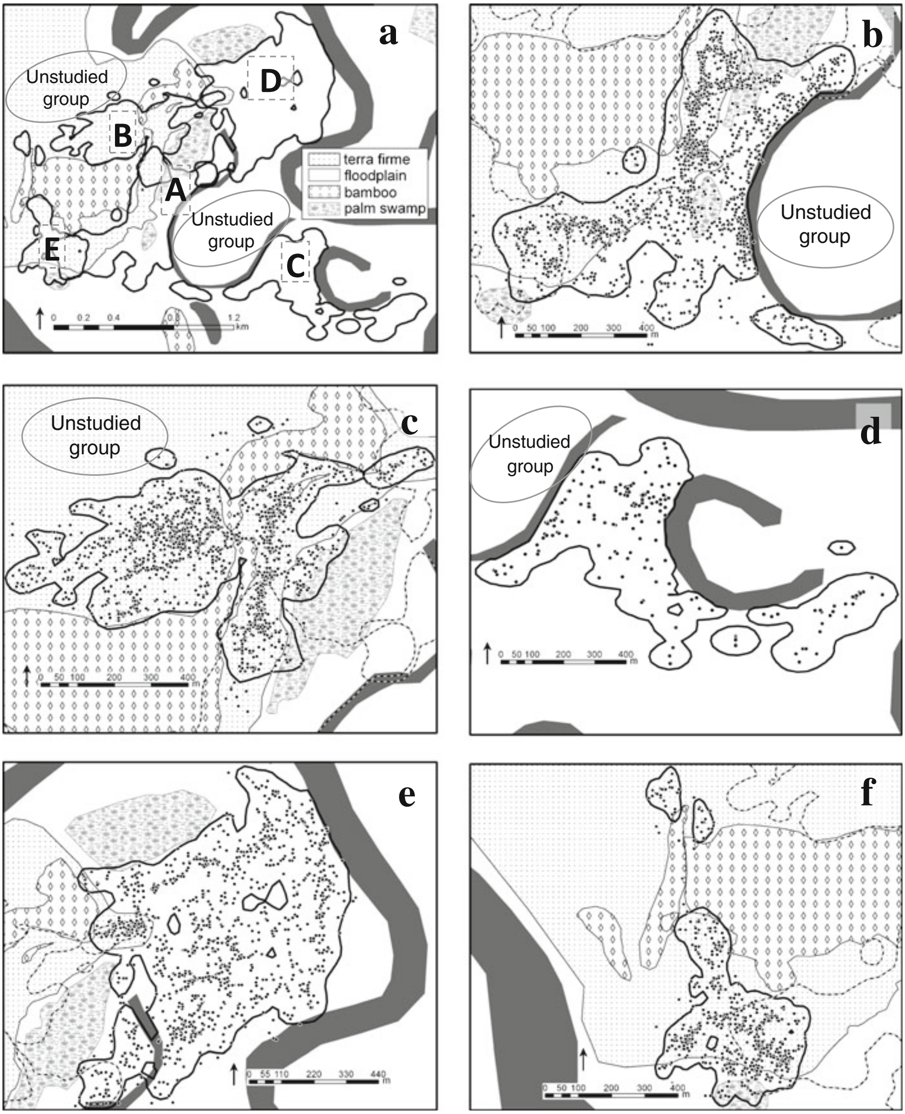

Fig. 1 HR polygons of individual bald-faced saki (*Pithecia irrorata*) groups A–E (**b–f**) at Los Amigos, southeastern Peru, expressed as 95% kernel polygons (solid lines) showing the spatial distribution of 15-min group locations and the 4 main forest types in the study area. Dashed lines represent HRs of adjacent focal groups. The HR boundaries of all 5 focal groups and neighboring unhabituated groups are also shown **a** (all groups together).

The terra firme domain was similarly covered primarily by mixed closed-canopy forest of 35–40 m in height (79 ha), but also included 2 open-canopy forest patches dominated by bamboo (*Guadua* spp.) stands (7 and 25 ha). We therefore defined 4 mutually exclusive habitat types in the study area: floodplain forest, palm swamp, terra firme forest, and bamboo forest.

Data Collection

To quantify saki movement patterns and behavior with respect to habitat type, we followed 5 previously habituated focal groups between January 2005 and December 2007. We monitored each group for 3–5 consecutive days per month, for between 6 and 28 mo (median≈22 mo) per group (Table I). A similar proportion (48±5.2 SD %) of scans for each group occurred in wet season months (October–March), and we monitored 4 groups in all calendar months and during all 3 yr of the study. Although our focal groups were habituated, we were unable to follow them continuously every sample day, obtaining *ca.* 6.2 (± 0.2 SD) contact hours per sample day. We followed focal groups continuously from either their sleeping tree or at first contact during the day until they entered their subsequent sleeping site. We systematically monitored these groups by following them with 1 or 2 observers recording a single group location, habitat type, and activity pattern (resting, moving, foraging/feeding, or social) every 15 min throughout all contact hours using instantaneous scan sampling (Altmann 1974). In total, we obtained *ca.* 3000 h of observation during the entire study.

