Determinants of primate distribution and abundance in south-western Amazonia, with a focus on bald-faced saki monkeys (*Pithecia irrorata*)

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Contents

Abstract

Despite its obvious importance, an understanding of species and community distribution patterns at a scale with sufficient resolution for conservation planning is often lacking, even for relatively well-known taxa. This thesis examines potential drivers of primate distribution and community heterogeneity at two spatial scales in south-western Amazonia: at the scale of a major watershed, analysing occurrence and abundance of 12 species of primates at 37 survey sites and, at the home range scale, quantifying the habitat use, diet, and ranging and feeding patterns of five habituated groups of bald-faced saki monkeys (*Pithecia irrorata*).

Substantial primate community heterogeneity was observed in this relatively small region of Amazonia, reflecting species patchiness, rather than species turnover. Two species known to occur in the region were undetected at all 37 survey sites, while three others were present at fewer than half the sites. Habitat type and geographic location each affect community heterogeneity, and human hunting pressure increases heterogeneity by reducing the abundance of large-bodied species.

The bald-faced saki, one of three species displaying patchy distributions in the region, maintained a broad diet of over 220 plant species and consumed primarily the seeds of immature fruit. By feeding on unripe fruit, which was more consistently available than ripe fruit, sakis appeared to reduce competition with other larger fruit-eating primates and reduce the need to expend greater foraging effort or consume less desirable foods, even in periods of low fruit availability. Dietary overlap with another arboreal seed predator, the larger-bodied macaws (*Ara spp.*), appeared to be limited. Movement patterns of sakis appeared to be affected more by forest type than food availability. Use of terra firme forest overall was greater than expected, and large group size, small home range, and high home range overlap associated with this forest type all suggest that saki densities in south-western Amazonia will be highest in terra firme forest with well-developed vegetation structure. Areas preferred by sakis had greater, more uniform canopy structure, both within study group home ranges and in the surrounding landscape, suggesting that habitats that facilitate movement and reduce detectability for a species with high vulnerability to predation and cryptic colouration and behaviour are preferred.

Habitat and dietary preferences must be considered together with other factors in determining occurrence and population densities at the landscape level. In accordance with these findings, regional barriers to dispersal, such as rivers, and finer-scale ecological specialisation, such as a preference for taller, more uniform canopy, may limit the utility of coarse-scale data, such as species range maps, for regional-scale conservation planning, even for relatively well-studied taxon like primates.

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Chapter 1: Introduction

Spatial patterns of communities and species distributions

Two of the basic puzzles of animal ecology are how species are distributed across a landscape and what determines their distribution patterns. Both are essential for effective conservation planning (Currie et al. 1999, Margules and Pressey 2000). If species distribution patterns vary in heterogeneous natural communities across a region of interest, conservation efforts must focus on ensuring that high conservation value areas that best capture species diversity and community heterogeneity are represented in conservation planning and implementation (Pressey 1994, Gaston 2003, Groves 2003, Brooks et al. 2004).

Despite its obvious importance, an understanding of distribution patterns at a scale with sufficient resolution for meso-scale (10^3–10^5 km^2) conservation planning within the Amazon basin is often lacking, even for relatively well-known taxa (Emmons 1999, Phillips et al. 2003a, Peres 2005, Tuomisto 2007). Patchy distribution patterns resulting from a species' specialization on spatially restricted habitats, such as bamboo or palm swamp forests (Emmons 1984, Kratter 1997) or on ephemeral habitats created by fluvial dynamics (Salo et al. 1986, Peres 1993, Tuomisto et al. 1995) are well documented and can be estimated through analysis of satellite images, vegetation maps, and similar tools. In contrast, assessing species presence or absence and, consequently, the level of community heterogeneity within a spatially dominant habitat, such as unflooded terra firme or floodplain forest, remains a major challenge to conservation planners. Range maps based on coarse occurrence data delineate species distributions and have been used for conservation planning, yet their level of precision may not be sufficient for regional-scale planning (Hurlbert and White 2005, 2007, Jetz et al. 2008). Consequently, documenting and understanding the drivers of the degree to which species vary in abundance, the structural heterogeneity of the communities they form, and the determinants of this variation can provide valuable insights for designing and implementing conservation strategies across large regions of tropical forest, such as the Amazon basin.

Spatial patterns of rare species

While discussion of rarity and patchy distribution patterns for a given taxon often focuses on the results of habitat loss and fragmentation (Peres 2001, Mbora and Meikle 2004, Michalski and Peres 2005), many species are naturally rare at different scales (e.g. Kunin and Gaston 1993, Yu and Dobson 2000, Harcourt et al. 2002, Borges 2006). These patterns of rarity vary from restricted range areas with high density, to wide geographic ranges with uniformly low density (Rabinowitz 1981, Dobson and Yu 1993, Pitman 1999), to natural patchiness in which species density varies from low to high at sites of close proximity relative to the species geographic range (Gentry 1988, Terborgh and Andresen 1998).

Habitat quality likely plays an important role in determining species abundance and distribution patterns. For example, habitat quality has been shown to be negatively correlated with primate home range size but positively correlated with population density (e.g. Struhsaker 1967-*Cercopithecus*, Stevenson 2006-*Lagothrix*). The availability of high-quality food is a known determinant of the ranging patterns of various primate taxa (e.g. Vedder 1984-*Gorilla*, Dietz et al. 1997, Stevenson 2006, Suarez 2006), particularly for frugivores, who specialize in an ephemeral resource, though the relationship between food availability and space use of primate groups is variable (Chapman 1988-*Cebus* and *Alouatta* in Costa Rica, Stoner 1996). Forest structure, which facilitates access to food, movement across a home range, and potentially predator avoidance for canopy residents, has been shown to affect the use of certain habitat types by primates (e.g. Lemos de Sá and Strier 1992, Porter et al. 2007) and other prey taxa (Fortin et al. 2008). Nevertheless, food, vegetation structure, and other features of suitable habitat are poorly known for many species, particularly in tropical forests.

The primates of Madre de Dios

Amazonian primates provide a good example of a taxonomic group that is relatively well known on a coarse scale, but remains poorly known at a scale that is fine enough for landscape conservation planning. Southeastern Peru boasts some of the highest primate alpha-diversities on earth (Terborgh 1983, Emmons 1999), with 13 resident species, ordered from smallest to largest body size: pygmy marmoset (*Cebuella pygmaea*), saddleback tamarin (*Saguinus fuscicollis*), emperor tamarin (*S. imperator*), Goeldi's marmoset (*Callimico goeldii*), Bolivian squirrel monkey (*Saimiri boliviensis*), brown titi (*Callicebus brunneus*), night monkey (*Aotus nigriceps*), bald-faced saki monkey (*Pithecia irrorata*), white-fronted capuchin (*Cebus albifrons*), brown capuchin (*C. apella*), Bolivian red howler monkey (*Alouatta seniculus*), Peruvian spider monkey (*Ateles chamek*), and grey woolly monkey (*Lagothrix cana*).

Within this diverse primate community, several species display patchy distributions across their geographic ranges that are poorly elucidated and largely unexplained. For example, the large-bodied frugivorous woolly monkey, which has been detected intermittently in regional surveys (e.g. Freese et al. 1982, Peres 1997), lives in large groups and may rely on large fruit patches to persist (Peres 1994a, Stevenson and Castellanos 2000). Although it is widely hunted by humans (Peres 1990, Ohl-Schacherer 2007) and is less abundant at hunted sites (Peres 1997, Kirkby 2004, Endo et al. 2010), it is absent from some historically nonhunted sites (Terborgh 1983) and purportedly from most of the MDD basin (Kirkby et al. 2000, Schulte-Herbrüggen and Rossiter 2003, Kirkby 2004). At the other end of the spectrum, the small-bodied *Callimico goeldii*, considered a bamboo / canopy gap specialist (Porter 2004), is seldom reported in MDD (Terborgh 1983, Pitman 2008) and only slightly more regularly in surveys in adjacent Pando, Bolivia (Christen and Geissman 1994, Buchanan-Smith et al. 2000). Finally, a medium-bodied seed predator, the bald-faced saki (*Pithecia irrorata*), one of the more enigmatic primates of the Amazon because of its cryptic, retiring nature, occurs at highly variable abundance in patterns that are unexplained, but seem to result in it being absent or rare in much of the region's extensive protected areas.

My first research objective, therefore, was to quantify the meso-scale heterogeneity of primate communities of the Madre de Dios basin, and to examine potential natural and anthropogenic drivers of that heterogeneity. Secondly, the outstanding lack of information about habitat and dietary requirements of *P. irrorata* led me to focus on this species and to investigate aspects of its ecology, particularly its habitat use, diet, and ranging and feeding patterns, that might affect its presence/abundance throughout its geographic range. This study thus attempted to determine why such variation in its density occurred within forests that, for now, remain relatively intact at a regional scale.

Bald-faced saki monkeys

Five species of saki monkey (*Pithecia aequatorialis*, *P. albicans*, *P. irrorata*, *P. monachus*, and *P. pithecia*) are currently recognized (Hershkovitz 1987), and their ranges span the Amazon from the northeast in French Guiana and Suriname, south and west to northern Bolivia and southeastern Peru. Sakis are medium-sized (1.8 – 2.3 kg) arboreal seed predators that live predominantly in family groups of 2 – 8 individuals, typically consisting of a male, one or more females, and one or more generations of offspring. Sakis south of the Amazon River are known primarily from mammal inventories (Branch 1983, Peres and Janson 1999, Heymann et al. 2002, Youlatos 2004, Haugaasen and Peres 2005, Sheth et al 2009), and synecological studies (Johns 1986, Soini 1986), with a few species-specific monitoring efforts (Happel 1982, Peres 1993). Their dispersal appears to be affected by major rivers, as the geographic ranges of all saki species are bounded at least partially by rivers (Branch 1983, Bennett et al. 2001, Heymann et al. 2002, Haugaasen 2004, Norconk and Conklin-Brittain 2004). For example, the geographic range of the bald-faced saki considered in this study includes the humid forests of the Amazon basin south of the Amazon River from the Tapajós River in east-central Brazil west to the Madre de Dios and Juruá rivers in southeastern Peru.

Importance of the study

This study is important or novel for several reasons:

(1) The relative integrity of the forested sites surveyed in this region allowed an assessment of the structure and composition of primate communities, as well as species-level habitat selection and sub-population dynamics without the confounding influence of forest fragmentation.

(2) Rarity in animals is still not well-understood and natural patchiness even less so, and this effort attempts to identify the characteristics affecting the distribution of one tropical forest vertebrate naturally distributed at low and sometimes highly variable densities.

(3) While frugivores must either shift their behaviour or their diets during periods of seasonal ripe fruit scarcity (e.g. Terborgh 1983, Symington 1988, Peres 1994b, Stevenson et al. 2000, Palacios and Rodriguez 2001, Porter et al. 2007), species

relying on more consistently available food resources, such as leaves or seeds, may be able to maintain their staple diet for a greater portion of the year (Norconk 1996). Seed predation is unusual in primates but is the principal dietary strategy for Pitheciines, potentially exposing them to reduced seasonal scarcity and allowing them to live sympatrically with larger or more aggressive frugivores. This strategy has to date been studied primarily in Pitheciines north of the Amazon River.

(4) This is the first long-term systematic study of *Pithecia* south of the Amazon River. The few longer-term studies of *Pithecia* ranging behaviour to date have monitored non-habituated groups (Peres 1993b), re-introduced individuals (Vié et al. 2001), chance encounters during synecological studies (Johns 1986, Soini 1986), or groups in habitat remnants (Oliveira et al 1985, Norconk 1996). The scarcity of systematic habitat use data for *Pithecia* species to date has precluded our understanding of essential relationships between them and their habitats and, consequently, our ability to make informed decisions relative to their distribution. Sakis in southern Amazonia are larger than *P. pithecia*, are generally allopatric with larger Pitheciines (*Chiropotes* and *Cacajao*), spend more time in the forest canopy and have adopted an appropriately quadrupedal means of locomotion, and may need to maintain larger home ranges than *P. pithecia*.

Study region

This study considers two main spatial scales: the Madre de Dios basin in southeastern Peru and a single site within it, in the sub-basin of the Los Amigos River (Figure 1). At the broader scale, I studied the heterogeneity of primate community composition and structure at sites across the Madre de Dios (MDD) basin. To complement the primate surveys that I led at 12 sites within the watersheds of the Las Piedras, Los Amigos, Madre de Dios and Tambopata rivers, I compiled data from surveys at 15 additional sites along these rivers (Kirkby et al. 2000, Schulte-Herbrüggen and Rossiter 2003, Nuñez-Iturri and Howe 2007), as well as in the Manu River basin (Kirkby 2004, Endo et al. 2010).

Madre de Dios biodiversity and conservation

The high levels of biological diversity and the relatively intact state of the forests of the MDD watershed make this region one of global importance for nature conservation. The region harbors some of the world’s highest numbers of species of various taxa, including birds (Terborgh et al. 1990), mammals, including the 13 primate species (Pacheco et al. 1993, Solari et al. 2006), amphibians (Rodriguez and Cadle 1990), and trees (Gentry 1988, Foster 1990).

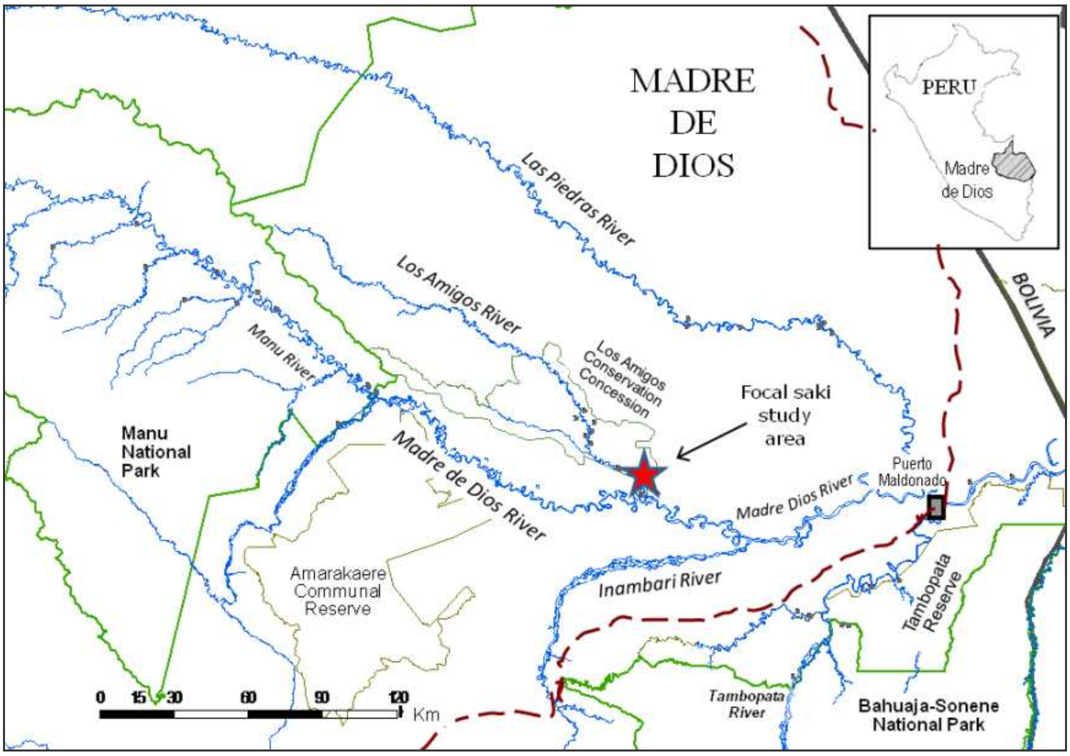

Figure 1. Orientation map of the study region in Madre de Dios, Peru. Primate community surveys were conducted across the region, while the focal area for the saki study is denoted by the star near the confluence of the Los Amigos and Madre de Dios rivers. The Inter-Oceanic highway is shown as a thick dashed line running through the main town of Puerto Maldonado and separating the conservation areas of the Manu/Madre de Dios and the Tambopata watersheds.

Legally designated areas for conservation or sustainable resource use, which cover approximately 60% of the 85,000 km^2 of the MDD region (Figure 1, inset), include three national parks, two reserves designated for communal use, an area for indigenous people in voluntary isolation, privately-managed conservation and tourism concessions, as well as various smaller concessions designated for extraction of Brazil nuts or timber that have restrictions on other uses. The high percent of forest cover (~90%, Phillips et al. 2006, Asner et al. 2010) means that most of the biodiversity is still also found outside, as well as within, protected areas.

Human population in MDD was historically sparse and concentrated into a few towns along the highway and larger rivers. Nevertheless, an untold number of temporary settlements housing legal and illegal mining and logging teams have become established across the basin. Overhunting of larger-bodied primates and subsequent decline in seed dispersal services has already affected forest regeneration at established settlements (Nuñez-Iturri and Howe 2007, Terborgh et al 2008), despite the absence of road transport and intensive development. Although land use change in the region has been moderate until recently (Dourojeanni et al. 2009), current development patterns and policies have prompted the rate of forest loss and degradation to rise precipitously (Asner et al. 2010). The paving of the Inter-Oceanic Highway, which connects Brazil with Peru's Pacific coast and cuts through the middle of MDD (Figure 1), has rapidly increased pressure for land use change in the region. Projections by the Amazon Scenarios study (Soares-Filho et al. 2005) include substantial forest conversion along the development corridor associated with this newly paved highway.

Focal study area for bald-faced sakis

Within the larger survey region, monitoring of saki study groups took place in a focal area of approximately 335 ha of unflooded (*terra firme*) and floodplain forest at the CICRA field station. The station sits at approximately 270 masl between the Madre de Dios and Los Amigos rivers in the southeastern corner of the Los Amigos Conservation Concession, at 12°34'07"S 70°05'57" W (Figure 1), which protects approximately 145,000 hectares of Amazonian lowland moist forest in the watershed of the Los Amigos River, a tributary of the Madre de Dios River.

Foster (2001) divided the vegetation zones of the Los Amigos watershed into three geologic formations: flat and hilly Amazon terra firme forest and floodplains. The high flat terrace, which occurs in the lower Los Amigos watershed and extends to the east, consist mostly of tall, highly-diverse, closed-canopy vegetation with some open bamboo stands on previously disturbed land. The dissected steep hills, large portions of which have an understory of spiny bamboo (*Guadua spp.*) occurring as open stands or under a sparse tree canopy or are covered with dense vine tangles, occupy much of MDD and stretch north into central-eastern Peru, western Acre, Brazil, and Bolivia (Nelson 1994, Smith and Nelson submitted/in press). These stands favour disturbed habitat specialists and may be unsuitable for mature canopy specialists. The Amigos floodplain, formed from a third geologic formation, supports tall floodplain forest as well as small stands of *Mauritia flexuosa*-dominated palm swamp along the Madre de Dios River. In this thesis, I therefore discuss four primary forest types in the focal group study area: tall, closed-canopy terra firme (upland) forest, *Guadua*-dominated bamboo stands (also upland), mature closed-canopy floodplain forest, and *M. flexuosa*-dominated palm swamp.

From 2000 to 2006, annual rainfall averaged between 2700 and 3000 mm. Rainfall patterns were seasonal: at least 80% of all rain fell between October and April while less than 80 mm per month fell in June, July, or August (Pitman 2008, BRIT 2010). Annual rainfall during this period ranged from 2,612 mm in 2001 to 3,498 mm in 2003. The first year of the study period, 2005, was an exceptionally dry year in the Amazon (Giles 2006, Aragão et al. 2007, Phillips et al. 2009), with relatively low rainfall in January, February and April, and unusually high rainfall in June (typically the "dry" season).

Despite increasing hunting, logging, and mining pressures both throughout the region and in nearby areas along the Madre de Dios river, the Los Amigos watershed is relatively undisturbed compared with other Amazonian watersheds, and a full complement of vertebrate species, including 11 of the region's 13 primate species, is found there (Pitman 2008). Of the primates, only woolly monkeys (*Lagothrix cana*) and pygmy marmosets (*Cebuella pygmaea*) are absent from the lower Amigos watershed.

Thesis aims and overview

The aim of this thesis is to contribute to our understanding of the patterns and underlying factors that affect the regional distribution of primates, in the absence of the effects of forest degradation, through complementary research on primate communities in MDD and the resource use and local and regional distribution of its most poorly-known primate species, the bald-faced saki monkey (*Pithecia irrorata*). This species is practically unstudied and, given a debate over its distribution and possible habitat specialisation (Mittermeier and van Roosmalen 1981, Terborgh 1983, Haugaasen and Peres 2005, Sheth et al. 2009), a second aim of this research was to better understand the ecological requirements of this species and, subsequently, help to interpret and estimate its distribution over larger areas.

The six data chapters are written in the form of peer-reviewed papers, the first two covering primate communities and remaining four investigating specific aspects of the ecology of *P. irrorata*. Chapter 2 assesses the fine-scale accuracy of species range maps for regional conservation planning by comparing published geographic range maps for 10 primate species to their occupancy at survey sites in Madre de Dios, emphasizing the importance of understanding ecological requirements of species. Chapter 3 further examines meso-scale heterogeneity of diurnal primate communities across lowland forested sites in the MDD watershed by quantifying patterns of species richness, abundance, and community structure with respect to environmental, geographic, and anthropogenic influences.

Chapter 4 is the first of several chapters to focus on one member of the Madre de Dios primate communities, the bald-faced saki, one of the most poorly-studied primates in the Neotropics. Sakis were thought to be terra firme forest specialists, so this chapter uses data from nearly three years of monitoring several study groups to examine the use of space by sakis, including home range size and movement patterns, relative to forest type. Findings may help to explain the high variance in group density observed in this region. As *Pithecia* is one of only a handful of primate genera for which seeds are the mainstay of the diet, Chapter 5 analyzes the potential advantages of eating seeds as an alternative dietary strategy to the traditional frugivorous diet that is comprised primarily of ripe fruit pulp. This chapter combines phenological data with saki feeding data to test whether immature fruit was available more consistently than ripe fruit and whether the patterns of saki feeding behaviour corresponded to fruit availability. Chapter 6 then compares the diets of *Pithecia* and large *Ara* macaws, the other main canopy seed predator in the region, and measures their overlap, to indicate the degree of potential competition between these bird and primate taxa. Chapter 7 examines the importance to sakis of forest structure, one key habitat characteristic that varies among forest types, by comparing the use of space within saki home ranges to canopy structure data derived from a high-resolution airborne light detection and ranging (LiDAR) system and attempts to apply the results to assessing habitat occupancy by sakis across a larger landscape. Chapter 8 presents the main conclusions of the thesis and future research directions.

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Chapter 2: Usefulness of species range polygons for predicting local primate occurrences in southeastern Peru

Abstract

Species distribution maps are widely used in predicting areas of conservation concern, particularly where species distributions are poorly known. However, the accuracy of range maps for regional/local planning is questionable. We compared published putative geographic range polygons of 10 primate species to their actual occupancy at 23 survey sites in southeastern Peru to assess the fine-scale accuracy of these polygons for regional conservation planning. We analyzed the proportion of sites at which each species was detected both inside and outside of its published NatureServe (Patterson et al. 2003) and IUCN (2008) range polygons. There were mismatches between our line-transect survey data and range polygon boundaries for nine of the 10 species (from 15% to 80% of cases), including both false presences and false absences. Each published dataset overestimated the presence of seven primate species and the absence of four species, though errors varied among species. Occupancy patterns of species with larger geographic ranges were no more accurately predicted than those of more narrow-range species. Regional barriers to dispersal, such as rivers, and finer-scale ecological specialisation may limit the applicability of range map polygons to regional-scale conservation priority-setting, even for relatively well-studied taxa. Despite the risk of errors, range polygons are still used as baseline data in conservation planning. We suggest some measures that could reduce the error risk.

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Introduction

Conservation planning typically uses both coarse-filter, habitat-based data and fine-filter, species-based data to identify priorities and assess representation gaps (Pressey 2004, Stoms et al. 2005). Maps of the geographic distributions of many species that are now available as downloads from conservation websites (Patterson et al. 2003, IUCN 2008) are considered to be fine-filter data (Rodrigues et al. 2004, Brooks et al. 2004, Higgins et al. 2004). As computers have facilitated interpolation of site-level data to broader areas, these species distribution maps have become widely used in predicting areas of conservation concern (Hurlbert and Jetz 2007, Rodrigues et al. 2004, Schipper et al. 2008), particularly in tropical forest regions where actual species distributions are poorly known.

Nevertheless, range polygons typically fail to capture local habitat variability, certain barriers to species movement, and other factors that determine the presence of a species at a given site and so may overestimate the degree to which its geographic range distribution is filled in terms of actual habitat occupancy (Jetz et al. 2008, Hurlbert and White 2005, Schipper et al. 2008, supplemental material).

Hurlbert and White (2005) found discrepancies in bird species richness patterns between analyses using geographic range maps and those using survey results. In a follow-up paper (Hurlbert and White 2007), they suggested that range map data alone may be insufficient to assess the capacity of existing or potential reserves to protect areas of species richness or species of interest, and they identified the potential for inappropriate application of range polygon data to questions of local-scale patterns and processes.

In this study, we examined the accuracy of species range maps for conservation planning at the landscape scale in the Peruvian Amazon. Specifically, we examined how range polygons of a relatively well-studied taxon − primates − compare to species occupancy patterns at survey sites. Diurnal primates are one of the few tropical forest taxa for which ecology and habitat use, as well as geographic ranges, are relatively well-known (Brooks et al. 2004, Higgins et al. 2004), and their conservation status is important to a broad audience, making them potentially good candidates for informing conservation planning efforts (Emmons 1999). We did not attempt to extend this analysis to whether primates can be used as indicators for other taxa or habitats as discussions of this concept are already available in the literature (e.g. Emmons 1999, Sebastião and Grelle 2009, and Moore et. al. 2003).

Methods

Study area

The department of Madre de Dios (MDD) in southeastern Peru (Figure 1) covers approximately 8,458,440 hectares and consists almost entirely of relatively intact moist forest cover. The region boasts one of the highest diversities of primates on earth (Terborgh 1983, Emmons 1984, Peres and Janson 1999) and a relatively high rate of protection -approximately 37% of MDD is covered by strict protected areas (WWF 2008 unpublished data, Figure 1). The region's two predominant habitat types are unflooded (*terra firme*) forest, typically found on dissected, steep-sided terraces, and supra-annually flooded forest (hereafter floodplain). All survey sites were located in relatively undisturbed areas between 250 and 400 m above sea level, except for three premontane sites (Figure 1, sites 11-13) positioned at 600-900m (Fernandez and Kirkby 2002).

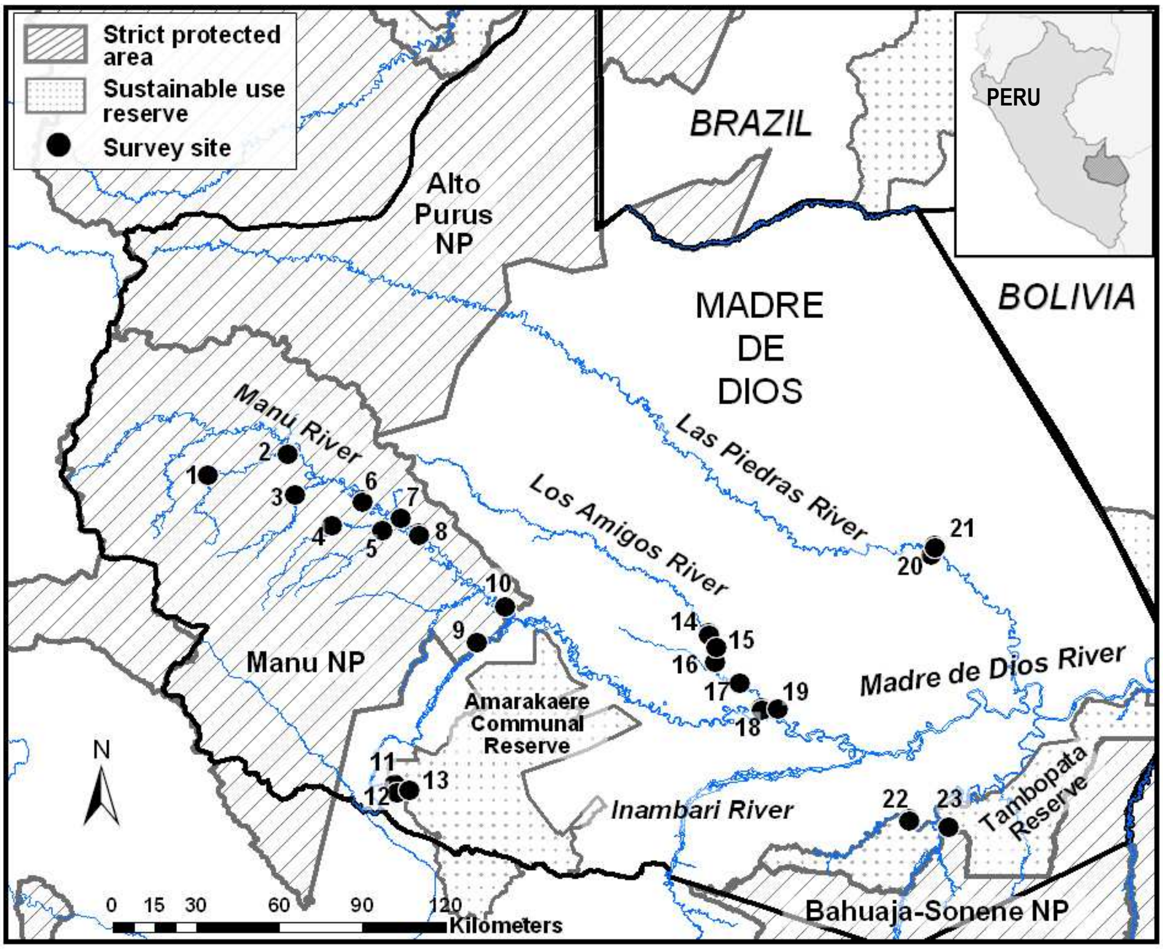

Figure 1. Study area in Madre de Dios, Peru. Dots represent the 23 sites (Table 1) at which mammal communities were surveyed along 55 line transects.

Table 1: Profile of 23 mammal survey sites in Madre de Dios, Peru.

Site number (Fig 1)	Site	Latitude (S), Longitude (W)	Survey length (km)	Primate species found*	Overlying IUCN ranges*	Overlying NS ranges*
1	Yomybato	11°48' 71°55'	139	8	6	7
2	Tayakome	11°44' 71°39'	126	10	7	7
3	Cumerjali	11°52' 71°38'	131	9	6	7
4	Upper_Panagua	11°58' 71°31'	135	8	5	7
5	Lower_Panagua	11°59' 71°21'	106	8	5	7
6	Cocha_Cashu	11°53' 71°24'	118	9	7	9
7	Pakitza	11°57' 71°17'	149	8	8	9
8	Salvador	12°00' 71°13'	26	5	8	9
9	Pusanga	12°21' 71°02'	31	4	6	7
10	Limonal	12°14' 70°56'	25	6	8	8
11	Salvación	12°50' 71°18'	35	4	5	6
12	Yunguyo	12°48' 71°19'	35	5	5	6
13	Paujil	12°50' 71°16'	31	4	5	6
14	Amigos_3-4	12°20' 70°16'	80	7	8	9
15	Amigos_5-6	12°22' 70°14'	72	9	8	9
16	Amigos_7-8	12°25' 70°15'	64	9	8	9
17	Amigos_1-2	12°29' 70°10'	100	9	8	9
18	Cicra	12°34' 70°05'	61	9	8	9
19	CM1	12°34' 70°02'	54	8	8	9
20	Piedras_south	12°04' 69°32'	275	8	9	10
21	Piedras_north	12°03' 69°31'	98	7	9	10
22	Malinowski	12°56' 69°36'	122	7	4	7
23	Chuncho	12°57' 69°28'	96	6	5	7

* Considers 10 analyzed species only. IUCN= International Union for the Conservation of Nature. NS=NatureServe.

Field surveys

Between 1998 and 2008, primate communities were surveyed at 23 sites representing both *terra firme* and floodplain forests on both banks of the Madre de Dios River (Table 1; Figure 1). Five separate studies, spanning wet and dry seasons, conducted diurnal line transect surveys (Peres 1999), a standard mammal inventory method in tropical forests. At each site, between one and four linear transects 2000 − 5300 m in length and >1 km apart, were walked 3-12 times each by trained observers. Data on species identity, group size, and distance from transect were collected following field procedures outlined by Peres (1999). These and all research protocols reported in this manuscript were reviewed and approved by Peru’s Institute for Natural Resources

(INRENA) and adhered to the American Society of Primatologist ethical principles for the treatment of nonhuman primates. Neotropical primates are usually highly conspicuous, group-living species, and their intrinsic detectability, even in lowland Amazonian forests, is relatively high, with the exception of the most habitat-specialist species (Peres and Janson 1999; C.A. Peres, unpublished data). In our field surveys, all habitat-generalist species recorded at any given site were detected before the last day of census effort, so Type I errors (false absences) were likely severely reduced in this study for the 10 species that we considered.

Data analysis

The two primate range map datasets we used for comparison were published by NatureServe (Patterson et al. 2003)- created by scanning or digitizing published species range maps- and IUCN (Schipper et al. 2008)- created by updating the NatureServe maps through literature searches and expert knowledge.

We used a species-by-site matrix to identify predicted and confirmed presences and absences at each site. We calculated the proportion of survey sites for which field and range data coincided, both inside and outside of the IUCN (Schipper et al. 2008) and NatureServe (Patterson et al. 2003) range polygons. We used t-tests to compare the number of species correctly predicted for each site and the number of sites correctly predicted for each species by the two range polygon datasets.

We assessed overlap of the two range datasets using Morisita's overlap index [$O = 2 \sum(x_i y_i) / (\sum x_i^2 + \sum y_i^2)$, Morisita, 1959, cited in Horn, 1966] in two ways. First, x_i and y_i were the proportions of survey sites at which species i was correctly predicted by the IUCN and NatureServe maps, respectively. Second, x_i and y_i were the proportions of the total number of species correctly predicted to occupy survey site i by each of the two species range datasets. Morisita's O varies between 0.0 and 1.0, with higher values indicating greater overlap.

Using a simple regression approach, we tested whether the two sets of range map polygons predicted the occupancy of species with larger geographic ranges better than those with smaller geographic ranges using a one-way ANOVA. We compared survey encounter rates of any given species to the proportion of successful predictions by the two published datasets using pairwise Spearman's correlations. We also used

Spearman's correlations to compare species' home range size with their mean encounter rates and the proportion of sites at which they were detected.

Species nomenclature follows Groves (2005), as the IUCN and NatureServe datasets differed in their treatments of species names.

Results

Field surveys

Over 2,000 km of line-transect census walks were conducted in the 23 forest sites (mean 86.5 ± 48.0 km SD per site, Table 1). Ten of Madre de Dios (MDD)'s 12 diurnal primate species (Table 2), plus black-headed night monkeys (*Aotus nigriceps*), were detected in at least one transect. The range maps predicted Goeldi's marmoset (*Callimico goeldii*) and pygmy marmoset (*Callithrix (Cebuella) pygmaea*) to be present throughout MDD (IUCN 2008, Patterson et al. 2003). Our failure to detect these two species may reflect their high degree of habitat specificity or low detectability due to their cryptic nature. In addition, night monkeys (*A. nigriceps*) were rarely detected during diurnal surveys. We therefore excluded these three species from the analysis.

Species occupancy

Overall, the IUCN and NatureServe range polygon datasets did not differ in correctly predicting either the number of species at each survey site (t=1.76, *df*=44, p=0.09, Table 1) or the number of sites occupied by each species (t=0.52, df=18, p=0.61). Values of Morisita's overlap index between the two datasets supported this result, indicating high overlap in the proportion of correct predictions of both the sites occupied by the 10 primate species (O=0.85) and the number of species detected at the 23 survey sites (O=0.98).

Table 2. Geographic ranges (IUCN + NatureServe) and regional occupancy data for 10 analyzed primate species, with their respective percentages of correct predictions of species occupancy. Species are ordered by their geographic range size.

Species / Common name	Geographic Range (km^2)	% of range in MDD	IUCN status	Home range (ha)	% sites present (n=23)	IUCN (%)	Nature Serve (%)
Cebus apella Tufted (Brown) capuchin	6,194,345	1.38	LC	80[1]	100.0	100.0	100.0
Cebus albifrons White-fronted capuchin	3,724,795	2.27	LC	150[1]	69.6	69.6	69.6
Ateles chamek Peruvian spider monkey	2,466,828	1.95	EN	150-250[3]	91.3	21.7	91.3
Saguinus fuscicollis Brown-mantled (Saddle-back) tamarin	1,735,472	4.74	LC	30[1]	87.0	87.0	91.3
Lagothrix cana Grey woolly monkey	1,383,941	5.06	EN	108-124[4]	30.4	43.5	34.8
Saimiri boliviensis Bolivian squirrel monkey	1,378,488	6.14	LC	250[1]	87.0	87.0	87.0
Pithecia irrorata Rio Tapajós (Bald-faced) saki	1,309,981	3.64	LC	37[5]	47.8	65.2	56.5
Alouatta sara Bolivian red howler	408,156	13.41	LC	182[6]	87.0	13.0	73.9
Callicebus brunneus Brown titi	245,043	20.00	LC	2-12[2,7]	87.0	65.2	21.7
Saguinus imperator Emperor tamarin	234,430	21.41	LC	30[1]	39.1	82.6	73.9

* LC=Least Concern, VU=Vulnerable, EN=Endangered. MDD=Madre de Dios department, Peru. Sources for home range data: 1= Terborgh 1983; 2= Wright 1986; 3= McFarland Symington 1988; 4= DiFiore 2003; 5= Palminteri, unpublished data; 6= Palacios and Rodriguez 2001; 7= Lawrence 2007.

Overall coincidence between the survey data and range map prediction was not significantly higher for species with larger geographic ranges for either the IUCN ($F_{1,8}$=1.27, p=0.29) or the NatureServe ($F_{1,8}$=2.98, p=0.12) dataset. Both range maps did match completely with survey results of one species, the wide-ranging brown capuchin (*Cebus apella*, Figure 2, Table 2).

Overestimation:

Both the IUCN and the NatureServe range polygons overestimated the occurrence of seven of the 10 primates (Figure 2, Inside-Absent), most particularly *C. albifrons*, *L. cana*, and *P. irrorata*. *C. albifrons* was predicted to occur throughout MDD by both the IUCN and NatureServe datasets but was absent at seven of the 23 sites. While *L. cana* was predicted to occur at 21 (IUCN) and 23 (NatureServe) sites, it was detected at only seven sites (Figure 1, sites 1-5, 7,11).

Underestimation:

Each range map dataset also underrepresented areas of occurrence of four species (Figure 2, Outside-Present). The IUCN dataset excluded the range of *A. sara* from MDD almost completely, and it terminated the range of *A. chamek* in the northern part of MDD department, yet both of these species are common throughout MDD, and each was detected in at least 20 forest sites. In contrast, the older NatureServe ranges for these two species coincided with survey results at 74-90% of sites, but the NatureServe range for *C. brunneus* excluded the species from 18 of the 20 sites at which it was detected.

We examined whether the population abundance of any given species affected the degree to which its site occupancy could be predicted. However, we found no significant correlation between species-specific encounter rates (groups per 10 km of census walks) and the proportion of overall correct predictions by either the IUCN (R_s=0.055) or NatureServe range maps (R_s=0.598, p>0.05 in both cases). Correlation between the NatureServe prediction of species presence and species' encounter rate was just significant (R_s= 0.648, p=0.043).

Species' home range size (Table 2) did not correlate with mean encounter rate (R_s=0.109), number of sites found (R_s=0.241), or the proportion of correct predictions by either IUCN (R_s=-0.248) or NatureServe (R_s=0.310, p>0.05 in all cases).

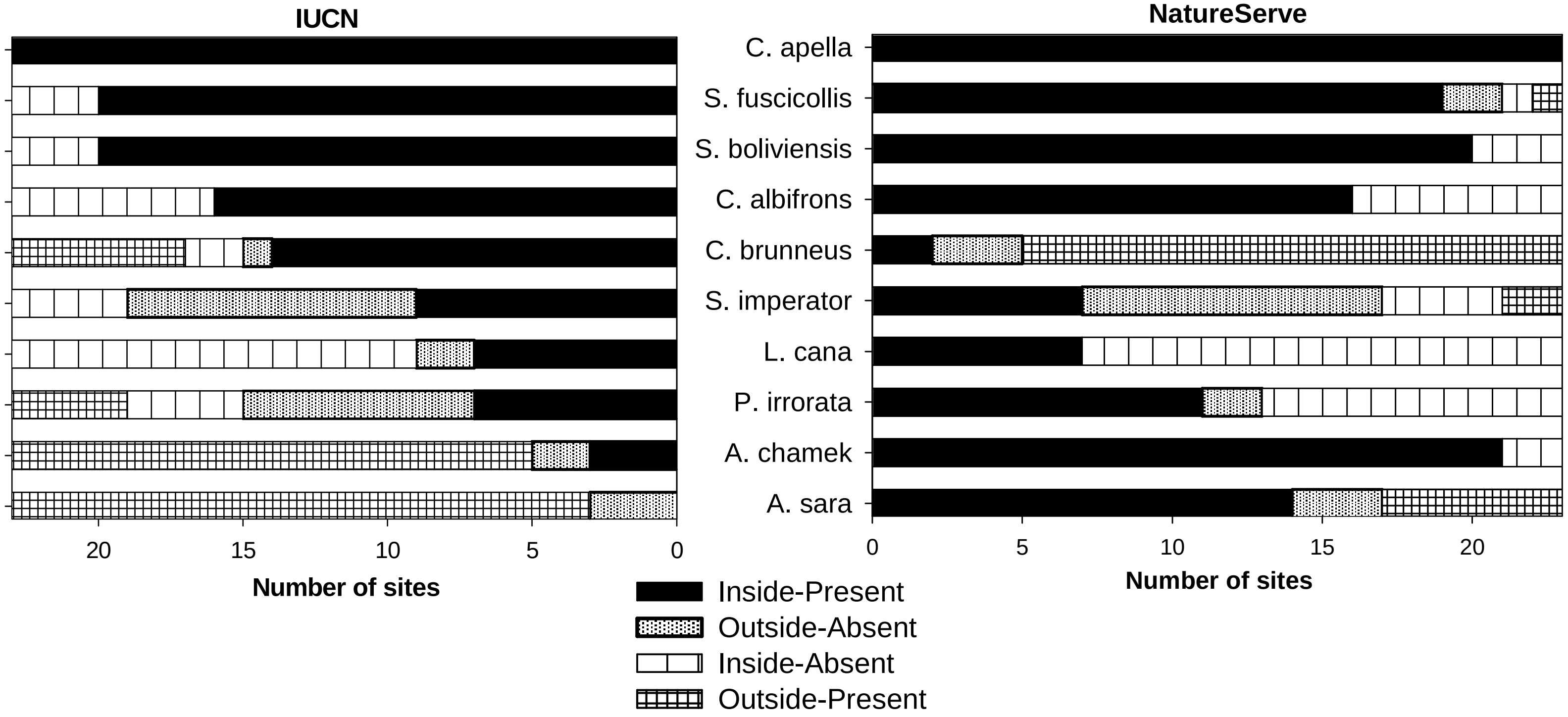

Figure 2. Number of survey sites (n=23) in Madre de Dios, Peru at which primate species were either present or absent, both inside and outside their respective predicted range polygons. Inside-Present and Outside-Absent represent correct predictions of species' occupancy records. Species are ordered by the number of sites at which the IUCN range correctly predicted their presence, from the best to the worst fit.

Discussion

Range maps as tools for conservation planning

Schipper et al. (2008, supplemental material) describe the IUCN range map data as sufficiently accurate to evaluate global spatial patterns of mammalian distribution but warn that, by their coarse-scale nature, these maps may overestimate species ranges. Our study supports this caveat in demonstrating the relatively poor fit between published range maps and presence/absence data from field surveys, even for a relatively well-known taxonomic group. Only one species, *C. apella*, was present along all MDD transects within its expected range boundary. Mismatches between survey data and range boundaries for the remaining species varied from 15% to 80% of the cases and included both overestimation and underestimation. For some species, particularly *C. brunneus*, the 2008 IUCN range maps overlapped more with survey data than the maps generated previously by NatureServe (Patterson et al. 2003). For *A. chamek* and *A. sara*, however, the IUCN range polygons severely underestimated their real-world occupancy. Any analysis of species protection status using these polygons would exclude protection afforded by the Manu and Bahuaja-Sonene National Parks, as well as additional reserves in central Peru and northern Bolivia (Figure 1).

Why false positives?

Sites at which the range maps predicted an undetected species to be present (Inside-Absent, Figure 2) are of particular conservation concern, as inclusion in the range implies that the area supports the species when, in fact, it may not. Various factors might limit the presence of a species within its predicted range (Brown et al. 1996) thereby resulting in such Type II errors (“false positives”) between range and survey data.

Range boundary edges:
The difficulty for range maps to accurately capture changes in species occupancy occurring at peripheral parts of their geographic ranges might explain some of the discordance between survey data and range maps. The consistency of species occupancy tends to decrease at the edges of their geographic ranges (Brown et al. 1996) and may

also change over time (Gaston 2003). Therefore, users of range maps for conservation planning or other purposes should take into consideration the likelihood of inaccuracies when using data from range boundary areas.

Dispersal barriers:

Another potential source of discordance may be failure of the range maps to take into account potential physical barriers to dispersal. The role of rivers as dispersal barriers is still under debate, with studies both supporting (Ayres and Clutton-Brock 1992, Peres et al. 1996) and challenging (Gascon et al. 2000) the impact of rivers on gene flow. East of the Andes, the Madre de Dios river system appears to limit the distribution of several primate species. Two species- *P. irrorata* and *S. imperator*- were absent south of the main Madre de Dios River channel (Figure 1). *L. cana* was absent on the south side of the east-west arch formed by the Madre de Dios River and its major tributary, the Inambari River, where NatureServe predicted it would occur. Both the upper Madre de Dios and the Inambari are braided, rather than meandering, rivers and therefore lack the process of avulsion, in which lateral river channel migration, coupled with meander cut-off dynamics, shift resident populations across opposite banks of the same river (Puhakka et al. 1992, Hamilton et al. 2007). The absence of avulsion may greatly elevate the effectiveness of fluvial barriers for arboreal species such as primates. The IUCN dataset captured the influence of this process on regional primate distribution by cropping the ranges of *P. irrorata* and *L. cana* at the Inambari and lower Madre de Dios rivers. Future range descriptions should pay close attention to species occupancy on opposite banks of rivers, particularly those with stable or wide braided channels, within range polygons.

Habitat specialization:

Species-specific patterns of habitat selection may also confound the use of coarse-scale range polygons because they may create large voids in the distribution maps, particularly for habitat-specialists. For instance, both IUCN and NatureServe range maps predicted *C. albifrons* to occupy sites throughout MDD, yet this species was absent from all three higher elevation sites (sites 11-13, Figure 1), as well as five additional higher-elevation sites surveyed by Kirkby (2004), suggesting an avoidance of higher-elevation forests.

Each of the primate species we surveyed in MDD used both floodplain and *terra firme* habitats. In contrast, two species that were not included in the analysis- *C. pygmaea* and *C. goeldii*- are known to exhibit high levels of habitat specialization (Peres 1993, Porter 2006). These rare species were predicted to occur at virtually all sites surveyed, yet *C. pygmaea* is known for only a small portion of Cocha Cashu Biological Station within Manu National Park (less than 2% of a 1000 ha study area: Terborgh 1983; Endo et al. 2009). While *C. goeldii* has been recorded regularly during line-transect surveys in northern Bolivia (Porter 2006, Buchanan-Smith 2000, Christen and Geissman 1994), reports of its presence at sites in MDD are extremely rare (Terborgh 1983), anecdotal, or limited to general species lists (Solari et al. 2006, Pitman 2008). The applicability of putative range maps for species with highly patchy distributions even in apparently suitable habitat, like these small-bodied primates, is even more questionable. Greater habitat specialization among other taxa, such as smaller vertebrates, invertebrates or plants, may further limit the applicability of coarse-scale range maps for regional conservation of these taxa.

Hunting pressure:

The sites used in this study had been exposed to limited or no hunting pressure. Therefore, species absences were not likely to have resulted from over-hunting. For example, both *A. chamek* and *A. sara* are widely hunted species, yet they were found at over 20 sites. Three of the seven sites occupied by *L. cana*, another preferred game species, were hunted sites (sites 1,-2, and 11, Figure 1).

Survey underestimation:

The potential for false absences due to non-detection is unlikely because the survey efforts (kilometers walked) used here were comparable with the distances surveyed elsewhere (Branch 1983, Christen and Geissman 1994, Peres 1997, Galetti et al. 2009) and thus considered to be sufficient to detect presence of the 10 analyzed species in our survey areas. Additionally, we found no correlation between species' home range size and encounter rate or between either home range size or encounter rate and the percent of correct predictions of their occupancy by the published datasets. In any case, failure to detect cannot explain the severe occupancy underestimation of the genera *Alouatta* and *Ateles* by the IUCN ranges, or *Callicebus* by the corresponding NatureServe range.

Use of range maps at the landscape scale

Despite widespread recognition that species range maps imply a uniform distribution that often severely overestimates true occupancy of these ranges (Brown et al. 1996, Schipper et al. 2008), range polygons continue to be a staple of broad-scale conservation planning (Rodrigues et al. 2004, Burgess et al. 2006, Hernandez et al. 2008, Vázquez et al. 2009). Positional data on primates are far more abundant than are data on lesser-known taxa (Jetz et al. 2008), yet this study shows that they still are insufficient to predict individual species distributions within a landscape. Overestimation and underestimation of species distributions occurred using both NatureServe and IUCN range data. Thus, even for relatively well-studied taxa like primates, current species range polygons run the risk of being too coarse to be relied upon for landscape-level conservation planning. Hurlbert and White (2007) and Jetz et al. (2008) reached similar conclusions based on their analysis of bird distributions.

On-the-ground sampling is necessarily taxa-specific (i.e. line-transect surveys for large mammals, live-trapping for small mammals) and therefore a relatively intensive method of assessing regional accuracy of species range maps. Initiating mammal community surveys at existing research sites may minimize their cost, though such sites are rarely randomly selected or representative of a region's biodiversity. The accuracy of range maps might be enhanced by the use of species gazetteers (Hernandez et al. 2008), which might expand the number of sites at which some species were confirmed to be present, though it would not contribute to knowledge of species absence. Use of long-term monitoring (LTM) data has been suggested to improve species distribution models, particularly for more specialist species (Brotons et al. 2007). Another potentially cost-effective alternative mechanism for updating and refining these maps may be to combine species distribution models with regional expert input, as NatureServe has initiated for endemic species in the Andes-Amazon region (Young, ed. 2007, Hernandez et al. 2008).