During each 15-min scan, we recorded the group's location and predominant activity pattern because not all group members were necessarily observed during each scan. Group locations were either recorded directly using a Garmin 12XL GPS or calculated in ArcView 3.3 (ESRI, Redlands, CA) using the distance and angle from known coordinates within a network of 30 km of georeferenced trails spanning the

Table I HR estimates for 5 focal groups of bald-faced sakis (*Pithecia irrorata*) at Los Amigos, Madre de Dios, Peru

Group	No. of sample months	No. of 15-min scans	No. GPS locations[a]	Mean group size (± SD)	MCP[b] (ha)	95% kernel (ha)[c]	50% kernel (ha)	% of HR shared[d]	Density (ind./ km^2)[e]
A	27	3600	2803	4.7±0.5	75.8	42.4	9.8	25.5	11.1
B	28	3329	2756	6.5±0.8	53.1	30.6	6.5	16.3	21.2
C	6	579	380	2.1±0.3	38.5	31.1	6.4	0.0	6.8
D	22	2453	1989	4.0±0.3	84.3	59.6	16.5	4.5	6.7
E	18	1388	1191	2.6±0.5	30.2	15.6	2.9	32.8	16.7
Median	22	2453	1989	4.0	53.1	31.1	6.5	16.3	11.1
Mean	20.2	2270	1824	4.7±1.5	62.9±25.4	35.9±16.3	8.4±5.1	15.8±13.8	12.5±6.4

[a] GPS locations used to generate HR estimates.

[b] Minimum Convex Polygon, excludes water.

[c] 95% kernel HR polygons, excludes water.

[d] Percent of 95% kernel HR overlapping with other focal groups.

[e] Density estimates are based on 95% kernel HR, and exclude HR overlap.

study area. To test the accuracy of incomplete scans in representing the collective behavior of an entire group, for a subset of observations (300 scans during 70 d), a second observer recorded the activity pattern of outlying members of the group, and we converted the number of matching simultaneous observations between the 2 data sets into a percentage of matching cases. Activity and habitat data acquisition by the auxiliary observer matched simultaneous data obtained by the principal observer in 90% of cases, indicating not only that data gathered during scans restricted to only 1–2 individuals in view could be used to define the primary overall group behavior, but also that activity patterns of group members were largely synchronized.

The relatively monomorphic coloration and size among *Pithecia irrorata* made definition of age categories difficult. Therefore, we categorized group members as adults, juveniles, and dependent infants. While adult males were clearly larger than younger males, we used evidence of reproduction to identify adult parous females. We defined dependent infants as those carried by their mothers and did not include them in group counts.

Data Analysis

Patterns of Habitat Selection

Habitat Availability We defined the amount of habitat available to a given group as the area within the minimum convex polygon (MCP) enclosing all locations for that group. The 5 MCPs served as each group's area of availability for habitat selection analyses (Thomas and Taylor 2006) while also enabling comparisons with other studies. MCPs included the areas groups were known to use and would have reasonable access to, while excluding areas not physically accessible to the groups, such as territories of unstudied groups or unsuitable habitats (lakes, rivers, etc.; Aebischer *et al.* 1993; Buskirk and Millspaugh 2006). To determine the area of each habitat type accessible per group, we intersected each group's MCP with a vegetation map (ACCA 2007). The map was first refined in the GIS by correcting the habitat type along the terra firme–floodplain forest boundary according to the fine-scale habitat data we recorded at *ca*. 860 (≈ 9%) georeferenced saki locations during 2 yr of saki group follows. For analyses of habitat selection and activity patterns, we considered each forest type as a categorical variable, whereas for correlations, forest type was represented by the proportion of scans in each sample-day that the group allocated to terra firme forest.

Habitat Use To quantify habitat use, we summed the amount of time spent (number of 15-min scans) by each group in each habitat within its HR. To test whether temporal autocorrelation in habitat use data was biasing the analyses, we used a Monte Carlo routine (PopTools ver 3.1.1, Hood 2009) to resample randomly 100 times the habitat type of all 15-min locations for each of the 4 saki groups whose HRs contained multiple forest types (Aebischer *et al.* 1993; Thomas and Taylor 2006). For each group, we then compared the observed count of scan locations within each habitat type to the median counts from the resampled data set using a Pearson χ^2 test. The resampled count data in the 4 habitat types did not differ from those of the overall data set for any of the 4 groups (A: $\chi^2=0.03$, df=3, $p=0.99$; B: $\chi^2=0.01$, df=3, $p=0.99$; D: $\chi^2=0.002$, df=3, $p=0.99$; E: $\chi^2=0.01$, df=3, $p=0.99$); we therefore used the full data set for all groups (Crowley 1992; Powell 2000).

For each focal group, we calculated HR sizes from all GPS locations using 95% fixed kernel analysis (Worton 1989) and core area sizes using 50% fixed kernel analysis (Hooge *et al.* 1999). MCP and kernel ranging polygons were generated using the Home Range Extension (HRE; Rodgers and Carr 1998) for ArcView (ver. 3.3, ESRI 2002). *Ad hoc* and least-squares Cross Validation smoothing factors—2 automated statistical methods used to generate kernel analysis probability curves (Seaman and Powell 1996; Worton 1989)—oversmoothed and undersmoothed our point data, respectively, a problem observed elsewhere (Gitzen *et al.* 2006; Hemson *et al.* 2005; Rodgers and Carr 1998). We therefore multiplied the *ad hoc* smoothing factor by 0.4 (Carr and Rodgers 1998; Fieberg 2007), which generated HR polygons that adequately fitted the location data for each of the saki groups without creating discontinuous islands of use (Hemson *et al.* 2005). To calculate HR overlap between adjacent focal groups, we used pairwise intersections of the HR polygons of neighboring groups. We tested whether saki groups spent more time (defined as proportion of 15-min scans) than expected by chance in their areas of HR overlap using a χ^2 goodness-of-fit test. We calculated expected time based on the proportion of each HR within overlap areas with all neighboring groups.