Our results point to the need to make regional ecological knowledge, as well as existing field locality and species ecology data, more available for conservation planning and species distribution modeling, so that so-called, “fine-scale” species distribution data are sufficiently fine scale for conservation use.

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Chapter 3: Regional-scale heterogeneity in primate community structure at multiple undisturbed forest sites across south-eastern Peru

Abstract

The forests of western Amazonia support high site-level biological diversity, yet regional community heterogeneity is poorly understood. Using data from line transect surveys at 37 forest sites in south-eastern Peru, we assessed whether local primate assemblages are heterogeneous at the scale of a major watershed. We examined patterns of richness, abundance and community structure as a function of forest type, hunting pressure, land-management regime and geographic location. The primate assemblage composition and structure varied spatially across this relatively small region of Amazonia (≈ 85,000 km^2), resulting from large-scale species patchiness rather than species turnover. Primate species richness varied among sites by a factor of two, community similarity by a factor of four and aggregate biomass by a factor of 45. Several environmental variables exhibited influence on community heterogeneity, though none as much as geographic location. Unflooded forest sites had higher species richness than floodplain forests, although neither numerical primate abundance nor aggregate biomass varied with forest type. Non-hunted sites safeguarded higher abundance and biomass, particularly of large-bodied species, than hunted sites. Spatial differences among species assemblages of a relatively generalist taxon like primates in this largely undisturbed forest region imply that community heterogeneity may be even greater in more species-rich taxa, as well as in regions of greater forest habitat diversity.

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Introduction

The patterns and drivers of regional-scale heterogeneity of biological communities in the mega-diverse western Amazon basin remain poorly understood (Terborgh and Andresen 1998, Tuomisto *et al*. 2003), and assessing the level of meso-scale community heterogeneity within spatially dominant habitat types, such as unflooded (terra firme) and floodplain forests, is a major challenge (Vormisto *et al*. 2004). There has been considerable discussion of patterns of Amazonian plant community heterogeneity at the meso-, or landscape, scale (Hubbell 2001, Phillips *et al*. 2003, Pitman *et al*. 2001, Tuomisto *et al*. 1995) but comparatively little on patterns of vertebrate diversity.

The composition and structure (relative species abundances) of Amazonian primate communities have been studied at local scales (Bennett *et al*. 2001, Emmons 1984, Haugaasen and Peres 2005a, Peres 1993, Soini 1986) and at the regional scale ($>10^5$ km^2, Freese *et al*. 1982, Peres 1997). Little is known, however, about patterns of variation in Amazonian primate community structure at the meso-scale (10^3–10^5 km^2), and the only published primate surveys at this scale (Buchanan-Smith *et al*. 2000, Christen and Geissmann 1994, Heymann *et al*. 2002) did not quantify species abundance or biomass. As sessile primary producers, plants would be expected to be sensitive to fine-scale changes in abiotic conditions (Fine *et al*. 2004, Tuomisto *et al*. 1995) and may also experience dispersal limitation (Hubbell 2001), whereas vertebrate taxa such as primates may be able to adjust to meso-scale variation in resource availability with limited change in their community composition and structure. We might therefore expect primate communities to be stable with respect to microhabitat change or geographic distance at spatial scales ranging from hundreds of thousands to millions of hectares.

To test this hypothesis, we synthesized published and unpublished primate species composition and aggregate abundance and biomass data from surveys collected across the department of Madre de Dios (MDD) in south-eastern Peru and quantified community spatial heterogeneity. The region encompasses millions of hectares yet represents only a fraction of 1% of the Amazon basin. This scale is well below that typical for turnover in Amazonian primate species (http://www.iucnredlist.org/mammals/data_types, Patterson *et al*. 2003), thereby allowing us to measure community heterogeneity, independent of species replacements.

While primate species richness is only a fraction of that of plants, south-western Amazonian primate communities are among the world's most diverse (Emmons 1999, Terborgh 1983) and may be sufficiently species-rich to display variability in community structure at this scale. To assess how habitat heterogeneity may affect primate communities across the region's relatively intact tracts of tropical forest, we examined patterns of primate community similarity as a function of geographic location, sub-basin position, location north or south of the Madre de Dios River (to assess its potential as a dispersal barrier), and major forest type (terra firme vs floodplain).

While the forest of MDD remains largely intact and therefore appropriate as a landscape to assess natural community heterogeneity, a rapidly growing human population has begun to impact primate populations at sites throughout the basin. To investigate how hunting interplayed with natural community heterogeneity, we also assessed community composition and structure as a function of hunting pressure and forest management regime. Based on previous studies, we expected that hunters would selectively remove the most abundant large-bodied species (Ohl-Schacherer *et al*. 2007, Peres 2000, Schulte-Herbrüggen and Rossiter 2003). Based on evidence suggesting density undercompensation of non-hunted medium-bodied species in moderately hunted sites elsewhere in Amazonia (Peres and Dolman 2000), we predicted that abundances of smaller and rarer species would increase at hunted sites to compensate for hunting-induced reduction of relatively abundant larger species. We further predicted that hunting-induced population declines in larger species would increase the structural heterogeneity of primate communities.

Methods

Study area

We compiled data from line-transect surveys at 37 forest sites in the Madre de Dios (MDD) watershed of south-eastern Peru (Figure 1, Appendix), 12 of which were conducted by SP. This transition region between the Andean foothills to the west and the vast Amazon lowlands to the north and east encompasses an area of approximately 85,000 km^2. Seven of the sites lie south of the main channel of the Madre de Dios River, while the rest were grouped into four additional subregions, all north of the river. Annual rainfall averages 2200-2700 mm, with a distinct dry season between May and

September (Botanical Research Institute of Texas (BRIT) 2007 http://atrium.andesamazon.org, Osher and Buol 1998). Elevation ranges from 190 to 440 m asl along an east-to-west gradient. All sites were located within largely intact primary lowland rain forest, as the MDD department retains over 90% forest cover (Phillips *et al*. 2006).

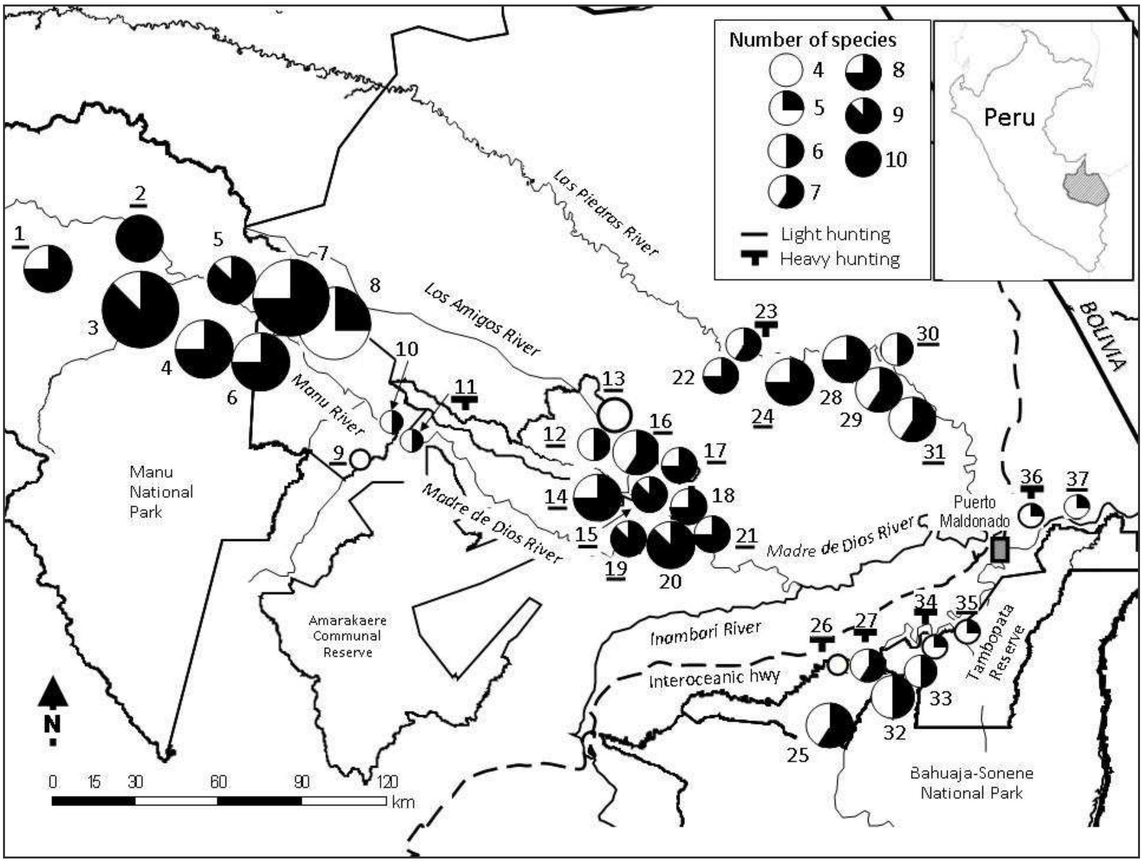

Figure 1. Study area in Madre de Dios, south-eastern Peru, including the 37 survey sites considered in this study (Appendix 1). Pie charts indicate primate species richness, whereas symbol sizes are proportional to the aggregate biomass of each primate assemblage (0-50 kg, 50-100 kg, 100-300 kg, 300-500 kg, >500 kg per 10 km surveyed). The dashed line indicates the Inter-Oceanic Highway, which is currently being paved.

The basin’s two predominant habitat types are elevated, unflooded terra firme forest, and supra-annually flooded, well-developed floodplain forest (Terborgh and Andresen 1998, Thieme *et al*. 2007). Floodplain forests of the south-western Amazon are inundated far less frequently and for much shorter periods than those of the central and western Amazon, though they still receive nutrient-rich suspended sediments from the Andes, rendering their soils more productive than those of surrounding terra firme forest

(Hamilton *et al*. 2007, Salo *et al*. 1986, Terborgh 1983). The percentage of terra firme forest at our survey sites ranged from 0% to 100%. Transect lines at 16 sites were established in a single known forest type; for all others, we overlaid the transect lines with a forest cover map in a GIS to calculate the percentage of terra firme forest along transects. Two less common habitat types — *Guadua* bamboo thickets in upland forest and *Mauritia flexuosa*-dominated palm swamps in floodplains — also occur in this region but were excluded from the surveys.

Approximately 37% of the study region is registered under strict protection, while another 8% is managed for sustainable use (MINAM 2010), 6% is privately managed for restricted-use activities that preclude hunting (conservation, Brazil nut and tourism concessions, BRIT 2007 http://atrium.andesamazon.org, E. Tatum-Hume pers. comm., MINAM 2010, Sociedad Peruana de Derecho Ambiental (SPDA) unpubl. data), and 11% is within an uncontacted indigenous reserve. However, de facto land-use restrictions vary across all land management categories. For example, subsistence hunting by Matsigenka Indians is permitted within the otherwise strictly protected Manu National Park. In addition, some areas of restricted use were heavily hunted prior to reserve establishment and immediately prior to our sampling. Remaining areas, including areas of contacted indigenous groups, face unrestricted (direct) human resource use and have been subjected to varying levels of hunting pressure.

Field surveys

Primate communities at all sites were surveyed using line transects of 2-7 km in length, between 1997 and 2007, with observers systematically alternating transects to avoid observer bias. Transects were surveyed an average of 15.6 (± 11.4 SD) times each. Diurnal surveys were conducted on mornings with no precipitation from 06h00 to 11h00, thereby excluding the night monkey (*Aotus nigriceps*), the only nocturnal primate in the region. For each primate group detected, we recorded the time, species identity, group size, sighting location, perpendicular distance from the transect, and detection cue. Field procedures used in our surveys are described in detail in Peres (1999a). For the purpose of analysis, individual transects within a subregion were considered unique sites if they represented a unique combination of river bank, habitat type and hunting pressure. Total survey effort per site ranged from 25 to 315 km (mean 123 km, Appendix 1), with a cumulative survey effort of 4537 km across 81 individual transects at 37 sites. Sites were grouped into five subregions [corresponding to the

Manu, Los Amigos, Las Piedras and Tambopata sub-basins and a section of the main channel of the MDD River (North-MDD subregion), Figure 1], as well as two main forest habitats, three levels of hunting pressure and three forest management regimes.

Data analysis

We used a kilometric index of groups encountered per 10 km walked (elsewhere referred to as encounter rate, sensu Buckland *et al*. 2001) to control for overall differences in sampling effort (Peres 1997). Due to small sample sizes for some species and variability in perpendicular distances that prevented pooling data among sites, our data did not meet the minimum prerequisites for estimation of density (Buckland *et al*. 2001) for all sites. Relative estimates of animal abundances were therefore used to allow comparison of community heterogeneity across the study region. We quantified a relative measure of species abundance at each site (hereafter, abundance) by multiplying the site-specific number of groups of each species encountered per 10 km walked by its mean group size, using values from all reliable group counts at each site for which data were available (Galetti *et al*. 2009). Data for one site (Boca Manu) were derived from published density estimates of three size-graded groupings of primate species (Nuñez-Iturri 2007, Nuñez-Iturri and Howe 2007, Terborgh *et al*. 2008). We multiplied the proportion of each species in its size class across three hunted sites in MDD by the abundance estimate of the same size class at Boca Manu to derive the abundance estimates for individual species at this site. For each site, we also calculated the aggregate relative biomass of each species (hereafter, biomass: Galetti *et al*. 2009) by multiplying the mean adult body mass of each species in the region by its abundance value at each site.

To estimate the extent of spatial structure in our data, we ran a partial spatial regression using the Spatial Analysis in Macroecology software (SAM, v 4.0, Rangel *et al*. 2010) with hunting pressure, forest habitat type, subregion, latitude and longitude to identify the amount of variance in species richness, aggregate abundance and aggregate biomass explained by geography and environmental variables, respectively.

We compared species richness of survey sites north and south of the MDD River using a t-test. We evaluated species richness and $\log_{10}$-transformed aggregate abundance and biomass at sites with different forest types (expressed as percentage of terra firme forest), management categories, hunting pressure (three ordinal categories based on information from landowners, researchers, guides, forest guards, published and unpublished reports and personal observations; Peres 2000), and subregions, entering the predictors both individually, using one-way ANOVA, and in combination, using a set of generalized linear mixed models (GLMMs). GLMMs for species richness and aggregate abundance/aggregate biomass used a Poisson and a Gaussian error structure, respectively. Given the wide variation in survey effort, we also included census effort (km walked) as a covariate in each set of models. Subregion was strongly correlated with elevation ($r = -0.83$), longitude ($r = -0.77$) and latitude ($r = 0.86$, $P < 0.01$ in all cases). Subregions thus served as both a measure of geographic location and as a proxy of environmental factors beyond the scope of this study, such as forest structure, tree species composition and soil types, all of which may affect primate assemblage structure. To account for possible effects of geography on community structure, we therefore treated subregion in each set of GLMM models as a random factor, within which the environmental covariates varied.

Following Burnham and Anderson (2002), we calculated the AIC, corrected for small sample size (AIC_c), for candidate GLMMs of each of the three response variables (species richness, aggregate abundance ($\log_{10} x + 1$), and aggregate biomass ($\log_{10} x + 1$)) using the AICcmodavg package (Mazerolle 2009) within the R statistical framework (R Development Core Team, v. 2.10.1). In each case, models were ranked according to their likelihood of being the best in each set of candidate models by rescaling the AIC_c values such that the model with the lowest AIC_c had a value of 0, i.e. $\Delta i = AIC_i - AIC_{min}$. Models for which $\Delta i > 2$ were considered unlikely to be appropriate (Burnham and Anderson 2002). We also computed Akaike weights (ω_i) for each model such that the sum of weights for all models for each response variable equals 1. These weights are approximate probabilities that a given model is the best model in its candidate set, so the values also provide an estimate of model selection uncertainty (Burnham and Anderson 2002).

We examined differences in abundance and biomass of individual species with respect to the same predictor variables using Kruskal–Wallis tests. To examine the likelihood of density compensation, we ran Spearman correlations among the abundance and biomass values of individual species.

We examined heterogeneity in primate species composition and abundance using Primer (v.6, PRIMER-E Ltd., Plymouth, UK). To evaluate similarities in species composition among sites, we constructed a pairwise similarity matrix of species occupancy, based on the Jaccard similarity index using species presence/absence data. We used a partial Mantel test (zt software, Bonnet and Van de Peer 2002) to examine pairwise species similarity values among sites located on the same side (either north or south) of the MDD River with those located on opposite sides of the river while controlling for geographic distance.

We assessed spatial patterns of community structure using non-metric multidimensional scaling (NMDS, Clarke and Warwick 2001). We initially square root--transformed the abundance and biomass data for each species at each site, to decrease over-dominance of abundant species, and converted these two datasets into separate pairwise similarity matrices based on the Bray-Curtis similarity coefficient, to exclude treatment of joint absences as a sign of similarity. We then tested whether patterns of community structure differed among sites as a function of forest type, hunting pressure, restrictions on human use, and subregion using Analysis of Similarities tests (ANOSIM, Clarke and Green 1988). The ANOSIM statistic (R) behaves like a correlation coefficient, ranging from –1 to +1, with significantly positive R-values implying that samples (sites) within groups are more similar than expected by chance. We examined the relative importance of the four main environmental variables, as well as geographic distance among sites, in determining primate community similarity, using Primer’s BIO-ENV function (Clarke and Warwick 2001) and a simple Mantel test, respectively. We also conducted partial Mantel tests to examine the significance of each of the environmental variables on community composition and structure, while controlling for pairwise distances between sites.

Results

Species richness and composition

We recorded 10 of the 13 primate species known to occur in Madre de Dios (Groves 2005, Table 1) in sufficient numbers to conduct analyses. Observations of the night monkey (*Aotus nigriceps*) were excluded from the analysis because detectability of this species is inconsistent during daylight hours, and Goeldi's marmoset (*Callimico goeldii*) and pygmy marmoset (*Cebuella* (*Callithrix*) *pygmaea*) were not recorded at any of the sites. We recorded between four and 10 primate species at each site (Figure 1, Appendix 1), with 10 species recorded at only one hunted site (Tayakome) within Manu National Park. Only one species, brown capuchin (*Cebus apella*), was found at all sites (Table 1), whereas three species—woolly monkey (*Lagothrix cana*), emperor tamarin (*Saguinus imperator*) and bald-faced saki (*Pithecia irrorata*)—were recorded at only 6, 12 and 18 sites, respectively, all north of the MDD river.

Table 1. Summary of 10 primate species occurring at 37 survey sites considered in this study, including mean (± SD) body mass, groups per 10 km walked, numerical abundance (individuals per 10 km walked) and biomass (kg per 10 km walked). Species are ordered by body mass, from smallest to largest. * Mean body mass values derived from the following sources (as available): [1] Clutton-Brock and Harvey 1977, [2] Emmons 1984, [3] Robinson and Redford 1986, [4] Ayres *et al*. 1991, [5] Mittermeier 1991, [6] Peres 1993, [7] Emmons 1997.

Species	English name	Body mass (kg) *	Number of sites found	Groups per 10 km	Abundance	Biomass
Saguinus fuscicollis Spix	Saddle-back tamarin	0.38	36	1.4 ± 1.0	7.5 ± 6.2	2.9 ± 2.4
Saguinus imperator Goeldi	Emperor tamarin	0.40	12	0.2 ± 0.4	0.9 ± 2.1	0.4 ± 0.8
Saimiri boliviensis I.Geoffroy and de Blainville	Bolivian squirrel monkey	0.84	31	0.5 ± 0.5	9.2 ± 13.3	7.7 ± 11.1
Callicebus brunneus Wagner	Brown titi	0.84	32	0.8 ± 0.8	2.1 ± 2.2	1.7 ± 1.8
Pithecia irrorata Grey	Bald-faced saki	2.35	18	0.3 ± 0.5	1.1 ± 1.7	2.6 ± 4.1
Cebus albifrons Humboldt	White-fronted capuchin	2.75	25	0.4 ± 0.5	3.9 ± 5.7	10.6 ± 15.6
Cebus apella Linnaeus	Tufted (Brown) capuchin	2.97	37	1.5 ± 0.8	7.6 ± 4.3	22.5 ± 12.9
Alouatta sara Elliot	Bolivian red howler	6.67	33	0.6 ± 0.5	2.5 ± 2.3	16.7 ± 15
Ateles chamek Humboldt	Peruvian spider monkey	8.13	29	1.7 ± 2.2	7.8 ± 12.1	63.4 ± 98.7
Lagothrix cana E. Geoffroy (in Humboldt)	Grey woolly monkey	10.20	6	0.4 ± 1.1	2.3 ± 6.9	23.4 ± 69.9

Sites north of the Madre de Dios River were thus more species-rich (mean ± SD = 7.3 ± 1.6; range = 4–10 species) than those south of the river (5.7 ± 1.1; range = 4–7 species, t-test: t = –2.47, df = 35, P = 0.018). Despite the absence of three species from all sites south of the river, pairwise similarity in species composition was not correlated with river bank once we controlled for geographic distance among sites (partial Mantel; r = –0.051, P = 0.278); geographic distance itself correlated weakly with species composition (simple Mantel: r = –0.164, P = 0.020).

Species richness was highest in the Amigos and Manu subregions ($F_{4,32}$ = 3.05, P = 0.03, Table 2, Appendix 1) and was positively correlated with proportion of terra firme forest (r = 0.463, P = 0.004, N = 37 sites). Although overall species richness did not differ among management regimes or levels of hunting pressure (one-way AVOVA, P > 0.05 in both cases), heavily hunted sites had fewer of the three largest species ($F_{2,34}$ = 4.44, P = 0.02) than the subset of 15 non-hunted sites, and at least one large-bodied species was likely driven to local extinction at five of the hunted sites (Sites 1, 26, 34, 36 and 37, Figure 1 and Appendix 1). Community composition was consequently more similar among the 15 non-hunted sites (mean pairwise similarity = 74.1% ± 13.1%, range = 38%–100%) than among the 22 hunted sites (mean similarity = 57.7% ± 16.6%; range = 25%–100%; t = –8.400, df = 228, P < 0.001).

Aggregate abundance and biomass

Primate abundance and biomass estimates across all 37 sites were highly variable (Figure 2, Table 2). We encountered between 1.7 to 17.8 groups per 10 km (mean ± SD = 7.9 ± 4.4) across all survey sites, while aggregate abundance ranged from 15.5 to 164.5 individuals per 10 km walked (Appendix 1). Aggregate biomass varied even more than abundance, ranging from a low of 14 kg per 10 km in a hunted site along the MDD River (Reserva Amazonica) to 615 kg per 10 km in a non-hunted site in Manu (Cumerjali); even among non-hunted sites, biomass varied by more than an order of magnitude (34-615 kg per 10 km). Aggregate primate abundance and biomass were higher in strictly protected areas than in zones of direct human use (abundance $F_{2,34}$ = 4.10, P = 0.025, biomass $F_{2,34}$ = 7.85, P = 0.002; Figure 2a), and higher at non-hunted than at hunted sites (abundance $F_{2,34}$ = 9.50, P = 0.0005, biomass $F_{2,34}$ = 7.83, P = 0.002; Figure 2c). Neither aggregate abundance nor biomass varied with the proportion of terra firme forest (P > 0.05 in both cases).