We overlaid all HRs, core areas, and overlap polygons with the refined habitat map. Areas within either the MCP or the 95% kernel polygon that extended into unusable habitat, e.g., lakes, were excluded from the final HR polygon (Irwin 2008). We then examined the relationships between the proportion of terra firme forest within the HR of each group and both the proportional HR overlap area of each group and the subsequent HR-level population densities (ind./km^2) using Pearson correlations.

Given the substantial variation in group and HR sizes (Table I), we analyzed habitat selection primarily by focal group. This approach also allowed us to include potential variability in habitat preference among groups in our analyses. Similarly, by assessing habitat use by 4 of the 5 groups across all calendar months, we reduced potential seasonal bias. For each group, we used a χ^2 goodness-of-fit test to compare the proportion of 15-min scans in each of the 4 forest types to the one expected, given the proportion of the group's MCP comprising each forest type. We applied a *Z*-test with Bonferroni-corrected 95% confidence intervals of the residuals (Byers *et al.* 1984; Neu *et al.* 1974) to determine which forest types were significantly preferred or avoided. We applied this process to the observed vs. expected proportion of each group's sleeping trees in each forest type, as well as the habitat composition of each group's overlap and core areas (Garshelis 2000).

Activity Patterns

We quantified habitat preference with respect to activity pattern by assigning each 15-min scan for each group to 1 of 4 mutually exclusive activity categories—resting, feeding/foraging, moving, and socializing—and comparing the number of scans of each activity recorded in each forest type to that expected based on the total number of observations in each forest type. We looked specifically at the distribution of agonistic intergroup interactions as a function of habitat type, as we expected more boundary disputes to occur in preferred habitat types. We omitted all scans for which the activity was either unknown or ambiguous (4.3% of 11,349 scans). Based on the overall time spent in each forest type, we used a χ^2 goodness-of-fit test to examine whether sakis used certain habitats for specific activities more or less often than expected by chance.

Results

Over the 3-yr study period, the 5 saki groups averaged 4.7±1.5 SD independent individuals and contained 2–8 individuals at a given point in time, consisting of 1 adult male, 1–3 adult females, and associated juveniles (Table I). Of all 15-min scans (N=11,349), we obtained group location data used for spatial analyses for 9119 scans.

Patterns of Habitat Selection

On the basis of 95% kernel polygons, mean HR size for the 5 groups was 35.9 ha (Table I), representing between 5 and 15 ha per individual. HR size was larger, but not significantly so, for group HRs encompassing proportionally less terra firme forest (r=–0.66, p=0.23, N=5). Habitat composition of the HRs varied substantially among study groups (electronic supplementary material [ESM] Table SI; Fig. 1), resulting in a strongly positive correlation between saki densities (ind./km^2, Table I) and the proportion of terra firme forest within each HR (r=0.97, p=0.01, N=5, Fig. 2). Neither total HR size (r=0.25, p=0.68, N=5) nor the group size to HR size ratio (density, r=0.58, p=0.31, N=5) correlated significantly with group size.

We conducted habitat selection analysis for each of the 4 saki groups that used >1 forest type, as floodplain forest was the only habitat available to group C. For each of these groups, the amount of time allocated to terra firme forest was greater than expected by chance for all activities combined and for foraging and feeding (χ^2 tests, Table SI; Fig. 3a). Groups used terra firme forest 1.6 (± 0.4 SD) times more often than expected, given the relative contribution of this forest type to each group's MCP, whereas they used bamboo forest 40 (± 33 SD) times less often than expected. Group D wholly avoided bamboo forest adjacent to its HR. Whereas groups A and B used all

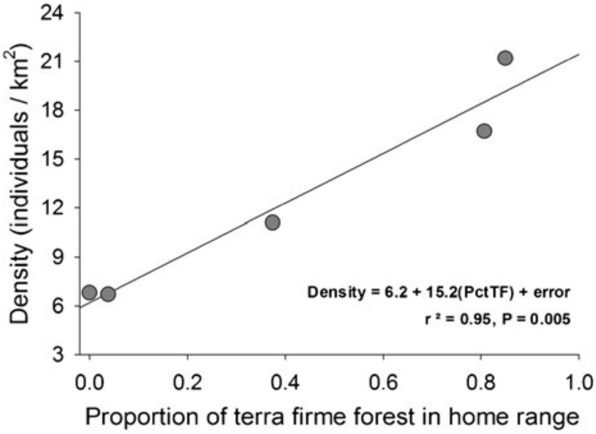

Fig. 2 Strong positive relationship between the proportion of terra firme forest in saki group HRs and the corresponding HR-scale density of individuals (per km^2), independent of HR overlap.

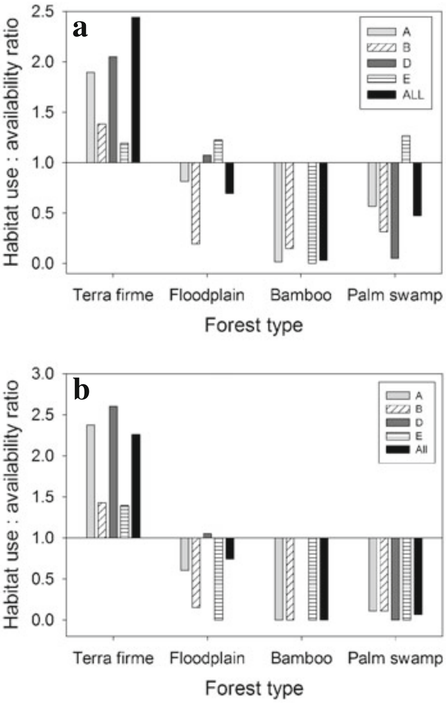

Fig. 3 Habitat selection ratios (Use: Availability; Manly *et al.* 2002) of 4 main forest types for each of 4 saki groups. Ratios >1.0 and <1.0 indicate positive selection (preference) and negative selection (avoidance), respectively. **a** Use = proportion of 15-min scans recorded in each forest type. Availability = proportion of area of group's MCP occupied by each forest type. **b** Use = proportion of sleeping sites (*N*=330) recorded in each forest type. Availability = proportion of area of group's MCP occupied by each forest type. Group C's MCP was entirely restricted to floodplain forest and is therefore not shown here. Bamboo vegetation was unavailable in the HR of group D and therefore lacks a selection value for this group. "All" denotes the overall values for all 4 groups with access to multiple habitat types.

other forest types less often than expected, given their relative availability, group E used all habitats except bamboo slightly more often than expected, given their respective proportions within its MCP.