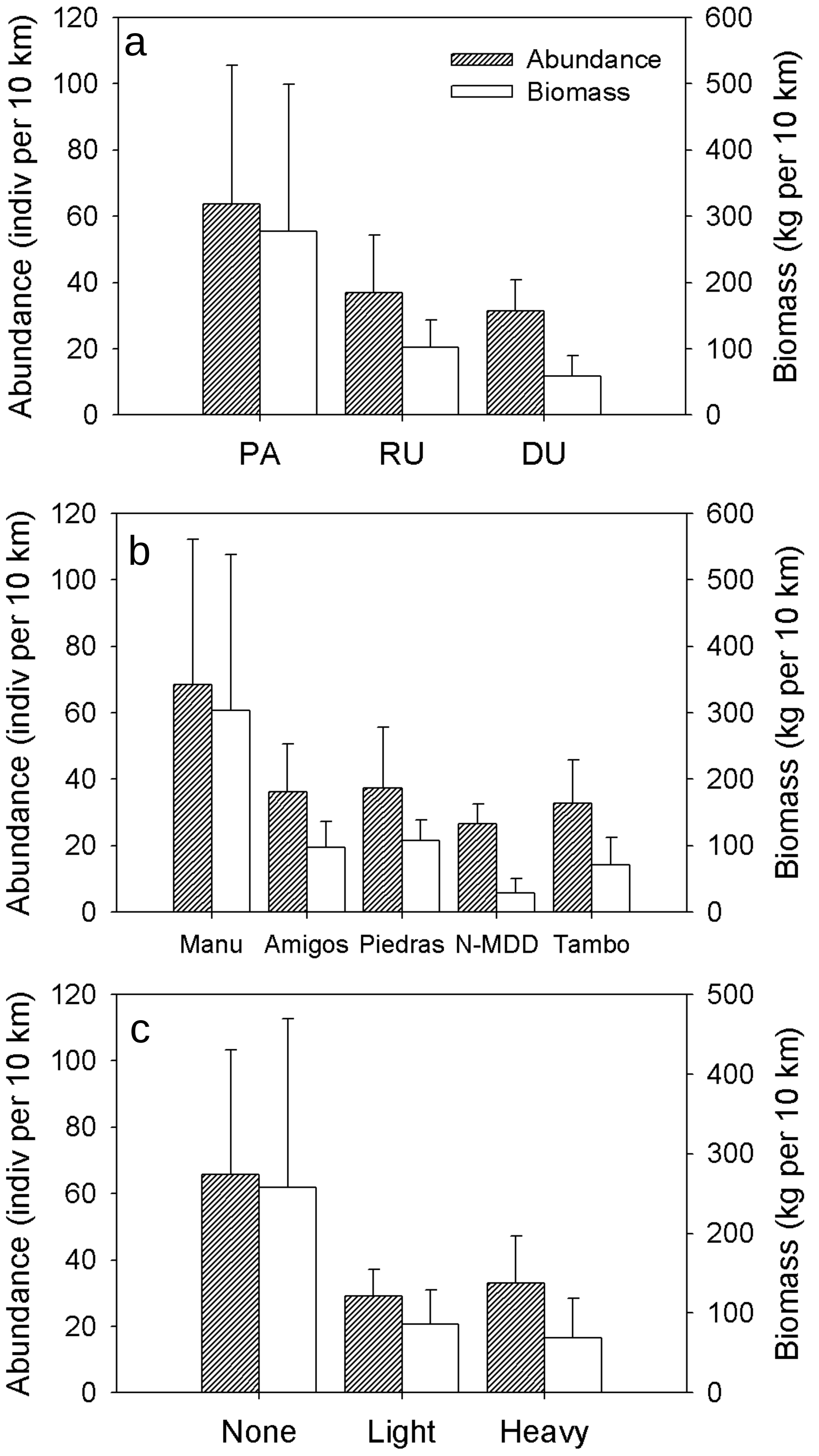

Figure 2. Mean (± SD) aggregate primate abundance (individuals per 10 km walked) and biomass (kg per 10 km walked) values: by land-management category, PA = strictly protected area, RU = restricted forest resource extraction, DU = direct forest resource extraction (a); by subregion, N-MDD = North bank of the Madre de Dios River, Tambo = Tambopata (b); and by level of hunting pressure (c).

Table 2. Summary statistics for mean species richness, aggregate abundance, aggregate biomass and Simpson diversity index (1 - λ') for survey sites across three levels of hunting pressure within each subregion. Tambopata is located south of the Madre de Dios River (all other subregions north of the river).

Subregion	Hunting pressure	Mean species richness	Mean abundance (individuals per 10 km walked)	Mean biomass (kg per 10 km walked)	Mean Simpson index
Manu	overall	7.4	68.4	303.5	0.87
	None	7.6	89.0	424.2	0.88
	Light	7.3	27.6	107.1	0.88
	Heavy	6.0	46.8	47.9	0.77
Amigos	overall	7.7	36.1	97.3	0.90
	None	8.5	48.8	120.7	0.90
	Light	7.5	30.8	81.5	0.90
	Heavy	7.5	39.4	121.5	0.90
Piedras	overall	7.3	37.4	108.0	0.90
	None	7.7	47.4	115.9	0.90
	Light	7.0	31.7	106.0	0.90
	Heavy	7.0	24.7	90.4	0.91
North-MDD	overall	5.0	26.5	29.0	0.79
	Light	5.0	30.8	44.0	0.84
	Heavy	5.0	22.3	14.0	0.75
Tambopata	overall	5.7	32.8	70.8	0.84
	None	6.3	40.7	103.4	0.87
	Light	5.0	15.5	32.1	0.88
	Heavy	5.3	30.8	51.1	0.80

Primate–environment relationships

The partial spatial regression using two environmental variables (hunting, per cent terra firme forest), together with latitude and longitude, to explain species richness and site-level abundance and biomass showed that geographic position was a contributing factor to any explanatory power of the environmental variables. Spatial location contributed 53%-79% of all explained variation in the three response variables and alone accounted for 24% of the total explained variation in species richness, 35.4% of aggregate abundance and 51.2% of aggregate biomass. These values decreased to 0.2%, 13.1% and 28.4%, respectively, when subregion was included as a predictor variable, which supported the nesting of random effects within subregion in the GLMM to help account for the spatial structure identified in the partial spatial regression.

No single explanatory model for species richness was clearly supported. The model including the single covariate, per cent of terra firme forest, was judged to be the best approximating model in the set of seven candidate models, although its Akaike weight of 0.36 suggests considerable model selection uncertainty (Table 3). The simplest models, with hunting pressure as a single covariate, were the only GLMMs supported by the data for both aggregate abundance and biomass. Hunting pressure accounted for over 97% and 85% of the modest amount of overall variance that could be explained in aggregate abundance (R^2 = 24.7%) and biomass (R^2 = 34.5%), respectively.

Patterns of community structure and heterogeneity

Primate community structure was highly variable across all 37 sites (Figure 3), but determinants of the heterogeneity were unclear. Community similarity over all 666 pairwise comparisons ranged from 19% to 90% (mean ± SD =59% ± 12%) using abundance values, and from 16% to 90% (56% ± 15%) using biomass values.

The potential drivers of community structure that we examined were, for the most part, significant but weak predictors of primate community similarity. Primate community structure across MDD could be grouped most clearly by subregion — based on either species abundance (Global ANOSIM $R_{abundance} = 0.248$, $P = 0.001$) or biomass (Global $R_{biomass} = 0.299$, $P = 0.001$, Figure 3). There were significant pairwise differences between most subregions, and differences between North-MDD and both Amigos and Piedras were marked (pairwise $R_{biomass} > 0.9$, $P < 0.05$ in both cases). The Manu subregion differed from the others by the high biomass values for the two largest-bodied ateline primates (spider monkey, *Ateles chamek*, and woolly monkey). Woolly monkeys were recorded only in the Manu subregion, and abundance of spider monkeys was significantly higher in the Manu subregion than in other subregions (Kruskal-Wallis test $H_4 = 10.4$, $P = 0.034$). High abundances of two rarer species (bald-faced saki and emperor tamarin) distinguished the Amigos subregion, while the Piedras subregion was characterized by highly variable abundances of several species.

Table 3. Summary of generalized linear mixed model (GLMM) selection results assessing the association between primate species richness, aggregate abundance, and aggregate biomass and a set of candidate GLMMs, assigning subregion as a random factor (see text and Figure 1). Model fit based on the global model is shown for each response variable as the percentage deviance explained (% dev).

Response variable	**Model description**	**LL**	**K**	**AIC$_c$**	**Δ_i**	**ω_i**	**Cum. ω**
Species richness	%TF	–5.66	3	18.06	0.00	0.36	0.36
% dev = 53.0	Hunt + %TF	–5.10	4	19.45	1.40	0.18	0.55
	Hunt	–6.49	3	19.71	1.66	0.16	0.71
	%TF + Effort	–5.62	4	20.49	2.43	0.11	0.81
	Effort	–7.11	3	20.94	2.89	0.09	0.9
	Hunt + %TF + Effort	–5.03	5	21.99	3.94	0.05	0.95
	Hunt + Effort	–6.42	4	22.08	4.02	0.05	1
Aggregate abundance (log$_{10}$ x + 1)	Hunt	1.33	4	6.60	0.00	1	1
% dev = 36.9	Hunt + %TF	–4.84	5	21.62	15.02	0	1
	%TF	–6.73	4	22.7	16.10	0	1
	Hunt + Effort	–5.52	5	22.98	16.38	0	1
	Effort	–6.90	4	23.05	16.45	0	1
	%TF + Effort	–13.04	5	38.02	31.42	0	1
	Hunt + %TF + Effort	–11.7	6	38.19	31.59	0	1
Aggregate biomass (log$_{10}$ x + 1)	Hunt	–14.2	4	37.7	0.00	1	1
% dev = 50.6	Hunt + %TF	–18.8	5	49.5	11.80	0	1
	%TF	–22	4	53.21	15.51	0	1
	Hunt + Effort	–20.70	5	53.33	15.63	0	1
	Effort	–23.7	4	56.63	18.94	0	1
	Hunt + %TF + Effort	–25.3	6	65.38	27.69	0	1
	%TF + Effort	–28.2	5	68.42	30.72	0	1

For each model, LL = log-likelihood; K = number of estimable parameters, AIC$_c$ = Akaike's information criterion for small sample sizes; Δ_i = the difference between a given model and the best model, in units of AIC$_c$; ω_i = Akaike weight, interpreted as the probability that the model best represents the data. %TF = Percentage of terra firme forest, Hunt = Hunting pressure (None, Light, Heavy), Effort = km of survey effort.

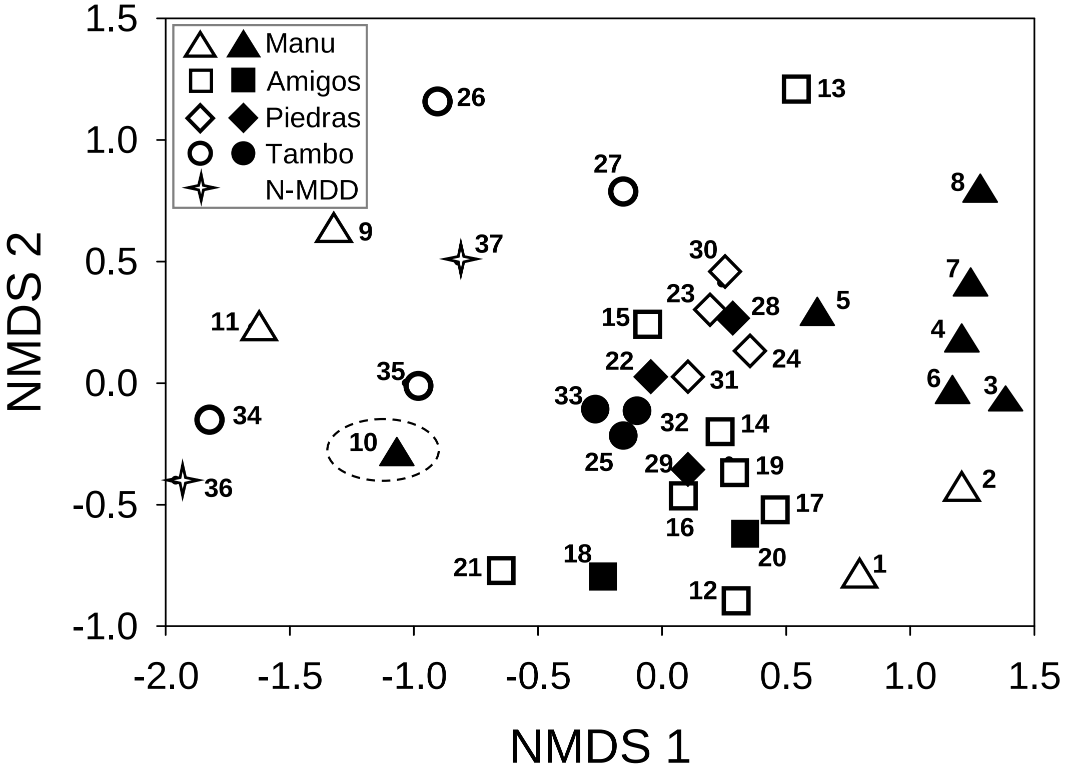

Figure 3. NMDS ordination of the primate community at 37 survey sites coded by location in one of five subregions. Stress = 0.17. Hunting increased community heterogeneity (displayed as relative distance between pairs of sites), both overall and within individual subregions. The grouping of the 15 non-hunted sites (filled symbols) by subregion shows spatial heterogeneity independent of the effects of hunting. Limonal (Site 10) appears as an outlier, and its extreme separation from all other non-hunted Manu sites and its location at the edge of Manu NP suggest that it has likely experienced greater hunting pressure than officially reported. Numbers correspond to site numbers, ordered west to east (Appendix 1). N-MDD = North-MDD; Tambo = Tambopata.

Virtually no difference was detected among sites with different amounts of terra firme forest (Global $R_{abundance} = 0.168$, $P = 0.05$, $R_{biomass} = 0.087$, $P = 0.07$), though communities at sites consisting entirely of either terra firme or floodplain forest were slightly more similar to each other than would be expected by chance (pairwise $R_{abundance} = 0.288$, $P = 0.001$, $R_{biomass} = 0.208$, $P = 0.002$). Hunting pressure and land-management category also had limited effects on similarity (Global $R_{abundance} = 0.148$–0.174, $P < 0.005$; Global $R_{biomass} = 0.146$–0.245, $P < 0.01$), although pairwise differences in community structure between non-hunted and heavily hunted sites were more pronounced (pairwise $R_{abundance} = 0.293$, $P = 0.002$, pairwise $R_{biomass} = 0.304$, $P = 0.06$). As expected, community structure was more similar among non-hunted sites (mean ± SD similarity 61.6% ± 12.7%, range = 29%–90%) than among the 22 hunted sites (mean similarity 52.2% ± 15.6%, range = 20%–83%, $t = -5.067$, $df = 228$, $P < 0.001$).

Higher abundances of large-bodied species separated the communities of protected and otherwise non-hunted sites from those at sites subjected to hunting pressure. Abundances of both the spider monkey and howler monkey (*Alouatta sara*) were significantly higher in non-hunted and strictly protected areas than in hunted sites and areas of direct human use, respectively (Kruskal-Wallis tests, $P < 0.05$ in all cases). Woolly monkey was recorded only within Manu National Park, where indigenous hunting was either light or absent, and the abundance of this species did not differ between these two levels of hunting pressure ($F_{2,8} = 0.610$, $P = 0.457$). Abundance and biomass values of larger-bodied species were not negatively correlated with those of medium- or smaller-bodied species ($P > 0.05$ or positive correlation in all cases), weakening support for density compensation in this region.

The influence of subregion on community structure was evident even among the relatively clustered non-hunted sites (Figure 3). Manu's non-hunted sites sustained outstanding primate biomass, even compared to other non-hunted sites. All Tambopata sites were located south of the Madre de Dios River, thereby lacking at least three species occurring only north of the river. BIO-ENV identified subregion as the most important single variable in explaining community structure using either the abundance or biomass data, though a limited relationship existed between structure and the best combination of variables (subregion + management + hunting, $r_s = 0.325$ using biomass data).

When partial Mantel tests were used to control for geographic position, subregion was no longer a significant predictor of community structure (Table 4). The negligible differences between these results and those of the individual ANOSIM tests indicate that the effects of forest type and hunting pressure on community structure were not confounded by geography. The significant relationship between inter-site distance and levels of community similarity for both abundance and biomass indicates that community structure among nearby sites was more similar than that among sites farther apart, even at this landscape scale.

Table 4. Partial Mantel test results showing relationships between primate community composition and structure and environmental variables, controlling for the effect of geographic distance among survey sites. Community composition is based on similarity in species richness, while structure is based on similarity in abundance or biomass.

	Composition (Richness)		**Structure (Abundance)**		**Structure (Biomass)**	
	r	**P**	**r**	**P**	**r**	**P**
Hunting[1]	–0.03	0.30	–0.141	0.01	–0.18	0.005
Habitat[2]	–0.13	0.001	–0.24	<0.001	–0.19	0.001
Management[3]	–0.04	0.18	–0.09	0.04	–0.15	0.006
Subregion[4]	–0.12	0.09	–0.01	0.45	0.001	0.51
Above variables combined	–0.11	0.08	–0.22	0.001	–0.26	0.001
Geographic distance only (simple Mantel test)	–0.16	0.02	–0.27	0.001	–0.22	0.001

r = Pearson correlation. [1] Hunting = None, Light, Heavy. [2] Percent terra firme forest at site. [3] Management = Strict protection, Restricted use, Unrestricted (direct) use. [4] Subregion = Manu, Amigos, Piedras, North-MDD, Tambopata.

Discussion

By intensively sampling a single major watershed of south-western Amazonia, this study revealed significant meso-scale biotic heterogeneity within an arboreal mammal taxon that was largely independent of species turnover. Despite the relatively short distances among sites, at least at a pan-Amazonian scale, species richness varied by a factor of two, species assemblage similarity by a factor of four, and aggregate biomass by a factor of ~45. These findings contradict our hypothesis that primate communities remain constant despite meso-scale variation in habitat structure and resource availability.

The variable primate community structure across MDD appears to be due to large-scale species patchiness, rather than actual replacements, even for some common species. The non-linear patterns of primate species occupancy observed in MDD agree with findings by Emmons (1984) of minimal turnover among mammalian genera across Amazonia, together with a tendency for consistently rare species to drop out at less favourable (usually nutrient-poor) sites. They were also consistent with floristic evidence on both trees and understorey plants of western Amazonia, the distributions of which have been shown to vary due to changes in microhabitats, such as edaphic gradients, within a broad forest type (i.e. unflooded terra firme forest, Phillips *et al*. 2003, Tuomisto *et al*. 1995). The inclusion in the analysis of extreme specialists of minor habitat types, such as pygmy marmoset (Peres 1993) and Goeldi's marmoset (Porter 2006), might have further amplified fine-scale variation in community composition and structure, but these species are rarely detected during censuses in the predominant forest matrix of western Amazonian forests, even at sites where they presumably occur (C.A. Peres, unpubl. data).

Environmental factors

The mechanisms behind the spatial heterogeneity observed in MDD are not yet known. The lack of support for density compensation seen within the hunted primate communities suggests that biogeographical and environmental factors, rather than interference or exploitative competition, drive community structure. In fact, each of the environmental variables we examined appeared to contribute to some component of this heterogeneity, yet none was an outstanding contributor. For example, the Madre de Dios River and its large tributary, the Inambari River, appear to serve as a barrier to dispersal for three rarer species (woolly monkey, bald-faced saki and emperor tamarin; Ayres and Clutton-Brock 1992, Palminteri *et al*. 2009), decreasing species richness south of the river, yet the inconsistent distribution of several species among sites north of these rivers remains puzzling.

Consistent with findings elsewhere that the spatial organization of primate communities is partly shaped by habitat heterogeneity resulting from variable inundation regimes (Ayres 1986, Haugaasen and Peres 2005b, Peres 1997), terra firme forest sites in MDD supported a higher mean number of primate species than adjacent floodplain forest. These differences were less pronounced than those reported for central Amazonia, as aggregate abundance, biomass and community structure did not differ significantly between these habitats. Flood pulses in MDD are typically supra-annual and short-lived (Prance 1979, Thieme *et al*. 2007), in contrast to the multiple-month seasonal flooding in the central Amazon. The western Amazon's shorter and less-frequent flooding regimes and generally more nutrient-rich soils (Peres 2008, Phillips *et al*. 2006, Terborgh and Andresen 1998) should produce smaller differences in both primary productivity and, consequently, an intermediate herbivore/frugivore community structure between terra firme and floodplain forests (Peres 1999b). The primate communities in mature floodplain forests of MDD are, in fact, more diverse than those of seasonally flooded forest (várzea) sites farther east (Haugaasen and Peres 2005a, Peres 1997), yet their high biomass levels are similar (Endo *et al*. 2010).

Inter-site similarity in community abundance and biomass correlated most strongly with subregion (ANOSIM). Subregions represented four sub-basins and the main MDD channel, thereby capturing potential differences in local edaphic conditions (Salo *et al*. 1986) and floristic composition (Kalliola *et al*. 1993). For example, Kalliola *et al*. (1993) reported that floodplain soils in the Tambopata river basin were highly weathered and more acidic than those of floodplain sites either on the mainstem MDD River or in the Manu River basin. Corresponding successional vegetation at the Tambopata site was also different from the other two sites. Similarly, Foster (1990) proposed that the 'conspicuous' abundance of tree species bearing mammal-dispersed fruits might underlie the relatively high density of primates and other mammals at Cocha Cashu, Manu (Site 5). Major soil-related floristic differences have also been observed among western Amazonian terra firme forests (Ruokolainen *et al*. 1997), and age of terra firme soils (Räsänen *et al*. 1990) was found to be a key driver of variation in tree species composition in MDD (Phillips *et al*. 2003).

Nevertheless, the importance of subregion and other drivers of primate species composition, abundance and biomass in the MDD basin was confounded by the effects of geographic location, which appeared to be an underlying key predictor of primate community similarity. The importance of geographic location at a fine scale reflects that of broad-scale patterns of primate community dissimilarity recorded across South America as a function of geographic distance (Peres and Janson 1999). Consequently, both local environmental variability and geographic distance appear to influence meso-scale patterns of primate community heterogeneity in MDD, as noted for other taxa (Phillips *et al*. 2003, Vormisto *et al*. 2004).

The BIO-ENV and partial Mantel test results indicated that a combination of environmental factors, rather than any one factor, drives the regional patterns of primate community structure (Table 4). The 18-fold difference in biomass among non-hunted sites illustrates considerable natural heterogeneity independent of hunting pressure. Such spatial heterogeneity in distribution patterns of a relatively generalist and widely-distributed vertebrate taxon like primates in the largely intact south-western Amazon forests implies that community heterogeneity will be even greater among more species-rich tropical forest taxa, as well as in regions of higher habitat diversity.

Anthropogenic factors

Consistent with other vertebrate studies (Freese *et al*. 1982, Peres and Palacios 2007), primate biomass in MDD was higher in non-hunted sites than in either lightly or heavily hunted sites. In both MDD and elsewhere in the western Amazon (Bennett *et al*. 2001, Freese *et al*. 1982, Heymann *et al*. 2002, Terborgh *et al*. 2008), large-bodied primates bear the brunt of the effect of hunting pressure. In MDD, this effect was observed both for the woolly monkey, which was restricted to Manu NP, and for the ubiquitous spider and howler monkeys. These latter two prey species are widespread in MDD (Levi *et al*. 2009, Ohl-Schacherer *et al*. 2007) and were recorded in each of our hunting categories but at lower levels of abundance and biomass in hunted sites.

The greater dissimilarity among primate assemblages at hunted sites suggests that primate biomass collapse induced by hunting paradoxically results in greater heterogeneity in community structure by selectively reducing the abundance of common and large-bodied primates to levels unrecorded in non-hunted sites (Figure 3). For example, while non-hunted Manu sites support uniquely high primate biomass and numbers of large-bodied species, the hunted Manu sites along the MDD River, Pusanga (Site 9) and Boca Manu (Site 11), lacked both spider and woolly monkeys, and they supported very low abundances of howler monkey and white-fronted capuchin (*Cebus albifrons*), two other hunted species. The ‘novel’ assemblages created by these changes in abundance of the most common, large-bodied species resembled those at hunted sites in North-MDD and Tambopata (Sites 26-27, 34-37) more closely than those of non-hunted Manu sites (Figure 3). Likewise, primate assemblages at the three non-hunted sites in the Tambopata subregion were remarkably similar to each other, while those of the hunted Tambopata sites downstream differed not only from the non-hunted sites but also from each other. Only one of 15 non-hunted sites, Limonal (Site 10), lacked both of the two largest-bodied species. The absence of spider monkeys, combined with the presence of the patchily-distributed emperor tamarin, rendered this community an outlier (Figure 3). In sum, hunting-induced population declines in otherwise abundant, large-bodied species, combined with the patchy regional distributions of certain less-hunted species (bald-faced saki, emperor tamarin), may have resulted in community signatures previously unknown in the region.

Our results support the key role of strictly protected areas in maintaining primate assemblage integrity, especially for large-bodied species, the disappearance of which has been shown to affect ecological processes, such as seed dispersal and associated tree recruitment, both in MDD (Nuñez-Iturri and Howe 2007, Terborgh *et al*. 2008) and elsewhere (Chapman and Onderdonk 1998, Holbrook and Loiselle 2009). While land management was highly correlated with hunting pressure (and therefore excluded from our abundance and biomass models), when analyzed separately, both aggregate abundance and biomass were significantly higher in sites with active conservation management than in those without. Moreover, although we found no significant relationship between survey effort and species richness, total abundance or total biomass for the 37 sites included in our analyses, separate ANOVAs restricted to only 25 sites with at least 48 km of census effort showed that, in addition to abundance and biomass, species richness also differed significantly among levels of hunting pressure and protection.

Primate communities at the edge of Manu NP differed from those in the park's interior. Within the park, large populations of primates, as well as other endangered vertebrates, occur at both non-hunted sites and those that are hunted by small, localized indigenous populations (Emmons 1984, Endo *et al*. 2010, Terborgh 1983). The sizeable populations of large-bodied primates surrounding the hunted catchments may be masking the local impact of hunting (Ohl-Schacherer *et al*. 2007). Immigration from source populations precludes local extinction of some species in at least one of these sites (Tayakome, Site 2, Figure 1) and maintains population densities that, while lower than those at non-hunted Manu sites (Appendix 1), were higher than at unprotected sites throughout the rest of MDD. On the other hand, any animals hunted at sites 9 or even 10, located within but at the edge of the park, may have experienced less recolonization from neighbouring populations, as their community structure was consistently different from those in the park interior.