The preference for terra firme habitat over other forest types was also pronounced for sleeping sites (A: $\chi^2=28.4$, df=2, $p<0.001$; B: $\chi^2=23.6$, df=2, $p<0.001$; D: $\chi^2=2.0$, df=1, $p=0.16$; E: $\chi^2=3.9$, df=1, $p=0.05$, Fig. 3b). Of the 330 sleeping sites recorded for all 5 focal groups during the entire study, 212 (64%) were in terra firme forest, 116 (35%) in floodplain, 2 (<1%) on the edge of a palm swamp, and sleeping sites were never recorded in bamboo habitat.

Habitat composition of the core area of each of these 4 groups also differed significantly from that of its MCP (χ^2 tests, ESM Table SI). The proportions of terra firme forest within the core areas of individual groups were 1.2–2.5 times greater than those in their respective MCPs, regardless of the overall habitat composition of the MCP.

Overlap among HRs similarly reflected the tendency of sakis to concentrate their time allocation into terra firme habitat. In fact, the HR of group C, which was entirely confined to floodplain forest, did not overlap with that of other groups. The proportion of time spent in overlap areas was greater than expected by chance for the other 4 focal groups, given the relative size of overlap areas (A: $\chi^2=69.6$, df=1, $p<0.001$; B: $\chi^2=13.9$, df=1, $p<0.001$; D: $\chi^2=48.4$, df=1, $p<0.001$; E: $\chi^2=110.7$, df=1, $p<0.001$; overall: $\chi^2=12.3$, df=3, $p=0.006$). HRs of these 4 groups overlapped between 5% and 33% (overall mean 15.8%, Table I). These percentages reflect only the overlap with other focal groups, as we were unable to quantify the additional overlap between habituated groups (particularly groups B and E) and neighboring unhabituated groups, which typically fled or hid from observers.

There was a weak positive correlation between the proportion of terra firme forest in the HRs of our 5 saki groups and their proportional overlap with neighboring study groups ($r=0.772$, $p=0.126$, $N=5$). Nevertheless, terra firme forest accounted for >75% of 3 of the 4 pairwise overlap areas (Table II). It also occupied between 37% and 85% of the combined overlap area of each group; these proportions were 1.2–7.9 times greater than expected (A: $\chi^2=1169.4$, df=3, $p<0.001$; B: $\chi^2=348.6$, df=3, $p<0.001$; D: $\chi^2=982.7$, df=2 [the HR of group D lacked bamboo forest], $p<0.001$; E: $\chi^2=251.3$, df=3, $p<0.001$). Terra firme forest comprised 82% and 85% of the overlap areas of groups B and E, respectively, and their overlap areas were used during 19% and 50% of their respective observations. Conversely, group D spent <10% of its time in its overlap zone, 37% of which was terra firme forest.

Activity Patterns

Feeding/foraging was the most frequent activity pattern, comprising 48±8% SD of scans (range 35–54%, $N=5$). The remaining time was spent resting (26±5%), moving (20±2%), or in social activities (5±1%), including grooming, playing and agonistic interactions with neighboring groups.

The use by 4 saki groups with access to multiple forest types of floodplain and terra firme forests for specific activities was similar to their overall use of those 2 habitats, except that they spent more time than expected socializing in terra firme forest (A: $\chi^2=64.5$, df=6, $p<0.001$; B: $\chi^2=32.9$, df=6, $p<0.001$; D: $\chi^2=20.3$, df=6, $p=0.002$; E: $\chi^2=7.3$, df=6, $p=0.30$; bamboo comprised <0.6% of all observations of any individual group, so it was excluded from this analysis; Fig. 4). Overall, 40% of scans classified as social behavior pertained to agonistic interactions between groups, and the percentage of agonistic interactions in terra firme forest (84%) was

Table II Pairwise overlap areas and proportion of each forest type in overlap areas between neighboring saki groups (A–E)

Pairwise overlap	Area (ha)	Terra firme	Floodplain	Bamboo	Palm swamp
A–B	4.01	0.78	0.07	0.08	0.08
A–D	1.67	0.00	1.00	0.00	0.00
A–E	5.12	0.85	0.12	0.00	0.03
B–D	1.00	1.00	0.00	0.00	0.00

Only pairs with overlapping HRs (defined as the 95% kernel polygons) are shown. All pairs could potentially overlap in terra firme and floodplain forest, except between groups A and D, the common boundary of which occurred exclusively in the floodplain.