Combining these results with our assessment of species richness illustrates that while primate communities in MDD are still largely intact, hunting pressure has begun to degrade them, particularly at sites near human populations (Sites 9, 11, 34-37, Figure 1). The MDD region is currently more than 90% forested and over 30% protected (MINAM 2010). The presence of substantial source populations of primates in the large protected areas and the relatively intact forest currently surrounding most of our unprotected sites has likely mitigated the impact of hunting pressure compared to other Amazonian regions. Spider monkeys, for example, occurred at 78% of our sites but were not recorded at most lowland rain-forest sites surveyed in north-eastern Peru (Bennett *et al*. 2001, Freese *et al*. 1982, Heymann *et al*. 2002), northern Bolivia (Christen and Geissmann 1994) and south-western Brazilian Amazonia (Peres 1990), absences that these authors attributed to hunting pressure.

Nevertheless, the currently high annual deforestation rate (~2%, G. Asner pers. comm.) along the region's infrastructure-development corridor is expected to increase due to the newly upgraded Inter-Oceanic Highway running through the centre of MDD (Figure 1). The projected expansion of the human population resulting from the paving of this road threatens to significantly increase hunting and forest fragmentation (Dourojeanni *et al*. 2009), reducing the possibility of recolonization by surrounding source populations of primates and other animals. Intervention focused on maintaining connectivity among faunally intact forest sites across MDD would help to stabilize forest retention and integrity across the region's development corridor. A major regional initiative, including a set of policies regarding development along the road, is urgently needed to prevent the deterioration of one of the largest single blocks of protected habitat in the Amazon basin.

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Appendix. Profile of 37 survey sites (ordered and numbered from west to east, Figure 1) considered in this study: subregion, bank of the Madre de Dios River, per cent terra firme (TF) forest, management regime (Mgmt), level of hunting pressure, number of transects, survey effort (km), number of species sampled (analyzed species only), mean number of groups per 10 km walked, aggregate abundance (individuals per 10 km walked), aggregate biomass (kg per 10 km walked), and Simpson diversity index (1-λ'). N/S = North or South of Madre de Dios River; PA = Protected Area, RU = Restricted Use - e.g. tourism, research, non-timber forest products, DU = Direct Use - e.g. buffer zone, logging concession; 0 = No hunting, 1 = Light hunting, 2 = Heavy hunting. [1]Numbers correspond to contributing dataset: 1 = Kirkby and Padilla 1998; 2 = Kirkby *et al*. 2000; 3. Schulte-Herbrüggen and Rossiter 2003; 4. Kirkby 2004; 5. Endo *et al*. 2010; 6. S. Palminteri, this study; 7. Nuñez-Iturri 2007.

Site number	**Site**	**Sub-region**	**Bank**	**TF (%)**	**Mgmt**	**Hunt-ing**	**Tran sects**	**Survey length (km)**	**Number of species found**	**Grps per 10 km**	**Abun dance**	**Biomass**	**Simpson index**
1	Yomybato[5]	Manu	N	100	PA	1	3	248	8	6.09	28.20	101.66	0.91
2	Tayakome[5]	Manu	N	100	PA	1	3	235	10	7.88	28.10	192.99	0.93
3	Cumerjali[5]	Manu	N	100	PA	0	3	227	9	17.78	98.44	615.53	0.88
4	U.Panagua[5]	Manu	N	100	PA	0	3	170	8	16.03	96.09	499.56	0.89
5	CochaCashu[5]	Manu	N	0	PA	0	3	218	9	12.24	68.32	277.28	0.89
6	L.Panagua[5]	Manu	N	100	PA	0	3	235	8	13.7	77.18	435.08	0.90
7	Pakitza[5]	Manu	N	0	PA	0	3	162	8	15.47	95.23	535.23	0.88
8	Salvador[4]	Manu	N	0	PA	0	2	26	5	16.67	164.47	572.69	0.80
9	Pusanga[4]	Manu	N	0	PA	1	1	31	4	4.19	26.41	26.67	0.81

Site number	Site	Sub-region	Bank	TF (%)	Mgmt	Hunt-ing	Tran sects	Survey length (km)	Number of species found	Grps per 10 km	Abun dance	Biomass	Simpson index
10	Limonal[4]	Manu	N	0	PA	0	2	25	6	6.48	23.48	34.13	0.90
11	Boca Manu[7]	Manu	N	0	DU	2	1	104	6	2.6	46.84	47.91	0.77
12	Amigos4[1]	Amigos	N	90	RU	1	1	40	6	5.5	16.75	68.14	0.90
13	Amigos3[1]	Amigos	N	25	RU	1	1	40	4	3.75	21.88	74.65	0.82
14	Amigos7[1]	Amigos	N	100	RU	1	1	32	8	6.88	36.89	119.52	0.93
15	Amigos8[1]	Amigos	N	0	RU	1	1	32	9	6.88	39.58	87.67	0.92
16	Amigos6[1]	Amigos	N	0	RU	2	1	36	7	8.33	58.23	163.27	0.87
17	Amigos5[1]	Amigos	N	100	RU	2	1	36	8	5	20.50	79.81	0.93
18	Puma[6]	Amigos	N	98	RU	0	1	47	8	9.93	42.18	73.13	0.90
19	Tigre[6]	Amigos	N	56	DU	1	1	53	9	5.33	25.73	76.43	0.93
20	Cicra[6]	Amigos	N	84	RU	0	1	61	9	13.4	55.35	168.19	0.91
21	CM1[6]	Amigos	N	100	DU	1	1	50	8	9.44	43.73	62.26	0.89
22	Piedras2_F[3]	Piedras	N	100	RU	0	2	220	8	3.77	19.45	62.40	0.94
23	Piedras2_E[3]	Piedras	N	100	DU	2	2	232	7	4.53	24.67	90.43	0.91
24	Piedras2_CD[3]	Piedras	N	100	RU	1	4	291	8	6.01	30.78	118.75	0.92
25	TRC[2]	Tambo	S	0	PA	0	5	181	7	5.25	45.35	106.30	0.85

Site number	Site	Sub-region	Bank	TF (%)	Mgmt	Hunt-ing	Tran sects	Survey length (km)	Number of species found	Grps per 10 km	Abun dance	Biomass	Simpson index
26	Mali_W[6]	Tambo	S	100	DU	2	1	48	4	4.79	29.24	35.09	0.78
27	Mali_N[6]	Tambo	S	90	DU	2	1	48	7	7.92	42.13	97.04	0.87
28	PiedrasA[6]	Piedras	N	95	RU	0	1	512	8	12.98	72.39	158.30	0.90
29	PiedrasC[6]	Piedras	N	49	RU	0	1	48	7	11.04	50.28	126.85	0.87
30	PiedrasB[6]	Piedras	N	53	DU	1	1	46	6	5.21	28.95	98.30	0.89
31	PiedrasD[6]	Piedras	N	44	RU	1	1	48	7	7.08	35.38	101.00	0.90
32	Chuncho_FL[6]	Tambo	S	0	PA	0	1	40	6	10.45	49.60	124.39	0.88
33	Chuncho_TF[6]	Tambo	S	100	PA	0	1	82	6	4.77	27.07	79.54	0.89
34	SachavacaInn[2]	Tambo	S	0	DU	2	5	296	5	1.72	21.00	21.31	0.75
35	ExplorersInn[2]	Tambo	S	0	RU	1	6	172	5	2.62	15.47	32.07	0.88
36	ReservaAmaz[2]	N-MDD	N	0	DU	2	5	315	5	2.79	22.26	14.03	0.75
37	EcoAmazonia[2]	N-MDD	N	0	DU	1	7	310	5	3.65	30.76	44.02	0.84

Chapter 4: Habitat effects on patterns of movement and use of space by a neotropical forest primate

Abstract

An understanding of landscape-scale population density and distribution in tropical forest vertebrates is directly linked to patterns of use of space relative to habitat structure and composition. To examine how forest type may explain the ranging behaviour and high variance in group density observed within the geographic range of the bald-faced saki monkey (*Pithecia irrorata*), we monitored the movement patterns and habitat use of five neighbouring study groups of this species in south-western Amazonia over three years. To test whether saki monkeys are unflooded (terra firme) forest specialists, we compared the spatial variation in home range use by our study groups to the corresponding availability of four main forest habitat types and estimated home range size and several movement metrics as a function of forest type. Home range size varied from 16 to 60 ha and was more strongly affected by forest type than by group size. Although sakis were not obligate habitat specialists, groups clearly avoided bamboo forest and consistently preferred terra firme forest. Terra firme forests were associated with large group size, small home ranges, more intensive than expected home range use, relatively long travel distances, and high home range overlap, all of which suggest that saki densities in south-western Amazonia will likely be higher in areas dominated by terra firme forest where large patches of bamboo (*Guadua* spp.) forest 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 specialists of mature terra firme forest like the saki monkey. Special attention will need to be given by regional conservationists to ensure that extensive blocks of terra firme forest are protected in areas that remain relatively free of bamboo.

Introduction

Patterns of movements and use of space in heterogeneous landscapes provide key insights into the resource and habitat requirements of animal populations (Powell 2000, Hemson et al. 2005). Specifically, the size and juxtapositioning of adjacent home ranges with respect to habitat type, combined with the occupants' use of different habitats within their home range, help us identify habitat preferences that affect the density, ecological distribution and, ultimately, the viability of a given population (Powell 2000).

Analyzing an animal's movements and behaviours relative to habitat type can be used to understand the determinants of density, and, consequently, help explain distribution patterns within a species' geographic range. 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 (e.g. Alldredge and Griswold 2006). Individuals of a species that consistently specializes on a particular forest type should thus maintain some minimum portion of their home range areas in that habitat and use it preferentially. Similarly, smaller home ranges and patterns of greater home range overlap within certain habitat types may serve as indicators of habitat preference (McLoughlin and Ferguson 2000); individuals would be expected to maintain larger home ranges where preferred forest type(s) are more sparsely distributed. In addition, the length, velocity, and linearity of an animal's movements and the propensity of individuals or group members to forage, rest, and interact agonistically with other conspecifics within different habitats of their home ranges can shed light on the relative value of habitat types to the species. For example, travel routes are likely longer and more sinuous in preferred forest types (Buskirk and Millspaugh 2006, but see Stevenson 2006), which may be more critical for foraging activities and more heavily defended. Conversely, in the case of habitat generalists, the density and patterns of travel and space use of individuals should be similar across habitat types.

Saki monkeys (*Pithecia spp*.) are medium-sized, small-group living forest primates distributed across the Amazon basin that specialize on immature fruit from a broad spectrum of plant species (Norconk and Conklin-Brittain 2004, Peres 1993, Palminteri et al. in press a). 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, and what little information is available is confounding. Some studies have suggested that sakis are habitat specialists of unflooded (hereafter, *terra firme*) forest (Mittermeier and van Roosmalen 1981, Terborgh 1983, de la Torre 1995, Sheth et al. 2009), whereas others have found that they occur within multiple forest habitats (Oliveira et al. 1985, Peres 1993a, Haugaasen and Peres 2005), though typically at low densities (Mittermeier and van Roosmalen 1981, Christen and Geissmann 1994, Peres 1997, Buchanan-Smith et al. 2000) or at uneven rates of occupancy (Freese et al. 1982, Johns 1986, Alverson et al. 2000, Chapter 3).

Here, we examine the patterns of habitat use and selection in bald-faced sakis (*Pithecia irrorata*) in the southeastern Peruvian Amazon. In particular, we investigate whether habitat preferences indicated specialization on terra firme forest and to what extent such preferences may explain the patchiness or variable group density reported for this species across its range (Branch 1983, Christen and Geissmann 1994, Chapter 3). Given the positive correlation between both group size (Milton and May 1976, Grant et al. 1992) and group metabolic requirements (Nunn and Baron 2000) and home range size in primates, we would expect groups with fewer individuals to maintain smaller home ranges than larger groups. We therefore measured the home range size, overall use of forest habitats relative to their availability, and behavioural attributes (movement rate, foraging time, and agonistic behaviour) of sakis as a function of both group size and forest type. An assessment of habitat use is likely to be biased by variation in ecological constraints, such as intraspecific competition or predation threat, that restrict or otherwise modify an individual's access to habitat (Van Horne 1983, Hobbs and Hanley 1990). Moreover, habitat preference may vary by group (Aebischer et al. 1993, McClean et al. 1998, Garshelis 2000), as well as by season or year. The monitoring of multiple groups over a three-year period in a naturally heterogeneous landscape helped to minimize these potential sources of bias while enabling between-group comparisons of space use within a single saki population. It also allowed us to measure home range overlap between the five adjacent groups to test whether overlap is positively associated with home range size (Nunn and Barton 2000) or forest type, and thus whether overlap estimates can refine saki density estimates.

Methods

Study area

The study took place in the south-western Amazon, between the Madre de Dios and Los Amigos rivers of the Madre de Dios region (MDD), Peru. The 450-ha study area (12°34’07”S, 70°05’57” W) is located in structurally intact moist forest ~270 masl within the 145,000-ha privately managed Los Amigos Conservation Concession. Mean annual rainfall at the site between 2005 and 2007 was 2,430 mm (http://atrium.andesamazon.org, BRIT 2009).

The study area was selected for its habitat diversity to facilitate examination of the relative use of different forest types (Figure 1). The study area was characterized by two major geomorphological formations, the contemporary floodplain of the Los Amigos and Madre de Dios rivers and a flat upland (terra firme) terrace, about 70 m above the floodplain and separated from it by a steep forested embankment. The supra-annually inundated floodplain was characterized primarily by a 25 to 30 m tall, closed-canopy evergreen forest but included two small patches (8 and 15 ha) of monodominant stands of the palm *Mauritia flexuosa* (hereafter, palm swamp). The terra firme domain was similarly covered primarily by mixed closed-canopy forest 35-40 m in height but also included two open-canopy forest patches dominated by bamboo (*Guadua* spp.) stands (7 and 29 ha). We therefore define four mutually exclusive habitat types in the study area: floodplain, palm swamp, terra firme and bamboo forest.

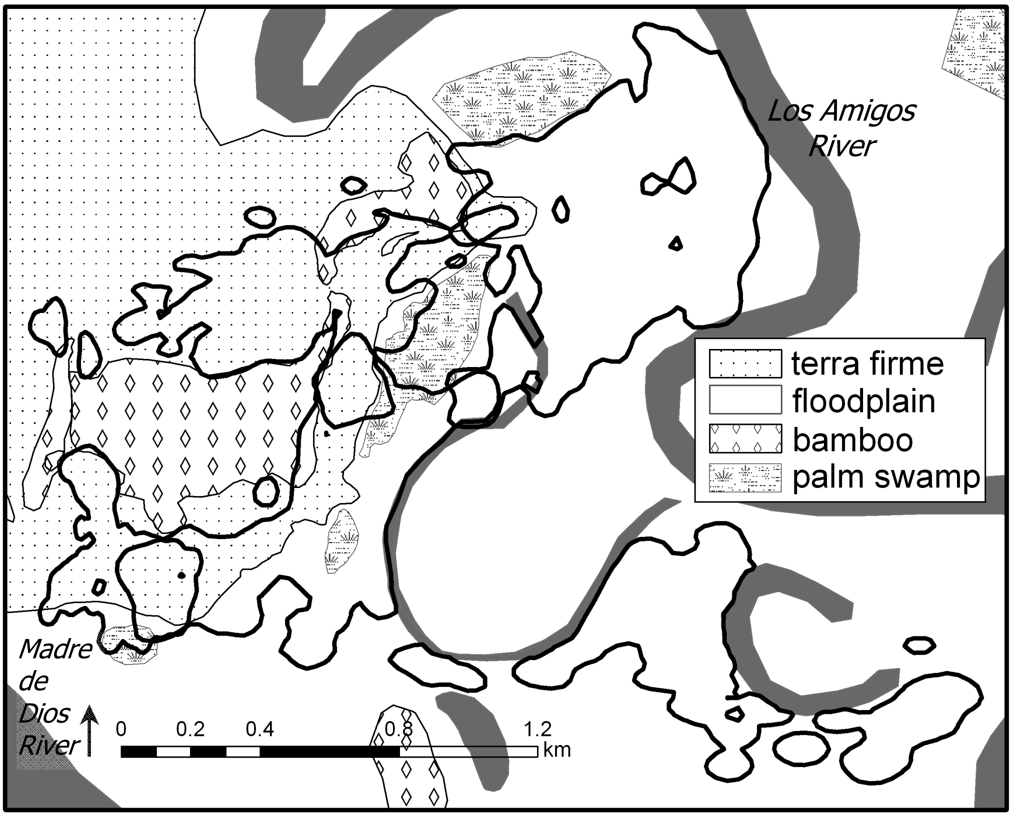


Figure 1: Study area at Los Amigos, southeastern Peru, with the spatial distribution of home range (HR) polygons of individual bald-faced saki (*Pithecia irrorata*) groups (solid lines) and the four main forest types available in the study area.

Data collection

To quantify saki movement patterns and behaviour with respect to habitat type, we followed five previously habituated study groups between January 2005 and December 2007. Each group was monitored for 3 to 5 consecutive days per month, for 6 to 28 months (median ~22 months) per group (Table 1). Although our study groups were habituated, we were unable to follow them continuously every sample day, obtaining approximately 6.2 (± 0.2 SD) contact hours per sample day. We followed study 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 one to two observers recording a single group location, habitat type, and behavioural pattern (resting, moving, foraging/feeding, or social/agonistic) every 15 min throughout all contact hours using instantaneous scan sampling (Altmann, 1974).

Table 1. Home range estimates for five bald-faced saki (*Pithecia irrorata*) study groups at Los Amigos, Madre de Dios, Peru.

Group	No. sample months	No. of 15-min. scans	No. GPS points[1]	Mean group size (± SD)	MCP[2] (ha)	95% kernel (ha)[3]	50% kernel (ha)	Percent of HR shared[4]	Density (ind/ km^2)[5]
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
Mean	20.2	2270	1824	4.7 ± 1.5	62.9	35.9	8.4	15.8	12.5
All [6]	31	11349	9119	19.9	334.6	167.2	40.8	14.1	11.9

[1] GPS locations used to generate home range estimates. [2] Minimum Convex Polygon, excludes lakes. [3] 95% kernel home range (HR) polygons, excludes lakes. [4] Percent of 95% kernel home range overlapping with other study groups. [5] Density calculation based on 95% kernel HR and excludes HR overlap. [6] All = aggregate values use all group scans and unions of the five groups' MCP, HR, and 50% kernel (core area) polygons, respectively, counting overlap areas once.

As individual recognition was effectively unreliable, we recorded the principal behaviour of all visible group members and the location of the approximate geometric centre of the group (Terborgh 1983, Stoner 1996, Matthews 2009), while recognizing that these scans were often incomplete. Group locations were either recorded directly using a Garmin 12XL GPS or calculated in ArcView 3.3 GIS (ESRI, Redlands California) using distance and angle from known coordinates of 30 km of georeferenced trails spanning the study area. To test the accuracy of incomplete scans in representing the collective behaviour of an entire group, for a subset of observations (300 scans during 70 days), a second, independent observer recorded the activity pattern of outlying members of the group, and the number of matching simultaneous observations between the two data sets was converted into a percentage of matching cases.

Data analysis

Habitat availability

The amount of habitat available to a given group was calculated as the area within the minimum convex polygon (MCP) enclosing all locations for that group. The five MCPs served as each group's area of availability for habitat selection analyses (Raboy et al.

2004, Thomas and Taylor 2006) while also enabling comparisons with other studies. The juxtaposition of various forest types and close proximity of adjacent saki groups that were not studied, rivers, and associated successional vegetation made the MCP a better choice than a more remote ecological or political boundary (Aebischer et al. 1993, Buskirk and Millspaugh 2006) that risked including areas not physically accessible to the groups. To determine the area of each habitat type accessible per group, we intersected each group's MCP with a vegetation map (ACCA 2007) that we refined in a GIS by correcting the habitat type along the terra firme–floodplain forest boundary according to the fine-scale habitat data recorded during approximately 860 (≈ 9%) of georeferenced saki locations. For habitat use, travel velocity and movement pattern analyses, we considered each forest type as a categorical variable, whereas for analyses of full-day travel paths, forest type was represented by the proportion of time in each sample-day that the group allocated to terra firme forest.

Patterns of habitat use

To quantify habitat use by each group within its home range (HR), we totalled time spent (number of 15-min locations) in each habitat. To test whether temporal autocorrelation in habitat use data was biasing the analyses (Aebischer et al. 1993, Thomas and Taylor 2006), we used PopTools (ver 3.1.1, Hood 2009) to randomly resample 100 times the 15-min locations for the four saki groups whose HRs contained multiple forest types. For each group, we then compared the median proportion of locations in each habitat type to those of the full data set.

For each study 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, the two automated statistical methods provided by standard GIS software to generate kernel analysis probability curves (Worton 1989, Seaman and Powell 1996), oversmoothed and undersmoothed our point data, respectively, a problem observed by others (Rogers and Carr 1998, Hemson et al. 2005, Gitzen et al. 2006, Tobler 2008). Therefore, we multiplied the ad hoc smoothing factor by 0.4 (Carr and Rogers 1998), which provided results that adequately represented the location data for all saki groups. Areas within either the MCP or the 95% kernel polygon that extended into unusable habitat (*e.g.*, lakes, rivers, or human clearings), were excluded from the final home range polygon (Irwin 2008). To calculate home range overlap between adjacent study groups, we intersected the HR polygons of pairs of neighbouring groups. We then overlaid all HRs, core areas, and overlap polygons with the refined habitat map.

We tested whether saki groups spent more time (determined by proportion of 15-min scans) than expected by chance in their areas of HR overlap using a chi-square goodness-of-fit test. Expected time was calculated based on the proportion of each HR within the overlap area. We examined the relationship between each group's proportional HR overlap area and subsequent HR-level population densities (ind. km^{-2}) with the proportion of terra firme forest within the HR of each group using a Pearson correlation. Given the substantial variation in group and HR sizes (Table 1), we analysed habitat selection primarily by study group. This approach also allowed us to include potential variability in habitat preference among groups in our analyses. Similarly, by assessing habitat use by four of the five groups across all calendar months, we avoided any potential seasonal bias.

For each group, we used a chi-square goodness-of-fit test to compare the proportion of 15-min scans in each of the four forest types to that expected given the proportion of the group's MCP comprised by each forest type. We applied a Z-test with Bonferroni-corrected 95% confidence intervals of the residuals (Neu et al. 1974, Byers et al. 1984) to determine which forest types were significantly preferred or avoided. We applied this process to the observed versus 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). To assess the overall habitat use by this *Pithecia irrorata* population, we treated all five groups as a single sub-population and repeated the process, comparing the sum of all scans in each forest type to the number expected within a single large MCP drawn around the locations of all groups (Buskirk and Millspaugh 2006).

Behaviour and movement patterns in different forest habitats

We quantified habitat preference with respect to behaviour by assigning all 15-min scans for each group to one of four mutually exclusive behavioural 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 omitted all scans for which the activity was either unknown or ambiguous (4.3% of 11,349 observations). Intergroup disputes were included in the social behaviour category. We used a chi-square goodness-of-fit test to determine whether sakis used certain habitats for specific activities more or less often than expected by chance.

To measure relationships between movement characteristics and habitat type, we organized the observations as daily travel paths. We estimated group travel distance and velocity in the different forest types by calculating the straight-line distance covered between each 15-min scan using the Pythagorean theorem. We used Hawth's Tools (Beyer 2004) to calculate turning angles (0^o – 180^o) for each of 4,659 movements (or step-lengths) between 15-min locations. In calculating travel velocity and turning angles, we included movements from 469 observation days allocated to the five study groups for which we had sufficient data points to represent movements. We examined group velocity and turning angles as a function of forest type, group identity, and group size using Kruskal-Wallis tests. Group size in this study (range = 2 – 8) is defined as the mean number of group members, other than dependent infants, per observation over the entire study period.

The daily travel path length (DPL) was defined as the sum of the straight-line distances between successive 15-min locations when a group was followed continuously between two consecutive sleeping sites (Irwin 2008, Boyle et al. 2009) or for days consisting of at least 8 h of observations terminating at a sleeping site, if the previous night's sleeping site was not determined. The ratio of straight-line distance (SLD) between consecutive sleeping trees to the corresponding DPL provided an estimate of daily travel path linearity (McKey and Waterman 1982, Normand and Boesch 2009), in which lower values represented more sinuous travel paths. We measured the relationships between three movement metrics – DPL, $\log_{10}$-transformed relative DPL (daily path distance/HR size, Kernohan et al. 1998, Wallace 2006), and linearity (the SLD:DPL ratio) – and two indicator variables – the percentage of each day's observations within terra firme forest and group size (which has been shown to explain primate DPL, Irwin 2008) – using Pearson correlations. Given the likely confounding effects of group size and percentage of terra firme forest each day, we used partial correlations to assess the relationships between the three movement metrics and each indicator while holding the effect of the other indicator constant. We further compared these three movement metrics as a function of group, using one-way ANOVA. Group C had only one full sample day so was excluded from the DPL analyses.

Data were analysed using JMP and SPSS statistical software; all tests are two tailed and based on an $\alpha = 0.05$ significance level.

Results

Over the 3-year study period, the five habituated groups averaged 4.7 ± 1.5 SD individuals, excluding dependent infants, and contained between two and eight individuals at a given point in time, consisting of one adult male, one to three adult females, and associated juveniles (Table 1). We recorded 9,119 georeferenced 15-min group locations over 2,837 observation hours of the five saki groups. Median values of habitat use intensity from our resampling test for autocorrelation did not differ from the overall data set; we therefore used the full dataset for all groups (Powell 2000). On the basis of 95% kernel polygons, mean HR size for the five groups was 35.9 ha (Table 1), representing between 5 and 15 ha per individual. Habitat composition of the HRs varied substantially among study groups (Table 2, Figure 2), resulting in a strongly positive correlation between saki densities (ind. ha^{-1}) and the proportion of terra firme forest in each HR ($r = 0.973$, $p = 0.005$, $N = 5$).