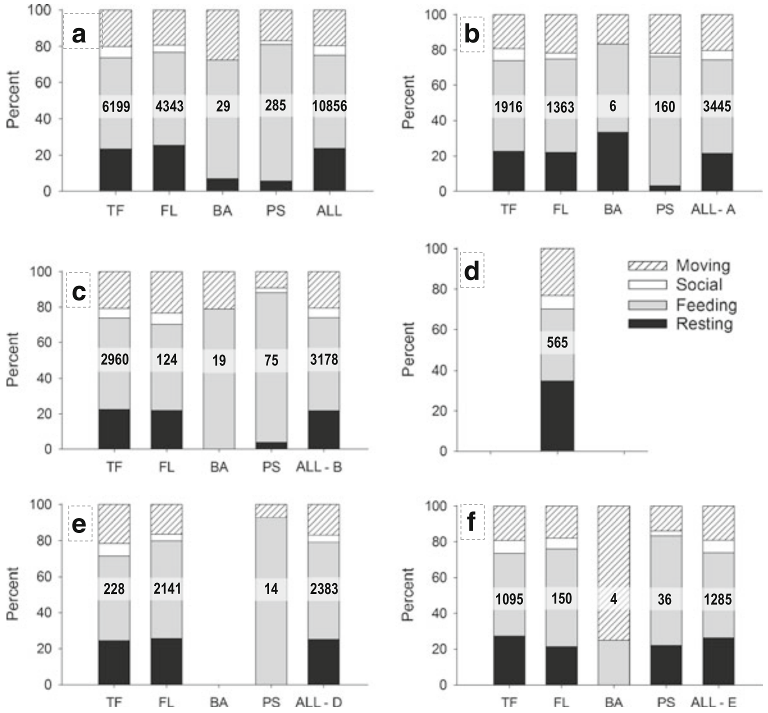

Fig. 4 Activity budget within 4 main forest types [terra firme (TF), floodplain (FL), bamboo (BA), and palm swamp (PS)] for 5 habituated groups of bald-faced sakis (**a** groups combined and groups **b**–**f** individually). Group **c**'s HR was entirely restricted to floodplain forest. Right-hand column (ALL) of each graph denotes the aggregate activity budget across all habitats. The number of scans in each forest type is listed over each column.

significantly higher than expected ($\chi^2=33.7$, df=2, $p<0.0001$). When intergroup interactions were excluded, social behavior did not occur more than expected by chance in any group or in any forest type ($p>0.05$ in all cases). No interactions occurred within bamboo-dominated forest. Sakis also spent more time feeding and less time resting in palm swamp than would be expected, given their overall use of this habitat type; for each of the 4 groups, feeding comprised 61–93%, and moving contributed another 7–22%, of time spent in palm swamp (Fig. 4).

Discussion

Patterns of Habitat Selection

Our results indicate that although *Pithecia irrorata* groups in southeastern Peru are not restricted to terra firme forest, they show a strong preference for this forest type. Although saki groups did not maintain a minimum threshold proportion of terra firme forest within their HRs and were not terra firme obligates, their HR size, overlap areas between neighboring HRs, patterns of habitat use, and spatiotemporal distribution of foraging activities and sleeping sites all indicated strong positive selection for closed-canopy terra firme forest over other forest types. Terra firme forest comprised a higher proportion than expected by chance of both occurrences and the distribution of core HR areas for all 4 groups with at least some access to this forest type. Although these trends were common across groups, the considerable variability in habitat composition we found in group HRs and the proportion of HR area shared with neighboring groups indicate that single-group studies are vulnerable to unrepresentative conclusions. Such studies also fail to assess heterogeneity within a population.

Given the variable access that the groups had to different habitat types, certain foods or other resources were presumably not available to all groups uniformly. As we were unable to monitor all groups for all 31 sample months, it is possible that some movement patterns affected by the availability of a particularly key food resource in a given month went undetected. However, we reduced this risk by monitoring 4 of the 5 groups in all calendar months, and the fact that seeds of unripe fruits, which are available for relatively long periods of time (Norconk 2007; Palminteri 2010), dominate the broad diet of sakis.

Although group size can affect HR size in large-group-living primate species (Dunbar 1988) and among species (Milton and May 1976), our results are more consistent with the negative relationship between HR size and habitat quality found for other primate genera (Dietz *et al.* 1997; DiFiore 2003; Struhsaker 1967). Our results at the group level indicate that habitat type, rather than group size, affects saki population density and ranging behavior in our study region. HRs dominated by terra firme forest tended to be smaller per individual, resulting in saki densities twice as high as those in floodplain forest. A comparison of ranging patterns with other populations of *Pithecia* south of Amazon is difficult, due to a severe paucity of studies and substantial differences in soil fertility, habitat heterogeneity, and level of group habituation (Peres 1993a; Soini 1986). However, smaller HRs recorded for white-faced sakis (*Pithecia pithecia*) north of the Amazon (Norconk 2007) are consistent with the lower body mass of this species, undersampling of unhabituated groups (Norconk *et al*. 2003), and possibly competition with larger-bodied sympatric pitheciines, such as bearded sakis (*Chiropotes* spp.: Peres 1993a).

While the positive correlation between the proportion of terra firme forest in the HRs of our 5 focal groups and their proportional overlap with neighboring study groups was weak, the addition of unknown overlap areas between groups B and E and those of unhabituated groups would have strengthened this relationship. We observed 2 of those elusive groups using portions of the HRs of these 2 focal groups, all in terra firme forest, thereby increasing the true intensity of use and density of *Pithecia* in this habitat. Quantification of these additional areas of overlap would likely have increased our HR overlap estimates from 33% (Table I) to nearly 50% for terra firme groups of *Pithecia irrorata*, as suggested by earlier studies on buffy sakis, *P. albicans* (A. Johns 1987 *unpubl. ms.*; Peres 1993a).