Table 2. Percentage of use, composition, and availability of four main forest types for five bald-faced saki groups at Los Amigos, Peru.

Group	**Measure**	**Terra firme**	**Floodplain**	**Bamboo**	**Palm Swamp**
A	Use	56.2***	38.9***	0.2***	4.7***
	Core	72.7	20.4	1.4	5.5
	Home Range	37.4	51.9	3.1	7.7
	Available	29.6	47.7	14.3	8.3
B	Use	92.7***	3.8***	0.6***	2.8***
	Core	98.8	0.0	1.2	0.0
	Home Range	85.0	3.7	7.5	3.8
	Available	67.1	19.9	4.1	9.0
C	Use	0.0	100.0	0.0	0.0
	Core	0.0	100.0	0.0	0.0
	Home Range	0.0	100.0	0.0	0.0
	Available	0.0	100.0	0.0	0.0
D	Use	9.7***	89.7***	0.0	0.6***
	Core	8.1	91.9	0.0	0.0
	Home Range	3.8	95.4	0.0	0.7
	Available	4.7	83.5	0.0	11.7
E	Use	85.7***	11.3*	0.0***	2.9
	Core	84.9	14.7	0.0	0.4
	Home Range	80.7	13.9	0.3	5.1
	Available	71.8	9.3	16.6	2.3
All groups[1]	Use	57.6***	39.4***	<0.3***	2.8***
	Core	39.4	58.8	0.5	1.3
	Home Range	28.8	66.9	1.3	3.0
	Available	34.7	52.1	7.0	6.3

Use = percentage of 15-minute scans (time) recorded in each forest type

Core = percentage of core area (50% probability zone from kernel analysis) in each forest type

Home Range = percentage of home range (95% probability zone from kernel analysis) in each forest type.

Available = percentage of Minimum Convex Polygon in each forest type

*, *** = Use differed significantly from Availability (p=0.05, p=0.001)

[1] = Represents the combined use (% of 15-min scans) of all study groups, within the aggregate Core, Home Range, and MCP areas of all groups.

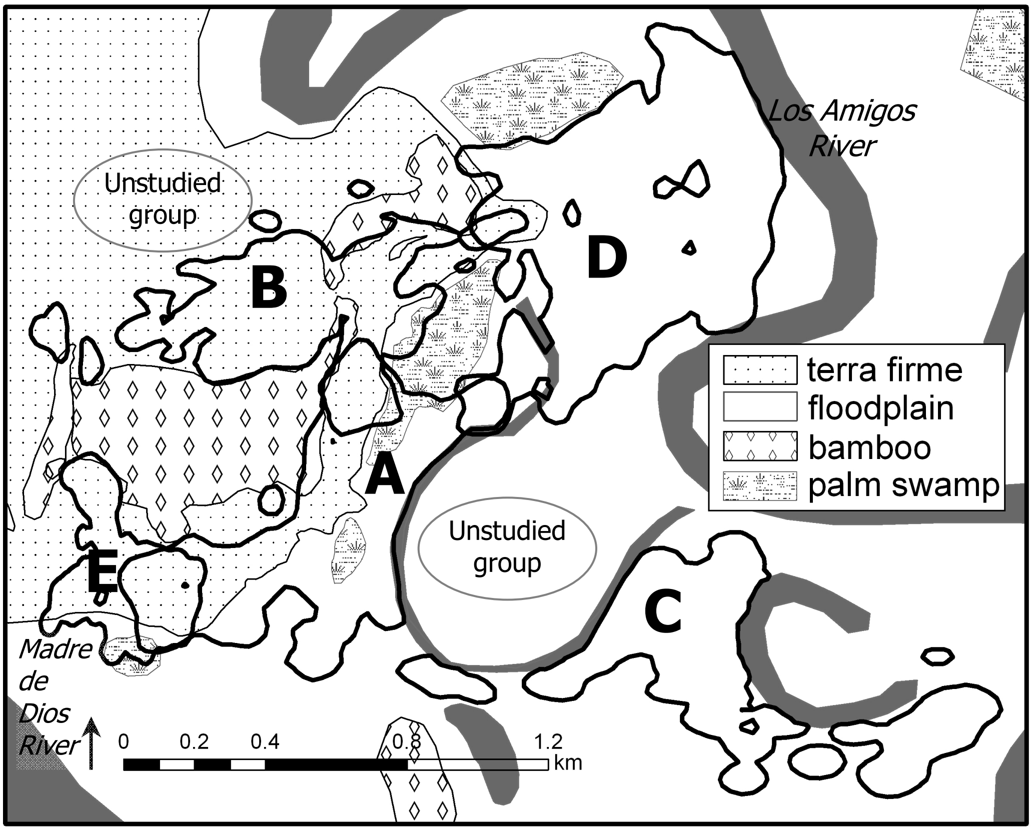
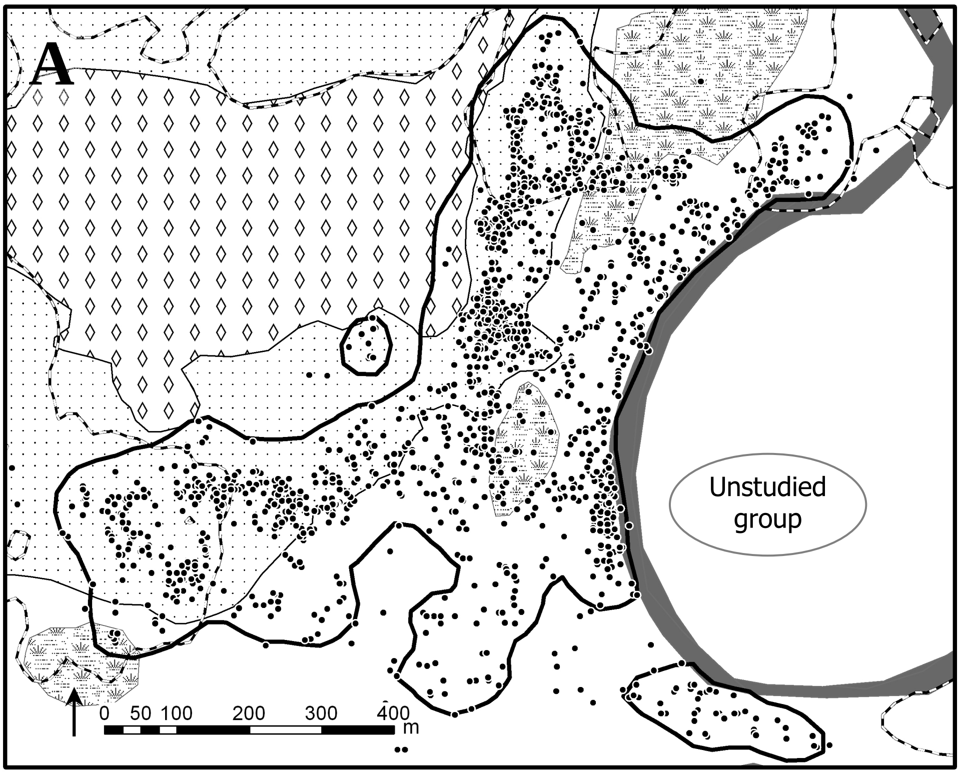
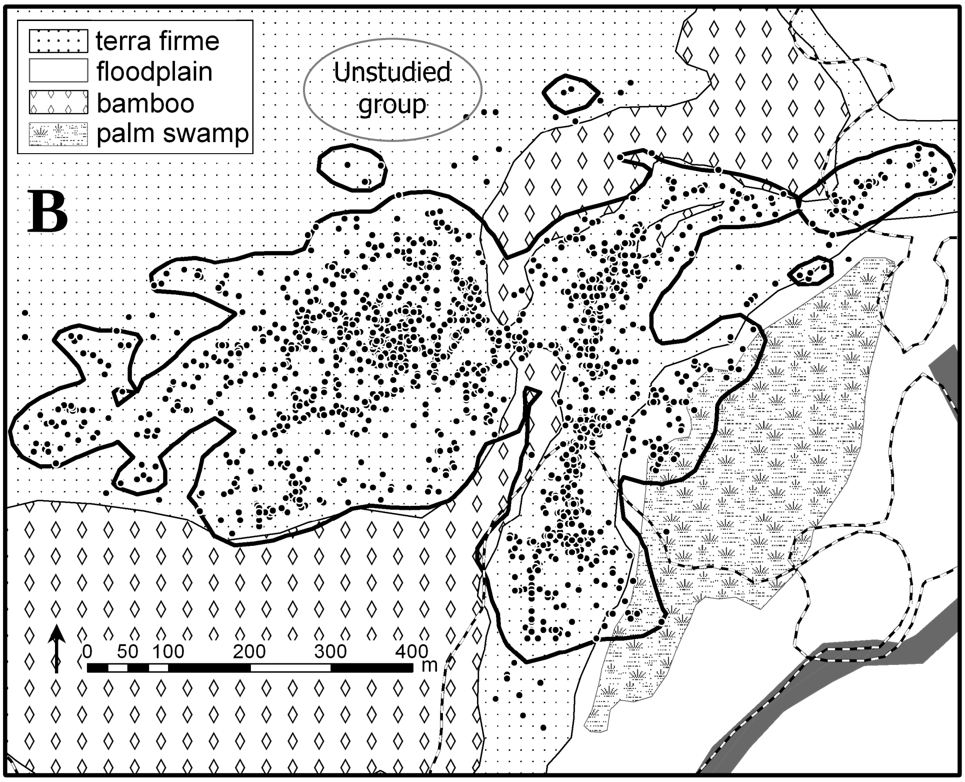
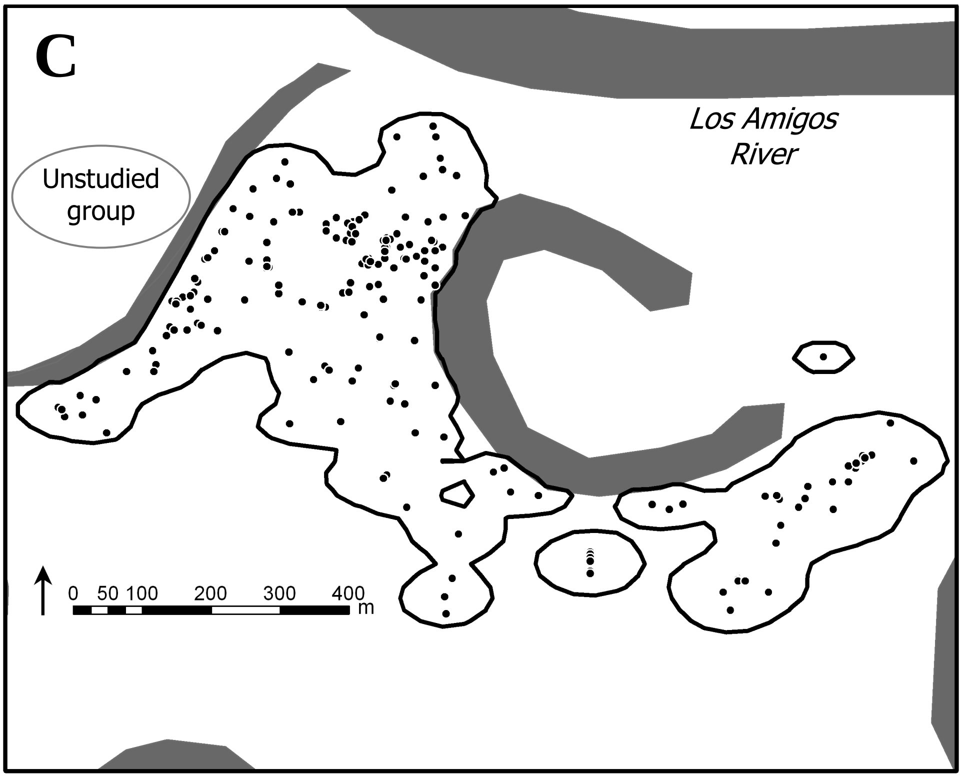
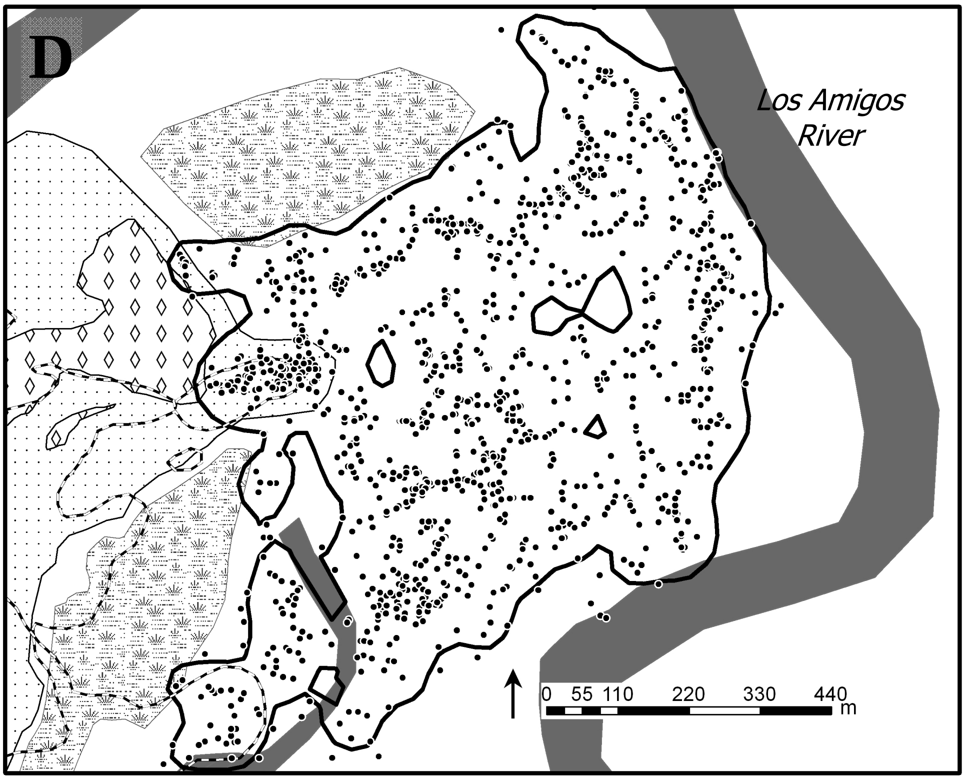


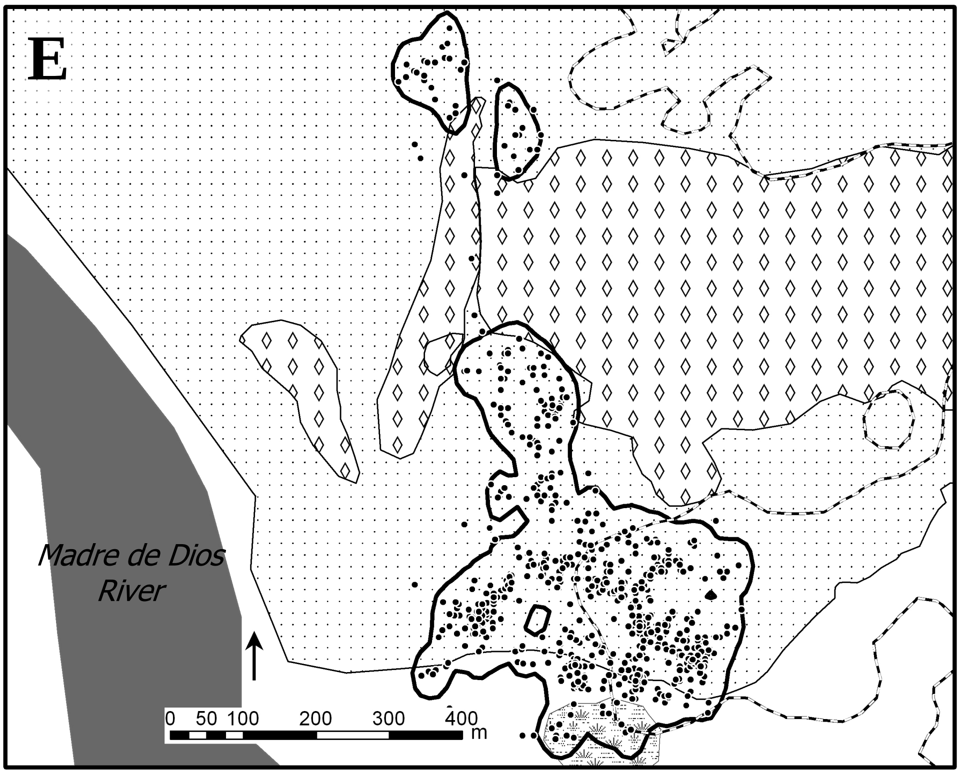
Figure 2: The home range (HR) boundaries (solid lines) of five habituated bald-faced saki (*Pithecia irrorata*) study groups and neighbouring unhabituated groups, between the Madre de Dios and Los Amigos Rivers, southeastern Peru. Mature floodplain forest (all white areas) dominates the HRs of groups C and D, while terra firme forest dominates the HRs of groups B and E. HR polygons of individual saki groups (A – E, below) expressed as 95% kernel polygons (solid lines) show the spatial distribution of 15-min group locations and forest types available for each group. On the following individual group maps, labelled by group, dashed lines represent home ranges of adjacent focal groups. Habitat symbols remain the same.


A
Unstudied group
0 50 100 200 300 400
m


terra firme
floodplain
bamboo
palm swamp
Unstudied group
B
0 50 100 200 300 400
m


C
Los Amigos
River
Unstudied
group
0 50 100 200 300 400
m


D
Los Amigos
River
0 55 110 220 330 440
m



Patterns of habitat use

Considering all groups, year-round use of the four main forest types indicated a strong preference for terra firme forest and an avoidance of bamboo habitat (χ^2= 3,071.4, df = 3, p<0.0001, Table 2), as did sakis' feeding and foraging time across all forest types (χ^2= 1,394.2, df = 3, p<0.0001). Together, the five groups used terra firme forest 2.4 times more often than expected, given the relative contribution of this forest type to the combined MCP, whereas floodplain forest, palm swamp, and bamboo forests were used 1.5, 2, and 32 times less often than expected, respectively (Figure 3). Habitat selection analysis was then carried out for each of the four saki groups that used more than one forest type, as the HR of Group C was entirely restricted to floodplain forest. For each of these groups, the amount of time allocated to terra firme forest was greater than expected by chance for both all activities combined and for foraging and feeding (p<0.05 in all cases; Table 2, Figure 3).

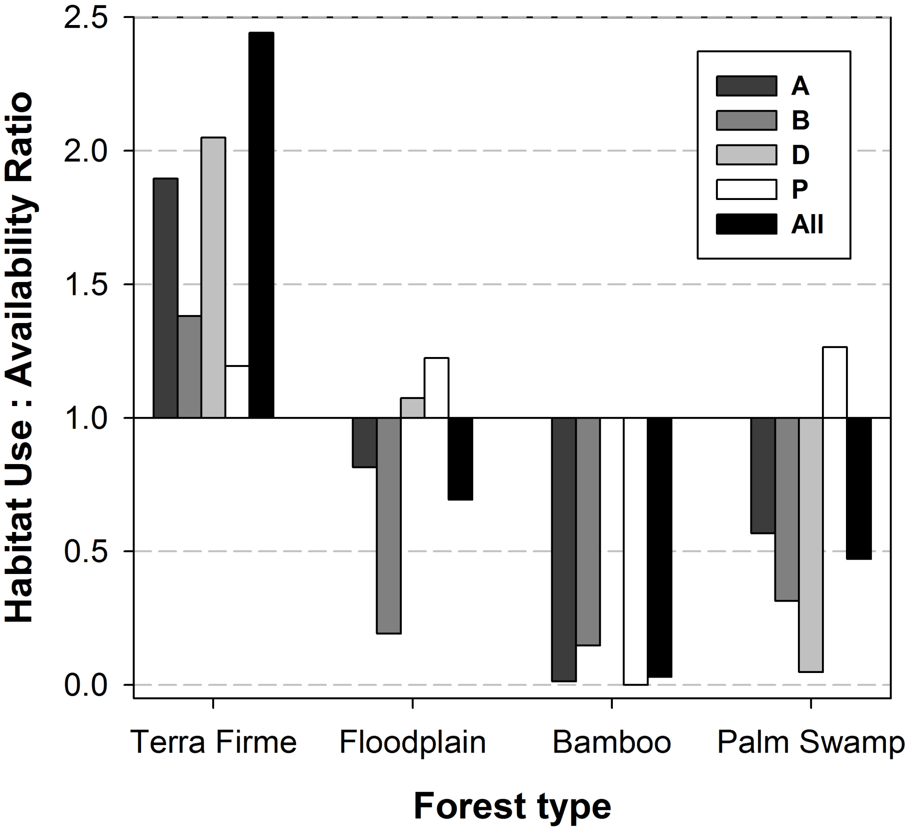


Figure 3. Habitat selection ratios (Use:Availability, Manly et al. 2002) of four main forest types for each of four saki groups. “All” denotes the overall values for all groups. Use = proportion of 15-min scans recorded in each forest type. Availability = proportion of area of group’s Minimum Convex Polygon occupied by each forest type. Ratios >1.0 and <1.0 indicate positive selection (preference) and negative selection (avoidance), respectively. TF=Terra firme, FL=Floodplain, BA=Bamboo, PS=Palm swamp. Group C’s home range was entirely restricted to floodplain forest and is therefore not shown here. Group D lacked bamboo vegetation and therefore lacks a value for that forest type.

Habitat composition of the core area (50% kernel polygon) of each of these four groups also differed highly significantly from that of its MCP (χ^2 tests, $p<0.0001$). On average, terra firme forest comprised 41% of the all core areas, or 1.4-fold higher than the proportion of this forest type available in all MCPs combined. The proportions of terra firme forest within the core areas of individual groups were 1.2-2.5 times greater than those in the groups’ respective MCPs, regardless of the overall habitat composition of the MCP.

Overlap among home ranges similarly reflected the tendency of sakis to concentrate their time allocation to 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. Home ranges of the other four study groups overlapped between 4.5% and 33% (overall mean 15.8%, Table 1). These percentages reflect only the overlap with other habituated groups, as it was not possible to quantify the additional overlap between habituated groups (particularly groups B and E) and neighbouring unhabituated groups, which typically fled or hid from observers.

Terra firme forest occupied between 37% and 85% of the combined overlap area of each group, and these proportions were 1.2-7.9 times greater than expected. Terra firme forest accounted for over 75% of three of the four pairwise areas of overlap (Table 3). The proportion of time spent in overlap areas was greater than expected by chance for all groups with overlap, given the relative size of overlap areas (χ^2 tests, p<0.001 in all cases). The overlap areas of groups B and E, which consisted of 82% and 85% of terra firme forest, respectively, were used during 19% and 50% of observations, respectively. Group D spent less than 10% of its time in its overlap zone, but this area encompassed only 37% in terra firme forest and only 4.5% of its HR size.

Table 3. Pairwise overlap areas and proportion of each forest type in overlap areas between neighbouring saki groups. Only pairs with overlapping home ranges (defined as the 95% kernel polygons) are shown.

Overlapping groups	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

Time budget and movements in different habitats

Feeding/foraging was the most frequent activity pattern, comprising 51.3% of all scans (between-group range 35.4% to 53.8%). The remaining time was spent resting (24%), moving (20%), or in social activities (5%), including grooming, playing and interacting with neighbouring groups. Over half of the time allocated to each of four main activities by all saki groups was in terra firme forest. Considering all groups, sakis spent more time resting in floodplain forest than expected, and less time in palm swamp and bamboo habitats; in fact, 75% of the relatively small amount of time in palm swamp was spent feeding (Figure 4). Social behaviour, 40% of which pertained to agonistic interactions between groups, was recorded more often than expected in terra firme forest (χ^2 = 115.5, df= 3, p<0.001), and the percentage of the agonistic interactions in terra firme forest (84%) was significantly higher than expected (S. Palminteri, unpublished data; χ^2= 33.7, df = 2, p<0.0001).

The preference of sakis for terra firme habitat and avoidance of bamboo and palm swamps was even more pronounced for their overnight sleeping sites (χ^2 = 124.0, df = 3, p<0.0001). Of the 330 sleeping sites recorded for all five study groups, 212 (64%) were in terra firme forest, 116 (35%) in floodplain, two on the edge of a palm swamp, and sleeping sites were never recorded in bamboo habitat.

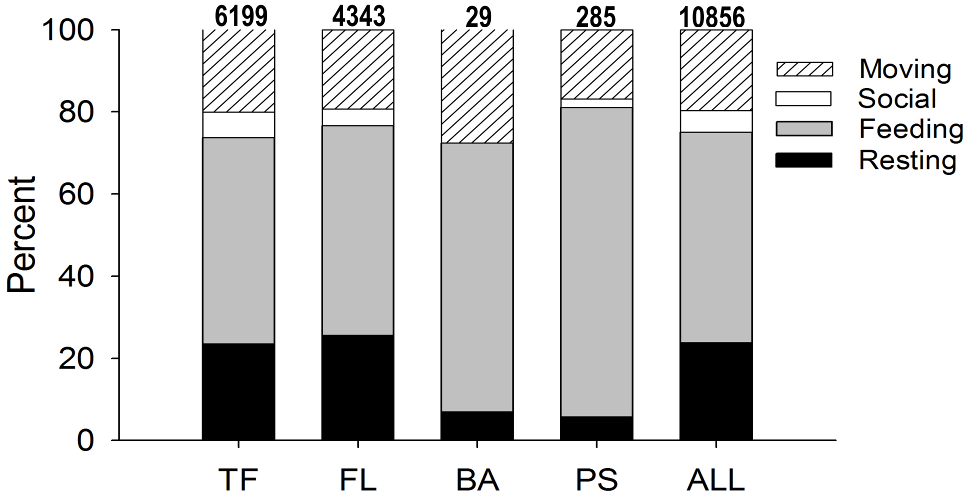


Figure 4. Activity budget (resting, feeding, moving, social) within four main forest types [terra firme (TF), floodplain (FL), bamboo (BA), and palm swamp (PS)] for five habituated groups of bald-faced sakis. Right-hand column (ALL) denotes the aggregate activity budget in all habitats. The number of observations in each forest type is listed above each column. Behavioural data collected by an 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 describe the overall group behaviour, but also that activity patterns of group members of were largely synchronized.

Sakis moved in a trajectory that usually took them from one boundary of the HR to another during the course of a day and included foraging in different habitats (Figure 5), rather than a single core area. The straight-line distance (SLD) between consecutive sleeping trees (306 m, range 0−838 m, N = 152) did not differ among saki groups ($F_{4,147}$ = 1.376, p = 0.245). However, the three groups using primarily terra firme forest travelled significantly faster and exhibited significantly longer daily path lengths (DPL, 1,108 ± 302.6 m) than the two groups with HRs dominated by floodplain forest (868 ± 187.8 m, $F_{4,129} = 5.03$, $p<0.001$; Table 4). Travel velocity, calculated for 15-min steps during which any forward movement occurred (median = 140.8 m/h; N = 5242), was not significantly different in terra firme, floodplain, and palm forest (137 - 141 m/h), but significantly faster in bamboo forest (251 m/h, H = 9.342, df = 3, p = 0.025).

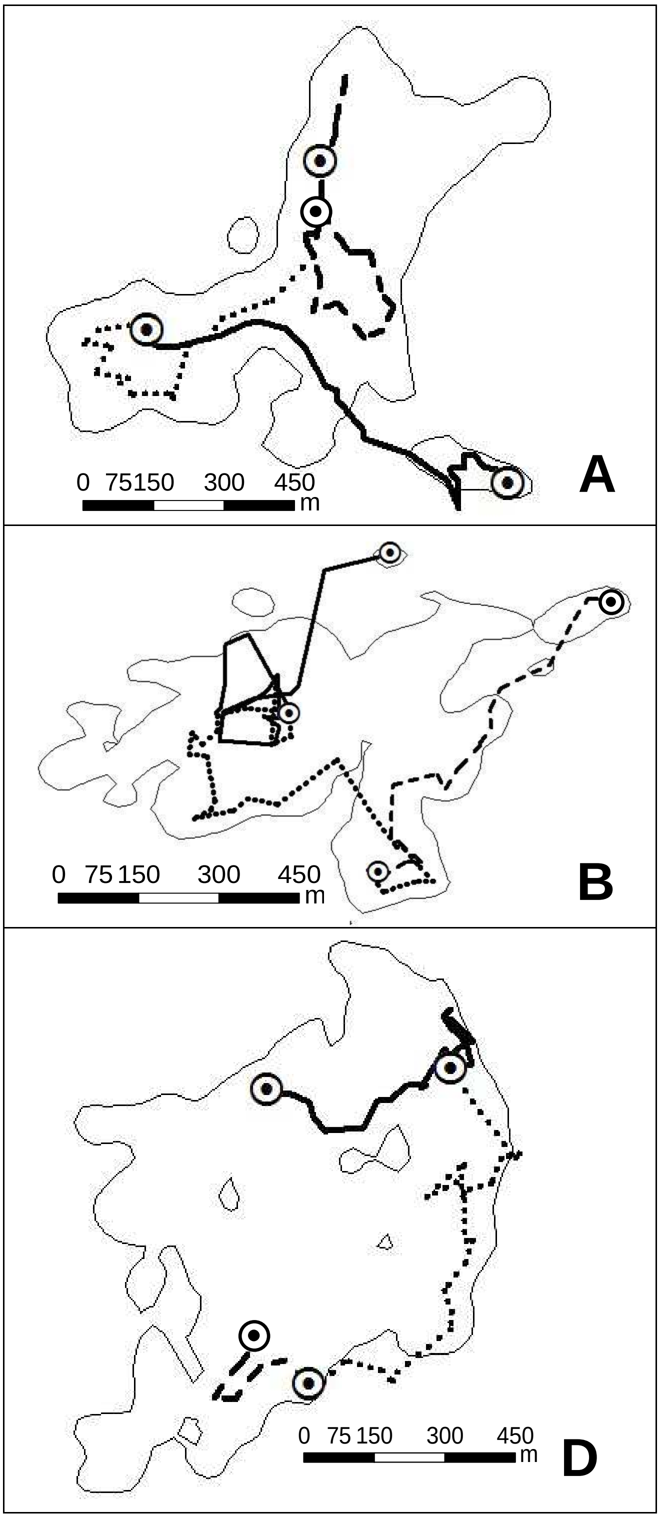


Figure 5. Sample travel paths of three consecutive full days of observation (solid, dotted, dashed lines = days 1, 2, 3) for three bald-faced saki groups showing typical group trajectories within their home ranges. Circled solid dots represent sleeping trees.

Table 4. Mean daily travel path lengths (DPL), relative day paths (DPL/HR), and straight-line distances (SLD) between consecutive sleeping sites of five saki groups, together with mean daily percentage of terra firme forest and median travel velocity.

Group	**No. sample days**[1]	**Mean daily % TF ± SD**[2]	**Mean DPL ± SD (m)**	**Range (m)**	**Relative DPL**[3]	**DPL / Group size**	**Mean SLD ± SD (m)**[4]	**Median travel velocity (m/h) (range)** [5]
A	140 / 51	61.0 ± 30.7	1,075 ± 298	593 – 1,741	25	229	321 ± 216	84 / 141 (0 – 969)
B	138 / 44	93.8 ± 8.2	1,176 ± 305	619 – 1,722	38	181	278 ± 146	100 / 156 (0 –1,072)
C	23 / 2	n/a	777 ± 2	775 - 778	25	370	193 ± 10	8 / 119 (0 – 543)
D	104 / 24	13.2 ± 22.0	872 ± 194	497 – 1,325	15	219	351 ± 162	72 / 128 (0 – 1,339)
E	55 / 13	86.9 ± 16.4	1,013 ± 287	579 – 1,489	65	390	237 ± 249	63 / 128 (0 – 924)
All	460 / 134	64.8 ± 36.8	1,062 ± 299	497 – 1,741	32	267	306 ± 189	80 / 141 (0 – 1,339)

[1] Sample days = all days used to assess travel velocity / "full" days used for DPL. [2] Daily % TF = percentage of each day's 15-min scans spent in terra firme forest. [3] Relative DPL = daily travel path (m) / home range (ha); [4] SLD = straight-line distance between consecutive sleeping sites. [5] Travel velocity based on distance travelled during 15-min steps, considering all steps / considering steps for which velocity > 0.

Across all groups, both group size and habitat type (percentage of observations in terra firme forest on a given day) were positively correlated with DPL and relative DPL [$\log_{10}$ (DPL / HR size)] and negatively correlated with day path linearity (Table 5), although in each case the partial correlations were either weaker or non-significant. The significant positive relationship between group size and DPL remained across habitat types, while the relationships between percentage of observations in terra firme forest on a given day and relative DPL and path linearity, respectively, remained significant, regardless of group size (Table 5). Likewise, groups B and E, with HRs dominated by terra firme forest, had significantly more sinuous (less linear) day paths than those of group D ($F_{3,114} = 5.43$, p=0.002), which primarily used floodplain forest. The turning angles between 15-min group locations (48.6°, range 0° – 180°, N = 4,659, mean 63° ± 51° SD) did not differ across forest types (H = 5.71, df = 3, p = 0.127) or groups (H = 4.51, df = 4, p = 0.341).

Table 5. Pearson correlation coefficients between three movement metrics for bald-faced sakis – day path length, relative day path length (day path length / home range area), and the straight line distance:day path length ratio – and two contrasting influences on movement patterns – habitat type (the percentage of each day's observations within terra firme forest) and group size (the number of individuals in the group each day). DPL = day path length , Log_{10}_RelDPL = $\log_{10}$-transformed relative DPL. SLD:DPL = Straight line distance:DPL ratio.

Movement Metric	**% terra firme**	**% terra firme (partial correlation)**	**Group size**	**Group size (partial correlation)**
Day Path Length	r = 0.201 P = 0.02 N = 134	r = 0.064 P = 0.47 df = 131	r = 0.311 P < 0.001 N = 134	r = 0.250 P = 0.004 df = 131
Log_{10}_RelDPL	r = 0.552 P < 0.001 N = 134	r = 0.534 P < 0.001 df = 131	r = 0.192 P = 0.03 N = 134	r = −0.097 P = 0.27 df = 131
SLD:DPL	r = −0.338 P < 0.001 N = 119	r = −0.291 P = 0.001 df = 116	r = −0.185 P = 0.04 N = 119	r = −0.043 P = 0.64 df = 116

Discussion

Patterns of habitat use

Our results indicate that while *Pithecia irrorata* in south-eastern Peru is not restricted to terra firme forest, groups show a strong preference for this forest type. Although saki groups did not maintain a minimum proportion of terra firme forest within their home ranges and were not terra firme obligates, their HR size, overlap areas between neighbouring HRs, patterns of habitat use, and spatiotemporal distribution of foraging activities and sleeping sites all indicated strong selection for terra firme habitat over other forest types. Terra firme forest comprised a higher proportion than that expected by chance for both overall occurrences and the distribution of core HR areas for all four groups with at least some access to this forest type.

While group size explains part of the variation in home range size in primates (Milton and May 1976), our results at the population level point to the importance of habitat type, rather than group size, in determining population density and ranging behaviour in our study region. Although group size can affect home range size in large-group living primate species (e.g. Dunbar 1988), our results are consistent with the negative relationship between HR size and habitat quality found for other primate species and genera (Struhsaker 1967, Dietz et al. 1997, DiFiore 2003). Terra firme-dominated HRs tended to be smaller, resulting in saki densities in terra firme forest that were double those in floodplain forest. A comparison of habitat selection and ranging patterns with other *Pithecia* populations 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 (Soini 1986, Peres 1993b). However, smaller HRs recorded for congeners north of the Amazon (*P. pithecia,* Norconk 2007) are consistent with the lower body mass of white-faced sakis, undersampling of unhabituated groups (Norconk et al 2003), and, possibly, competition with larger-bodied sympatric pitheciines, primarily bearded saki monkeys (*Chiropotes spp.*, Peres 1993b).

Although the correlation between the proportion of terra firme forest in the HRs of our five saki groups and their proportional overlap with neighbouring study groups was not statistically significant (r = 0.772, p = 0.126, N = 5), the addition of unknown areas of HR overlap of groups B and E with those of unhabituated groups would have strengthened this relationship. We observed two of those elusive groups using portions of the HRs of our study groups, all in terra firme forest, thereby increasing the overall intensity of use by *Pithecia* of this habitat. While HR overlap among our terra firme study groups reached only 33% (Table 1), quantification of the overlap area between groups B and E and unstudied neighbouring groups would have increased HR overlap estimates to levels closer to the 50% overlap of HRs of terra firme populations of buffy sakis (*P. albicans*) reported by previous studies (A. Johns, unpublished manuscript; Peres 1993b).

This contrasted with the situation among our floodplain forest groups, for which overlap was less than expected by chance. For example, an unhabituated group of only two individuals with a small HR in floodplain habitat adjacent to those of study groups C and D (Figure 2f) was never observed within the HR of either of these groups, despite interacting vocally with group C. In the extensive seasonally flooded forests of northern Peru, where terra firme forest was not available, the HR of a group of monk sakis (*P. monachus*) overlapped <1% and ~70%, respectively, with those of its two neighbours (Soini 1986), showing that extensive overlap among floodplain groups may occur under some circumstances. Nevertheless, our data indicate a general lack of HR overlap in floodplain forest, which further contributes to the observed variation in saki densities across the MDD region.

Time budget and movements in different habitats

Despite the smaller home ranges of bald-faced saki groups containing more terra firme forest, their absolute and relative day paths tended to be longer and more sinuous. These groups thus covered a larger area of their respective HRs each day than groups with more floodplain habitat. That 72% of known overlap area and 84% of observed agonistic interactions occurred in the terra firme portions of all HRs may indicate a greater propensity for groups to defend preferred terra firme forest habitat. The tendency of groups to move across opposite boundaries of the HR within a day, combined with the higher than expected use of overlap areas, which were terra firme dominated, further suggests higher time and energy allocation to exploitative and/or interference defence of higher-quality territories.

While more than half of the time spent by sakis in each of four main activities was in terra firme forest, other forest types were targeted for specific activities, a strategy seen in other primates (e.g. Porter et al. 2007). For example, sakis foraged significantly more often than expected by chance in palm swamp (Figure 4), where they primarily consumed *Mauritia* palm fruits. The canopy structure of *Mauritia* palm crowns, which are widely spaced with little horizontal connectivity, requires frequent leaps that make movement conspicuous and therefore risky for this otherwise behaviourally cryptic species. Sakis thus appeared to minimize their vulnerability in *Mauritia* palm swamps by largely restricting their time in this habitat to feeding bouts. The disproportionately high amount of time spent feeding and lack of forward movement in both palm swamp and bamboo forest and intensive use of the edges of these habitats (Figure 2) suggest that sakis entered these relatively open-canopy forest types to access a specific food source and return to closed-canopy floodplain or terra firme forest as directly as possible.

Landscape-scale detection and population density

In a series of mammal surveys across the Madre de Dios region of southern Peru, Palminteri et al. (Chapter 2) partly attributed the high variability in saki abundance among sites to their higher abundance at terra firme sites. Consistent with those findings, a number of behavioural traits identified here may elevate saki encounter rates in terra firme habitat. Saki groups are more tightly packed in terra firme forest habitat because of both smaller HRs per individual and the much higher overlap among HRs, which increased our group densities by 5 to 50%. While our habituated saki groups were similarly observable in mature flooded and unflooded forests, unhabituated groups are likely more detectable in terra firme forest, as they spend more of their time, feed more frequently, and tend to be more vocal (intergroup encounters) while in that habitat type, all of which may create an appearance of even greater densities for this normally highly cryptic species.

However, these factors are insufficient to explain all of the observed regional-scale variation in saki population densities. Sakis were absent from eight of eleven floodplain forest survey sites and from four of 19 terra firme forest sites in Madre de Dios (Chapter 2). Sakis in this region face little hunting pressure, habitat disturbance from forest fragmentation and logging, or potential competition from other seed-eating vertebrates (Chapter 6). Thus, the observed patchiness in regional-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 (e.g. fluvial barriers: Ayres and Clutton-Brock 1992), to better understand saki distribution and abundance at the landscape scale. Further studies of the habitat use and feeding ecology of *Pithecia*, in conjunction with the spatiotemporal distribution of food resources, in areas with varying saki densities (including absences), would help strengthen our understanding of this enigmatic species by elucidating, for example, how food availability in terra firme forest compares to that in other forest types and which canopy structure characteristics are favoured by sakis and how they are distributed across forest types.

Quantifying the patterns of use of space across different forest types can help explain the variation in *Pithecia* density 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, Peres 1997, Sheth et al. 2009, Chapter 2). 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. At Los Amigos, use by sakis of mature floodplain forest depended on the presence of highly-developed forest structure to a greater degree than their use of terra firme forest (Chapter 7). Our results suggest that the wider terra firme forest matrix spanning the vast interfluvial regions of lowland Amazonia will pack more *Pithecia* groups per unit area, thereby facilitating greater HR overlap and 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 *Guadua* bamboo predominates, including large portions of south-western Amazonia (165,000 km^2, Nelson 1994, Smith and Nelson, submitted/in press). Alarmingly, these areas are expected to expand under a scenario of increasing frequency and/or severity of seasonal droughts and wildfires (Barlow and Peres 2004, Asner et al. 2010, Smith and Nelson submitted/in press), as already witnessed in south-western 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 (Nepstad et al. 1999, Asner et al. 2010) 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-induced invasions of *Guadua* bamboo should become a regional conservation priority.

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Chapter 5: On the advantages of granivory in seasonal environments: feeding ecology of an arboreal seed predator in Amazonian forests

Abstract

Seed predation among arboreal vertebrates has been primarily considered a response to seasonal ripe fruit scarcity faced by most generalist frugivores. The suggestion that consuming seeds of immature fruits — that are available for relatively long periods compared to mature fruit — may reduce seasonal food scarcity experienced by primary consumers remains largely untested. To test whether immature fruit was available over longer periods or more consistently than ripe fruit, we examined the diet and feeding behaviour of bald-faced saki monkeys (*Pithecia irrorata*) in southeastern Peru based on systematic monitoring of five habituated groups over a 3-year period, and compared the relative availability of ripe and unripe fruits in their diet. Phenology data showed that immature fruits were available for longer periods within individual crowns of a given tree and liana population, in more species, and in greater quantities than ripe fruit. Fruit availability, however, did not substantially affect the feeding patterns or food preferences of sakis: fruits comprised an average of 95% of sakis' monthly diet, with seeds alone accounting for 75%, and no major monthly dietary shift was recorded despite pronounced community-wide seasonal changes in fruit production at our study area. The wide taxonomic spectrum of over 220 plant species consumed by sakis, comprised mainly of seeds of unripe fruits, likely minimizes both dependence on particular plant species and intra- and interspecific competition for individual food species or discrete food patches. The flexible exploitation by sakis of a relatively aseasonal food supply for which they face little competition may reduce their need to expend greater foraging effort or consume less desirable foods, even during prolonged seasons of fruit scarcity.

Introduction

Fruit is a key element in the diet of many tropical forest vertebrates, including virtually all diurnal primates, most of which consume ripe fruit pulp (Terborgh 1983, Cowlishaw and Dunbar 2000), which is typically a highly ephemeral resource (Fleming et al. 1987, van Schaik 1993, Peres 1994). Individual fruits remain in an immature stage for relatively long periods before maturation (Denne 1963, Bollard 1970), and trees and woody lianas bear immature fruit for longer periods than ripe fruit (Janson and Emmons 1990, Peres 1994, Haugaasen and Peres 2007). Norconk (1996) has suggested that feeding on seeds of immature fruit may be an adaptation to minimize seasonal variation in food availability. The relative rarity of specialised seed predators, compared to the overall seed availability, may also translate into reduced interspecific competition (van Roosmalen et al. 1988, Janson and Emmons 1990). Moreover, seeds tend to contain a higher nutritional value per unit volume than other plant parts, such as ripe fruit pulp and leaves (Janzen 1971, Fleming et al. 1987), including higher levels of both protein and lipids (Garber 1987, Kinzey and Norconk 1993). Animals that specialise on unripe fruits may therefore be able to use less ephemeral, more reliable fruit resources than pulp-eating generalist frugivores can. They may also exhibit less pronounced spatial, dietary and physiological changes that are considered to be seasonal responses to food scarcity. These include home range relocation into more favourable areas (Leighton and Leighton 1983); socioecological adaptations in group structure, such as fissioning into sub-groups (Symington 1988, Norconk and Kinzey 1994); increases (e.g. Peres 1994, Matthews 2009) or decreases (e.g. Stevenson et al. 2000, DiFiore and Rodman 2001) in daily travel distances; shifts to alternative food resources, such as arthropods, nectar, or leaves (e.g. Terborgh 1983, Symington 1988, Peres 1994, Stevenson et al. 2000, Palacios and Rodriguez 2001); and seasonal reduction in body mass (e.g. Goldizen et al. 1988) and/or metabolic rate (Schmid 2000). Yet the general hypothesis that vertebrate seed predators targeting unripe fruits are less likely to experience seasonal food scarcity than pulp-eaters (Janson and Emmons 1990, Norconk 1996) remains largely untested.

Despite the potential benefits of seed predation as a foraging strategy, specialised consumers of immature seeds are relatively rare in primates. In the Neotropics, only the larger Pitheciines (*Cacajao*, *Chiropotes*, and *Pithecia*) are known to specialise on seeds (van Roosmalen et al. 1988, Kinzey and Norconk 1993). There has been relatively little systematic research on the feeding ecology of these genera. While the feeding ecology of one of the five species of saki monkeys (*Pithecia* spp.) has been studied systematically in northern Amazonia (*P. pithecia*: Kinzey and Norconk 1993, Norconk 1996, Cunningham and Janson 2006), the remaining four species (*P. albicans*, *P. albicans*, *P. monachus* and *P. aequatorialis*), all of which occur in southern and western Amazonia, have been observed only through opportunistic sightings during synecological primate surveys and follows of unhabituated groups (Happel 1982, Johns 1986, Soini 1987, Peres 1993). In the two longest studies of these species, seeds comprised 40% of feeding observations for *P. monachus* in north-eastern Peru (Soini 1987) and 46% for *P. albicans* in central-western Brazilian Amazonia (Peres 1993). A preliminary study in southeastern Peru indicated that bald-faced saki monkeys (*Pithecia irrorata*, hereafter sakis) not only foraged primarily on seeds of immature fruits (>80% of overall diet) during the season of relative fruit scarcity but consumed seeds from a wider range of plant species, without switching to other plant parts (Chapter 6). This suggests that seed predation as a year-round dietary strategy may afford bald-faced sakis access to a broader spectrum of food species and perhaps a more reliable food supply.

In this study, we tested whether sakis, by consuming seeds of unripe fruits, experience reduced seasonal food scarcity by comparing the relative availability of ripe and unripe fruit in the study area, focusing primarily on the wide array of plant genera in the saki diet. We hypothesized that saki food plants would bear immature fruit for longer periods than mature fruit and that, at any given time, the richness of plant species bearing immature fruits consumed by sakis would be higher than that of ripe fruit. We further predicted that whenever fruit was available, each food plant species would supply larger crops of immature fruits per tree (hereafter referred to as productivity) than those of mature fruit. In sum, immature fruit would be available more consistently over time across food patches and in larger numbers within a given food patch than mature fruit. We also monitored the seasonal variation in the diet and feeding ecology of five habituated saki groups over a three-year period to test the corollary to the reduced seasonality hypothesis, that, as seed predators, their diet would (i) be largely independent of mature fruit availability, thereby including high intakes of fruit parts all year-round and (ii) remain taxonomically diverse, rather than show the pronounced seasonal dietary switches to alternative plant resources and/or arthropods that have been typically reported for sympatric primates that forage primarily on mature mesocarps. Finally, if unripe fruit parts are more consistently available over time, then territorial defence through agonistic interactions toward neighbouring groups would occur independently of food availability.

Methods

Study area

The study took place in south-western Amazonia, between the Madre de Dios and Los Amigos rivers in Madre de Dios (MDD), Peru on the 145,000-ha privately managed Los Amigos Conservation Concession. This region supports an exceptionally high species richness of trees (Gentry 1988) and primates (Emmons 1984, Terborgh 1983). The focal saki group study area (335 ha), described in more detail in Chapter 4, contains both mature floodplain forest subjected to a supra-annual flood pulse and unflooded terra firme forest. Phenological data were collected along 30 km of trails north of the Los Amigos River, adjacent to the saki study area (Figure 1). Over 70% of the year-round precipitation falls within 6 months (October and March), so for this study we distinguished two main seasons: wet (October – March) and dry (April – September).

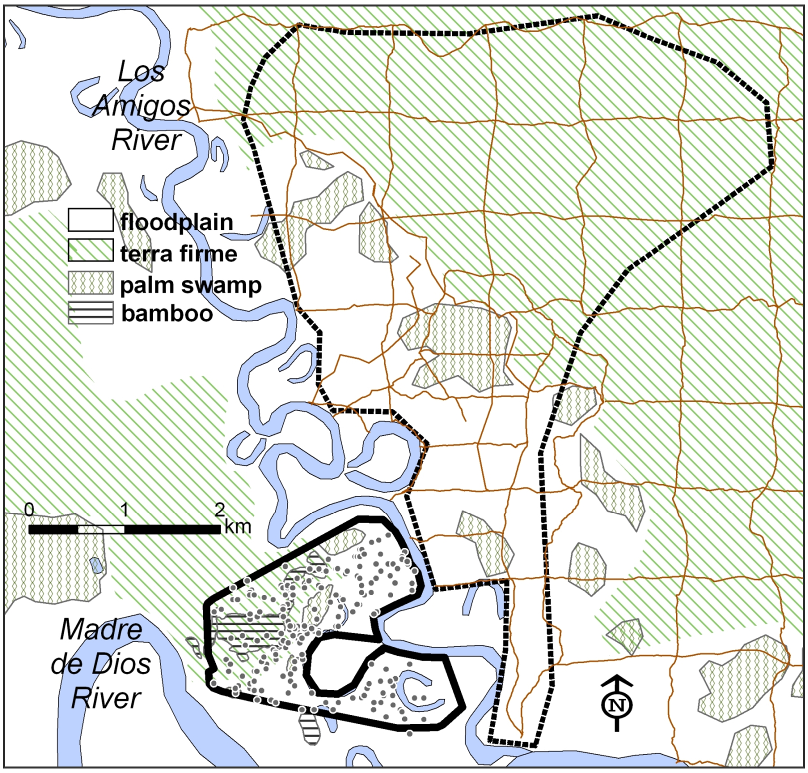

Figure 1. Map of the study area at Los Amigos, Peru, showing the focal saki group area (solid black outline) and the phenological data collection area (broken black outline) along adjacent trail systems. Floristic plots are represented by grey dots.