Conversely, overlap was less than expected by chance for our floodplain forest groups. For example, we never observed an unhabituated group of only 2 individuals occupying a small HR within floodplain habitat adjacent to those of study groups C and D (Fig. 1, All) within either of their HRs, despite it interacting vocally with group C. In the extensive seasonally flooded forests of northern Peru, where terra firme forest is not available, the HR of a group of monk sakis (*Pithecia monachus*) overlapped <1% and *ca.* 70%, respectively, with those of its 2 neighbors (Soini 1986), showing that extensive overlap among floodplain groups may occur under some circumstances. Nevertheless, our data indicate a general lack of overlap in floodplain forest, further contributing to the observed variation in saki densities across the MDD region.

Activity Patterns

The 72% of known overlap area and 84% of observed agonistic interactions occurring in the terra firme forest portions of all HRs may indicate a greater propensity for groups to defend this preferred forest habitat. The tendency of groups to move across opposite boundaries of the HR within a day (Palminteri 2010), combined with the higher than expected use of overlap areas, which were terra firme dominated, further suggests higher time and energy allocation to exploitative or interference defense, or both, of ostensibly higher-quality territories in upland forest.

Although in general sakis carried out specific activities in proportion to their overall use of each forest type, they may have targeted particular forest types for specific activities, a strategy seen in other primates (Porter *et al.* 2007). For example, sakis spent little time in palm swamp, but there they foraged significantly more often than expected by chance (Fig. 4), consuming primarily fruits of the palm *Mauritia*. The canopy structure of crowns of *Mauritia*, which are widely spaced with little horizontal connectivity, requires frequent leaps that make movement conspicuous and therefore risky for this otherwise behaviorally cryptic species. Sakis thus appeared to minimize their detection vulnerability in swamps of *Mauritia* by largely restricting their time in this habitat to feeding bouts. The relatively low use overall, intensive use of the edges, and disproportionately high amount of time spent feeding in palm swamp, combined with their general avoidance of bamboo-dominated areas, suggest that sakis entered these relatively open-canopy forest types to access a specific food source and returned to the relative safety of closed-canopy forest as directly as possible.

Landscape-scale Detection and Population Density

Quantifying the patterns of use of space across different forest types can help explain the variation in density of *Pithecia* observed in surveys across lowland Amazonia, which have typically found this small-group-living pitheciine to be most frequently associated with terra firme forests (Branch 1983; Christen and Geissmann 1994; Palminteri *et al.* 2011; Peres 1997; Sheth *et al.* 2009). Using data from mammal surveys across the Madre de Dios region of southern Peru, Palminteri *et al.* (2011) partly attributed the high variability in saki abundance among sites to their higher recorded abundance at terra firme sites. Consistent with those findings, a number of behavioral traits identified here will likely elevate saki encounter rates in terra firme forest. The distribution of saki groups in terra firme forest is more tightly packed because of both smaller HRs per individual and the much higher overlap among HRs, which increased our group densities by 5–50%. Whereas our habituated saki groups were similarly observable in mature flooded and unflooded forests, unhabituated groups are likely more detectable in terra firme forest, where they spend more of their time, feed more frequently, and tend to be more vocal (intergroup encounters), all of which lead to higher detectability and a perception of greater densities of this otherwise highly cryptic species.

These factors are nevertheless insufficient to explain all of the observed regional-scale variation in saki population densities. In Madre de Dios, sakis were absent from 8 of 11 floodplain forest survey sites and from 4 of 19 terra firme forest sites (Palminteri *et al.* 2011). Sakis in this region face little hunting pressure, little habitat disturbance from forest fragmentation and logging, and minimal competition from other seed-eating vertebrates (Palminteri *et al.* in press). Thus, the observed patchiness in large-scale distribution is likely independent of human disturbance and reflects true species-habitat relationships that remain largely unexplained. These habitat preferences must be considered together with other ecological and biogeographic factors, such as predation risk (Sheth *et al*. 2009; Terborgh 1983) or fluvial barriers (Ayres and Clutton-Brock 1992), to better understand distribution and abundance at the landscape scale. Further studies of the habitat use, feeding, and antipredation behavior of *Pithecia* in areas with varying saki densities (including absences), in conjunction with the spatiotemporal distribution of food resources, would help strengthen our understanding of this enigmatic species by elucidating, e.g., how food availability in terra firme forest compares to that in other forest types and which canopy structure characteristics are favored by sakis and how they are distributed across forest types.

At Los Amigos, use of mature floodplain forest by sakis depended on the presence of highly developed forest structure to a greater degree than their use of terra firme forest (Palminteri 2010). Similarly, Haugaasen and Peres (2005) occasionally found sakis in seasonally flooded várzea and igapó forests, but only at sites immediately adjacent to terra firme forest. Our results suggest that the wider terra firme forest matrix spanning the vast interfluvial regions of lowland Amazonia will pack more groups of *Pithecia* per unit area, thereby resulting in higher population densities (*cf.* Peres 1997; C. A. Peres, *unpubl. data*). In contrast, sakis' virtually complete avoidance of low-phytomass habitat types, such as bamboo stands, suggests that they are unlikely to persist in areas where the bamboo *Guadua* predominates, including large portions of southwestern Amazonia (165,000 km^2; Nelson 1994; Smith and Nelson 2011). Alarmingly, these areas are expected to expand under a scenario of increasing frequency or severity of seasonal droughts and wildfires (Asner *et al.* 2010; Barlow and Peres 2004; Smith and Nelson 2011), as already witnessed in southwestern Amazonia (Aragão *et al.* 2007; Phillips *et al.* 2009). The expansion of bamboo-dominated forest and increasing threats to mature terra firme forest from climate and human land-use change across the basin (Asner *et al.* 2010; Nepstad *et al.* 1999) potentially threaten the long-term viability of specialists of mature terra firme forest, such as sakis. Ensuring the protection of extensive intact blocks of terra firme forest in areas that will remain relatively resistant to fire-mediated invasions of *Guadua* should become a regional conservation priority.

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References

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology, 74*, 1313–1325.

Alldredge, J. R., & Griswold, J. (2006). Design and analysis of resource selection studies for categorical resource variables. *Journal of Wildlife Management, 70*, 337–346.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*, 227–267.

Aragão, L. E. O. C., Malhi, Y., Roman-Cuesta, R. M., Saatchi, S., Anderson, L. O., & Shimabukuro, Y. E. (2007). Spatial patterns and fire response of recent Amazonian droughts. *Geophysical Research Letters, 34*(L07701), 1–5.

Asner, G. P., Loarie, S. R., & Heyder, U. (2010). Combined effects of climate and land-use change on the future of humid tropical forests. *Conservation Letters, 6*, 395–403.

Asociación para la Conservación de la Cuenca Amazónica (ACCA). (2007). Mapa fisiográfico de la Concesión para Conservación Los Amigos – ACCA. Puerto Maldonado, Peru.

Ayres, J. M., & Clutton-Brock, T. (1992). River boundaries and species range size in Amazonian primates. *The American Naturalist, 140*, 531–537.

Barlow, J., & Peres, C. A. (2004). Ecological responses to El Niño-induced surface fires in central Amazonia: management implications for flammable tropical forests. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 359*, 367–380.

Botanical Research Institute of Texas (BRIT). (2009). Atrium® biodiversity information system version 1.7.1 ©2005–9 Botanical Research Institute of Texas. http://atrium.andesamazon.org/.

Branch, L. (1983). Seasonal and habitat differences in the abundance of primates in the Amazon (Tapajos) National Park, Brazil. *Primates, 24*, 424–431.

Buskirk, S. W., & Millspaugh, J. J. (2006). Metrics for studies of resource selection. *The Journal of Wildlife Management, 70*, 358–366.

Byers, C. R., Steinhorst, R. K., & Krausman, P. R. (1984). Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management, 48*, 1050–1053.

Carey, A. B., Reid, J. A., & Horton, S. P. (1990). Spotted owl home range and habitat use in southern Oregon coast ranges. *Journal of Wildlife Management, 54*, 11–17.

Carr, A., & Rodgers, A. (1998). *HRE: The home range extension for ArcView™ tutorial guide*. Ontario: Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources.

Christen, A., & Geissmann, T. (1994). A primate survey in northern Bolivia, with special reference to Goeldi's monkey, *Callimico goeldii*. *International Journal of Primatology, 15*, 239–275.

Crowley, P. H. (1992). Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Reviews of Ecological Systems, 23*, 405–447.

Dietz, J. M., Peres, C. A., & Pinder, L. (1997). Foraging ecology and use of space in wild golden lion tamarins (*Leontopithecus rosalia*). *American Journal of Primatology, 41*, 289–305.

DiFiore, 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.

Dunbar, R. I. M. (1988). *Primate social systems*. Ithaca, NY: Cornell University Press.

ESRI (2002) ArcView Version 3.3. Environmental Systems Research Institute (ESRI), Redlands CA.

Fieberg, J. (2007). Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology, 88*, 1059–1066.

Freese, C., Heltne, P., Castro, N., & Whitesides, G. (1982). Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *International Journal of Primatology, 3*, 53–90.

Garshelis, D. L. (2000). Delusions in habitat evaluation: measuring use, selection, and importance. In L. Boitani & T. K. Fuller (Eds.), *Research techniques in animal ecology* (pp. 111–164). New York: Columbia University Press.

Gitzen, R., Millspaugh, J., & Kernohan, B. (2006). Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *Journal of Wildlife Management, 70*, 1334–1344.

Grant, J. W. A., Chapman, C. A., & Richardson, K. S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology, 31*, 149–161.

Haugaasen, T., & Peres, C. A. (2005). Primate assemblage structure in Amazonian flooded and unflooded forests. *American Journal of Primatology, 67*, 243–258.

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

Hobbs, N. T., & Hanley, T. A. (1990). Habitat evaluation: do use/availability data reflect carrying capacity? *Journal of Wildlife Management, 54*, 515–522.

Hood, G. M. (2009). PopTools version 3.1.1. Wildlife and Ecology, CSIRO, Canberra. URL http://www.cse.csiro.au/poptools.

Hooge, P. N., Eichenlaub, W. M., & Solomon, E. K. (1999). *Using GIS to analyze animal movements in the marine environment.* Unpublished manuscript. U.S. Geological Survey, Alaska Science Center, Glacier Bay Field Station.

Horner, M. A., & Powell, R. A. (1990). Internal structure of home ranges of black bears and analyses of home-range overlap. *Journal of Mammalogy, 71*, 402–410.

Irwin, M. (2008). Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? *Biotropica, 40*, 231–240.

Johns, A. (1986). Notes on the ecology and current status of the buffy saki, *Pithecia albicans*. *Primate Conservation, 7*, 26–29.

Johns, A. (1987). Patterns of social organization in the buffy saki, *Pithecia albicans* Gray 1860. Unpublished manuscript, Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2002). *Resource selection by animals: Statistical design and analysis for field studies* (2nd ed.). Dordrecht: Kluwer Academic.

McClean, S. A., Rumble, M. A., King, R. M., & Baker, W. L. (1998). Evaluation of resource selection methods with different definitions of availability. *Journal of Wildlife Management, 62*, 793–801.

McLoughlin, P. D., & Ferguson, S. H. (2000). A hierarchical pattern of limiting factors helps explain variation in home range size. *Ecoscience, 7*, 123–130.

Milton, K., & May, M. L. (1976). Body weight, diet, and home range area in primates. *Nature, 259*, 459–462.

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

Nelson, B. W. (1994). Natural forest disturbance and change in the Brazilian Amazon. *Remote Sensing Reviews, 10*, 105–125.

Nepstad, D. C., Verissimo, A., Alencar, A., Nobre, C., Lima, E., Lefebvre, P., Schlesinger, P., Potterk, C., Moutinho, P., Mendoza, E., Cochrane, M., & Brooks, V. (1999). Large-scale impoverishment of Amazonian forests by logging and fire. *Nature, 398*, 505–508.

Neu, C. W., Byers, C. R., & Peek, J. M. (1974). A technique for analyses of utilization-availability data. *Journal of Wildlife Management, 38*, 541–545.

Norconk, M. A. (2007). Sakis, uakaris, and titi monkeys: Behavioral diversity in a radiation of primate seed predators. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 123–138). New York: Oxford University Press.

Norconk, M. A., & Conklin-Brittain, N. L. (2004). Variation on frugivory: the diet of Venezuelan white-faced sakis. *International Journal of Primatology, 25*, 1–26.

Norconk, M. A., Raghanti, M. A., Martin, S. K., Grafton, B. W., Gregory, L. T., & DeDijn, B. P. E. (2003). Primates of Brownsberg Natuurpark Suriname with particular attention to the Pitheciins. *Neotropical Primates, 11*, 94–100.

Nunn, C. L., & Barton, R. A. (2000). Allometric slopes and independent contrasts: a comparative test of Kleiber's law in primate ranging patterns. *The American Naturalist, 156*, 519–533.

Oliveira, J. M. S., Lima, M. C., Bonvincino, C., Ayres, J. M., & Fleagle, J. G. (1985). Preliminary notes on the ecology and behavior of the Guianian saki (*Pithecia pithecia*, Linneaus 1766: Cebidae, Primate). *Acta Amazonica, 15*, 249–263.

Palminteri, S. (2010). *Determinants of primate distribution and abundance in southwestern Amazonia*, *with a focus on bald-faced saki monkeys* (Pithecia irrorata). Ph.D. thesis, University of East Anglia. Norwich, UK.

Palminteri, S., Powell, G., Adamek, K., & Tupayachi, R. (in press). Competition between two specialist seed-eaters: The diets of Pitheciines and large *Ara* macaws. In L. M. Veiga, A. A. Barnett, S. F. Ferrari, & M. A. Norconk (Eds.), *Evolutionary biology and conservation of titis*, *sakis and uacaris*. Cambridge, UK: Cambridge University Press.

Palminteri, S., Powell, G. V. N., & Peres, C. A. (2011). Regional-scale heterogeneity in primate community structure at multiple undisturbed forest sites across south-eastern Peru. *Journal of Tropical Ecology, 27*, 181–194.

Peres, C. A. (1993a). Notes on the ecology of buffy saki monkeys *(Pithecia albicans*, Gray 1860): a canopy seed-predator. *American Journal of Primatology, 31*, 129–140.

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

Peres, C. A. (1997). Primate community structure at twenty western Amazonian flooded and unflooded forests. *Journal of Tropical Ecology, 13*, 381–405.

Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C. A., et al. (2009). Drought sensitivity of the Amazon rainforest. *Science, 323*, 1344–1347.

Porter, L., Sterr, S. M., & Garber, P. A. (2007). Habitat use and ranging behavior of *Callimico goeldii*. *International Journal of Primatology, 28*, 1035–1058.

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. In L. Boitani & T. K. Fuller (Eds.), *Research techniques in animal ecology* (pp. 65–110). New York: Columbia University Press.

Rodgers, A., & Carr, A. (1998). *HRE: The home range extension for ArcView™: User's manual*. Ontario: Centre for Northern Forest Ecosystem Research, Ontario Ministry of Natural Resources.

Seaman, D. E., & Powell, R. A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology, 77*, 2075–2085.

Sheth, S. N., Loiselle, B. A., & Blake, J. G. (2009). Phylogenetic constraints on fine-scale patterns of habitat use by eight primate species in eastern Ecuador. *Journal of Tropical Ecology, 25*, 571–582.

Smith, M., & Nelson, B. W. (2011). Fire favours expansion of bamboo-dominated forests in the south-west Amazon. *Journal of Tropical Ecology, 27*, 59–64.

Soini, P. (1986). A synecological study of a primate community in the Pacaya-Samiria National Reserve, Peru. *Primate Conservation, 7*, 63–71.

Struhsaker, T. T. (1967). Ecology of vervet monkeys (*Cercopithecus aethiops*) in the Masai-Amboseli game reserve, Kenya. *Ecology, 48*, 891–904.

Terborgh, J. (1983). *Five new world primates: A study in comparative ecology*. Princeton, NJ: Princeton University Press.

Thomas, D. L., & Taylor, E. J. (2006). Study designs and tests for comparing resource use and availability II. *Journal of Wildlife Management, 70*, 324–336.

Torre, S., de la Utreras, V., & Campos, F. (1995). An overview of primatological studies in Ecuador: primates of the Cuyabeno Reserve. *Neotropical Primates, 3*, 169–170.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. *Journal of Wildlife Management, 47*, 893–901.

Wallace, R. B. (2006). Seasonal variations in black-faced black spider monkey (*Ateles chamek*) habitat use and ranging behavior in a southern Amazonian tropical forest. *American Journal of Primatology, 68*, 313–332.

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