Data collection

Food availability

To estimate the temporal availability of saki food, we extracted data on 573 plants, comprised of 512 fertile trees ≥10cm in diameter at breast height (DBH), 9 lianas, and 52 arborescent palms, belonging to 129 species or morphospecies that were known or probable saki food plants from an unpublished 39-month phenology study (March 2005 – May 2008) on food plants for a suite of frugivorous bird and mammal species (G. Powell and R. Tupayachi, unpubl. data). Phenology plants were located within 10 m bands (30 m for exceptionally rare emergent trees) on either side of nine trails within a 30 km trail grid covering ≈18 km^2. Phenology plants were marked and identified to the level of species or morphospecies [range 1-25 individuals per (morpho)species, mean 4.4 ± 4.8 SD]. Each tree crown was visually monitored using a pair of 10x40 binoculars on a monthly basis and assigned a productivity value of 0−5 for each phenophase of reproductive plant parts (flowers, immature fruits, and mature fruits) where 5 was the maximum potential score (Fournier 1974). Mature and immature fruits were distinguished in each case on the basis of texture and colour of fruits still attached to the plant or the same traits plus smell and taste of fruits (or fruit fragments) collected on the ground following abscission or vertebrate consumption of whole fruits. However, only those fruits still attached to plants were recorded to derive availability metrics from phenology surveys. All phenology plants were usually observed within the same 5 – 6 day period each month, with intervals of 27 – 33 days between consecutive visits to the same tree. Whenever either the saki food item or the monitored phenology tree could only be identified to genus and morphospecies, trees belonging to the genus (congeners) were combined.

To independently estimate abundance of saki food plants in the study area, we located 192 floristic plots, totalling 2.81 hectares, by digitally overlaying a 25 x 25m grid on the study area and randomly selecting 60-65 grid cells in each of three levels of saki use intensity, based on initial two years of focal group monitoring. We obtained density data on additional plant species from 18 plots, totalling 1.8 ha, inventoried in the study area by BRIT (2010).

Feeding patterns

Five adjacent groups of bald-faced sakis (mean group size = 4.7 ± 1.5 SD, range = 2 – 8) were previously habituated and then followed for up to 5 consecutive days per month, for between 6 and 28 (mean 20.2 ± 8.9) months each, between January 2005 and December 2007 (see Chapter 4 for details on observational sampling). To investigate feeding patterns and food selection, we used instantaneous group scan sampling (Altmann 1974), taking a scan every 5 min, during which we recorded the group's location, modal activity pattern, forest type, and vertical position. We categorized all scans for each group as resting, feeding/foraging, moving, or socializing (including intergroup agonistic interactions), omitting all scans for which the activity was not known (4% of ≈36,000 total 5-min observations). Insect feeding was also excluded from this analysis. For all plant feeding bouts observed within a given food patch, we recorded the plant species (or morphospecies), plant part consumed (seed, mesocarp, whole fruit, flower, young leaf), and status of maturity of fruits or seeds consumed.

Data Analyses

Fruit availability

To estimate the overall monthly availability of immature and mature fruit, we first calculated the monthly productivity score for either immature or mature fruits produced by each phenology plant multiplied by its basal area (cm^2, Develey and Peres 2000), as tree DBH is a reliable predictor of both immature and mature fruit crop size (Chapman et al. 1992, Leighton & Leighton 1982). We calculated the mean of these scores for all trees in each species, to correct for uneven sample sizes, and summed the species means to produce a monthly fruit availability index (FAI). We then examined the monthly variation in both the number of species bearing immature and mature fruits and their FAI scores using one-way ANOVAs with Tukey post-hoc tests.

To examine whether the availability of immature fruits included in the diet of sakis was less ephemeral than that of ripe fruits, we used a paired t-test between the log-transformed numbers of sample months (N=39) during which each plant species produced immature fruit and mature fruit. Paired t-tests were also used to compare the number of species bearing immature fruit in each sample month to that bearing mature fruit, the mean monthly productivity values of immature and mature fruit for each species, and the FAI values for the two phases of maturity.

Feeding patterns

We tested for monthly differences in the proportion of time allocated to plant feeding using a one-way ANOVA and the proportion allocated to either seeds (predominantly immature fruit) or fruit pulp (almost exclusively from mature fruit) using a paired t-test, across the 31-month saki observation period. We used Pearson correlations to compare the availability of immature and mature fruit — represented by the number of plant species, productivity, and FAI scores for either immature and mature fruit — to patterns of feeding behaviour, including the proportion of time sakis spent feeding, the proportions of seeds and pulp in the diet, and the dietary species richness. Spearman rank correlations were used for parameters with non-normally distributed data. To standardize for varying observation effort across months, dietary species richness was represented by the number of food species per 100 five-minute observations. We evaluated the dietary importance of flowers and several key food genera (e.g. *Inga*, *Mauritia*, *Socratea*) by comparing their respective contributions in monthly diets (% time) to the overall and genus-specific availability measures on the basis of phenological surveys. To assess whether sakis allocated more time to agonistic interaction with neighbouring groups during times of fruit scarcity, we correlated the total number of intergroup encounters per 100 h of observation to our measures of overall fruit availability.

To assess the relationship between use and availability of a given food plant genus by sakis, we used the comprehensive vegetation data set obtained from the 210 floristic plots (≈ 4.28 ha), which were evenly distributed throughout the study area (Figure 1, BRIT 2010), to measure the abundance of 58 food genera representing 72% of all feeding observations on plant items (N = 6,703). To examine preference for a given food plant genus relative to its abundance in the study area, we extracted the residuals from a regression equation predicting the proportional contribution of each genus in the overall diet based on the overall density of trees of that genus in the vegetation plots. Positive residuals indicated preference or positive selection, whereas negative residuals indicated less use than expected, given abundance. Of the 129 plant food morphospecies recorded in this study, 100% and 60% were identified to genus and species, respectively. For our comparative analyses, we therefore restricted the taxonomic resolution of plant identification to genus because the number of morphospecies in both the plant diet and the floristic plots rendered species-level comparisons unreliable. To account for habitat specialisation of tree genera to a particular forest type – those for which >80% of feeding observations were restricted to either floodplain or terra firme forest (the two dominant habitat types used by sakis) –

we related the proportion of feeding time allocated to the genus in that forest type to its abundance in floristic plots in that forest type.

Finally, to determine whether preference for particular food plant genera was related to fruit availability, we correlated the preference score of each plant genus to the number of months in which fruits were available, the mean fruit productivity score, and the FAI score. We also compared preference scores to the number of months in which each genus was consumed by sakis and its respective proportion in the saki diet. For variables representing monthly availability and phenology scores, we applied genus-specific data for immature fruit unless sakis consumed only mature fruit from that genus. Using one-way ANOVAs, we also compared the saki preference score of each food plant genus to (1) the stage of maturity (immature, mature, both) in which fruits were taken; (2) fruit morphology (*sensu* Janson 1983: fleshy mesocarp or aril with a minimal pericarp; pods or fleshy pulp surrounded by a protective pericarp; and tough / sclerocarpic fruits); and (3) the principal habitat type in which the genus was used (terra firme forest, floodplain forest, or both).

Results

We observed the sakis feeding on fruit during >8,800 5-min. scans during 3,000 hours of observation, during which they consumed fruits or seeds of 216 species from at least 112 plant genera belonging to 53 families (Appendix). The combined proportions of seeds, pulp, and whole fruits taken each month averaged 95.8% ± 7.0% SD of the monthly plant-based diet, with seeds (187 species) comprising most (58 – 88%) of sakis' diet during all months, except May (early dry season, 47%, Figures 2 and 3). Sakis typically extracted seeds from unripe fruit, leaving the pulp unconsumed (71% of all feeding observations). Rarely, however, sakis continued to consume seeds of a species even after the fruit appeared to be mature to observers, but these cases comprised fewer than 50 feeding scans. Feeding on ripe fruit pulp, principally from the genus *Inga* and the palm *Mauritia flexuosa*, together with fruits from 19 other genera, comprised 25% of total plant feeding time and peaked in May. Flowers and young leaves contributed just 3% and 1%, respectively, to the overall diet.

Fruit availability

Based on monthly phenology data from 573 plants representing 129 species (62 genera in 31 families), the number of species bearing immature and mature fruit showed marked seasonal variation. The number of species bearing immature fruit was highest in September (late dry season, mean ± SD = 42.7 ± 6.1 species) and declined through March (late wet season, 22.5 ± 9.2), with the exception of a possible second peak in January, before increasing again ($F_{11,27} = 3.17$, P = 0.01, Figure 1). This pattern was mirrored in the immature fruit availability index (FAI, productivity x basal area), which was significantly higher in the late dry season (August-September) than late wet season (March-April, $F_{11,27} = 5.14$, $P < 0.001$). The number of species with mature fruit tracked a similar trend, but the second peak (25.0 ± 2.0 SD species) was in February, rather than January, declining thereafter through June ($F_{11,27} = 4.00$, P = 0.002, Figure 2). The FAI score for mature fruit was highly variable across years and did not differ significantly across months ($F_{11,27} = 0.60$, P = 0.81).

Immature fruit was more consistently available to arboreal consumers than mature fruit using all three measures of availability. The number of species per sample month (*N* = 129) with immature fruit (mean ± SD = 32.0 ± 8.5 species) was double that with mature fruit (15.6 ± 5.1 species, paired t-test: t = 12.16, df = 38, $P<0.0001$). Fruiting periods for immature fruit of each species were also longer (median = 7 months, range = 0 – 39 months) than those of mature fruit (median = 2 months, range 0 – 39 months, paired t-test: t = 11.90, df = 128, $P<0.0001$), suggesting a substantial potential advantage to consuming immature seeds rather than, or in addition to, ripe fruit pulp. Trees bore immature fruit not only for longer periods but also in greater quantities than mature fruit. Across all trees in 129 monitored plant species, the mean monthly productivity score for immature fruit (mean ± SD = 0.31 ± 0.13) was significantly higher than that for mature fruit (0.09 ± 0.04, paired t-test: t = 10.14, df = 38, $P<0.0001$). Per capita productivity scores adjusted for tree basal area greatly amplified this difference. Mean FAI scores for immature fruit (380.0 ± 152.2) were far greater than those for mature fruit (126.8 ± 78.0) in every sample month (paired t-test, t = 10.90, df = 38, $P<0.0001$).

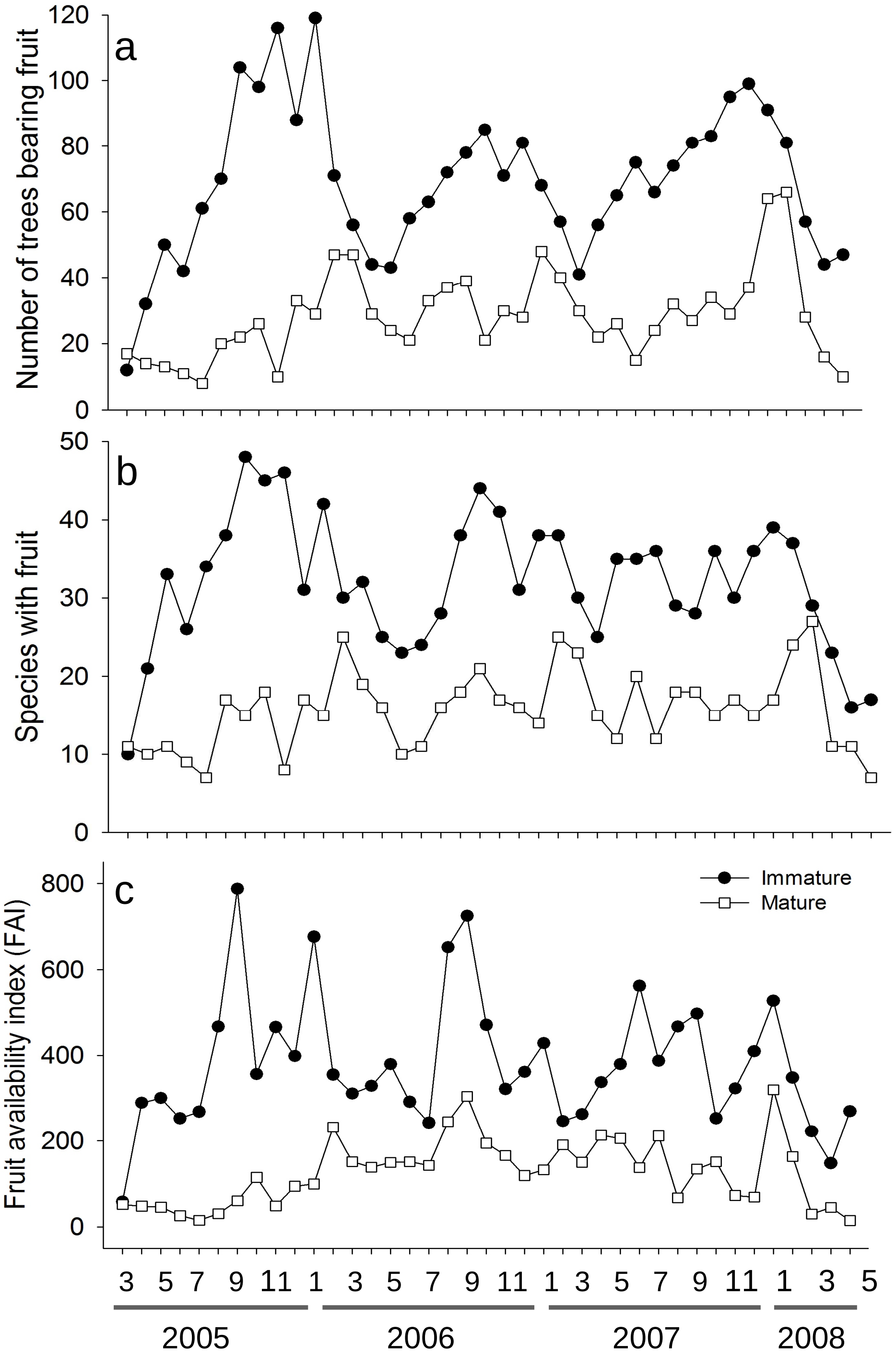

Figure 2. Monthly indices of immature and mature fruit availability, calculated for 573 saki food plants (98% trees ≥ 10cm DBH) over 39 months at Los Amigos. (a) Individual plants (predominantly trees) with fruit, (b) species with fruit, and (c) index of fruit availability (FAI). Months are numbered, beginning in March 2005.

Feeding patterns

The composition and diversity of the diet of sakis reflected the prolonged availability of immature fruits. The monthly proportion of time allocated to plant feeding (mean ± SD = 25.9% ± 5.9%) varied from 21.0% of all scans in February to 35.3% of scans in August but did not differ significantly among months (one-way ANOVA $F_{11,19} = 1.93$, P = 0.10). However, mean proportion of time allocated to plant feeding was not correlated with our measures of fruit availability or the number of tree species bearing either immature or mature fruit (Pearson correlations, N = 29, P>0.10 in all cases, Table 1). The proportion of feeding time dedicated to seeds was higher than that dedicated to pulp in all sample months, and usually considerably higher (paired t-test: t = 7.704, df = 30, P<0.0001). The proportion of immature fruit (seeds) in the diet remained high throughout the year (70.8% ± 17.1%, *N* = 31 months, Figure 3); excluding the values for May (47.3% ± 17.6% over the study period), this proportion rose to 72.3% (± 16.1%, *N* = 29). While consumption of pulp appeared to track mature fruit availability, it varied widely by month (5 − 39%) and was not significantly correlated with either the number of species bearing mature fruit or mature fruit availability (Table 1). The two months in which sakis consumed the lowest amount of immature fruit (April and May) were also those with the second and third highest levels of consumption of mature fruit (Figure 3). Consumption of flowers — 93% of which were from a single arborescent palm species (*Socratea exorrhiza*) — peaked from a base level of < 1% of feeding time to 16% when that palm flowered. Flower consumption, in fact, correlated most strongly with the availability of flowers of *S. exorrhiza* ($r_s = 0.851$, P = < 0.001, Table 1), suggesting that flowers were actually consumed preferentially, rather than as a fallback food. Flower consumption in June, in particular, was greater than predicted according to residuals of the positive linear relationship between *Socratea* flower availability and consumption. The positive correlation with overall productivity of immature fruit further indicates that flowers were consumed when other foods were also available.

To investigate possible links between the percentage of feeding time allocated to unripe and ripe fruit and seasonality in food availability, we assessed whether sakis might have altered their dependency on individual plant species during April and May. During this period, sakis fed more heavily upon ripe pulp of *Mauritia flexuosa,* a large palm forming monospecific stands of up to 15 ha that produced mature fruits all year-round. Sakis fed on *Mauritia* fruits at low to moderate levels throughout the year but sharply increased their use during April and May, when *M. flexuosa* accounted for 25% and

28% of their plant feeding time, respectively. In fact, the monthly proportion of *M. flexuosa* in the saki diet was strongly correlated with the percentage of both immature (seeds) and mature fruit (pulp) in the diet (immature, $r_s = -0.676$, $P < 0.001$, mature: $r_s = 0.753$, $P < 0.001$, $N = 31$). Neither overall consumption of immature or mature fruit nor the proportion of *M. flexuosa* in the sakis' diet correlated with the monthly availability score for mature *M. flexuosa* fruit (Spearman correlations $P > 0.10$ in all cases). The 26 species of the genus *Inga*, the other major source of ripe fruit pulp, accounted for 9.5% of the overall plant diet and comprised 5 - 19% of the monthly saki feeding time. The overall amount of ripe fruit pulp consumed each month correlated positively with both the productivity of *Inga* ($r_s = 0.468$, $P = 0.01$) and the contribution of this genus to the saki diet ($r_s = 0.446$, $P = 0.01$), yet both use and availability of *Inga* were lower in April and May, the period of lowest seed consumption.

Table 1. Spearman rank correlations between monthly variation (*N* = 29) in rainfall and fruit availability and the feeding patterns of bald-faced sakis. Feeding is defined as time allocated to feeding and foraging on plant material. Seeds and pulp are taken predominantly from unripe and ripe fruit, respectively.

Behavioural pattern	**Rainfall**	**Spp. with Imm**[1]	**Spp. with Mat**[2]	**Imm_F**[3]	**Mat_F**	**Imm_ FAI**[4]	**Mat_ FAI**
Prop. time feeding	-0.415*	0.117	0.006	0.025	-0.240	0.229	0.124
Feed time seeds (%)	0.056	0.284*	-0.033	0.344	0.131	0.252	-0.219
Feed time pulp (%)	0.304	-0.030	0.194	-0.443	-0.027	-0.285	0.289
Seeds / Pulp ratio[5]	-0.317	0.255	-0.202	0.420*	-0.098	0.216	-0.325
Feed time flowers (%)[5]	-0.426*	-0.052	-0.383*	0.427*	0.057	-0.008	-0.248
Species / 100obs	-0.076	-0.395*	0.105	-0.491*	0.081	-0.230	0.184
Genera / 100obs	-0.144	-0.408*	-0.087	-0.519*	0.110	-0.284	0.088
Max from 1 genus (%)[5]	0.203	0.007	-0.110	-0.076	-0.190	0.002	0.126
Intergr. interactions / h[5, 6]	0.259	0.146	0.295	-0.148	-0.185	0.255	0.419

* P ≤ 0.05. [1]Imm = Immature fruit, [2]Mat = Mature fruit, [3]F = Mean productivity/phenology score (0 – 5, Fournier 1974). [4]FAI = mean fruit availability score. [5]Pearson correlation. [6]Intergr. interactions / h = number of agonistic interactions between saki groups per hour of observation

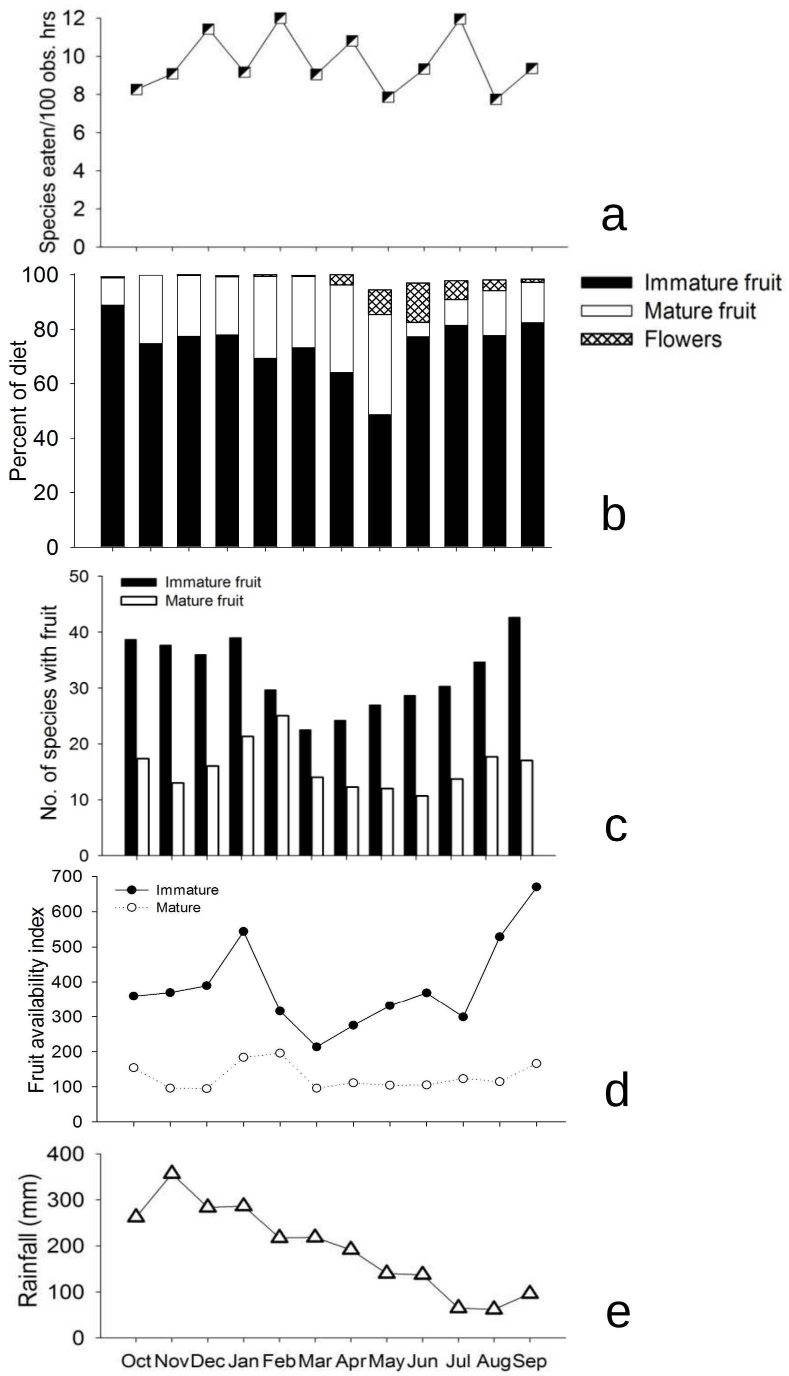

Figure 3. Mean monthly fruit availability and consumption patterns by bald-faced sakis, across 39 months (fruit availability) and 31 months (sakis), respectively: (a) mean number of species consumed per 100 h of observation; (b) mean proportion of feeding time allocated to seeds, pulp, flowers; (c) mean number of plant species with immature and mature fruit present; (d) mean fruit availability (FAI) of immature and mature fruit; and (e) rainfall (2005 – 2007). Given the relatively predictable seasonality to fruit availability (Figure 2), we combined all months of phenology and feeding data to a 12-month period to display annual cycles of resource availability and use. FAI = Monthly mean of productivity (phenology) score x basal area for each tree, averaged by species to correct for uneven sample sizes.

Dietary preference

Based on the floristic plot data, we were able to quantify the densities of 58 saki food plant genera comprising 72% of all plant foraging observations. Although *M. flexuosa* was a favoured species contributing an additional 9.3% of all plant feeding observations, it was excluded from the preference analysis because it accounted for virtually all trees in three small monodominant palm swamps in the study area but was rare in other forest types. The remaining 47% of the food genera were not found in the plots, so we were unable to independently estimate their densities. The densities of food plant genera occurring in the vegetation plots were positively correlated with their respective contributions to the sakis' diet ($r_s = 0.33$, $P = 0.01$, $N = 58$). The median preference score, represented by the residuals of the regression equation relating density to dietary contribution, was −0.006 (range −0.055 for *Iriartea* to +0.074 for *Inga*, Table 2, Appendix), and most plant genera were consumed slightly less than expected, given their overall abundance in the vegetation plots. In contrast, a few genera were both relatively abundant and highly preferred. For example, the five most preferred genera in the analysis — *Inga*, *Pseudolmedia*, *Brosimum*, *Eschweilera*, and *Pouteria* (range of preference scores: 0.04 – 0.07) — comprised 35% of sakis' total feeding time, and their mean overall dietary rank (4) was greater than their relatively high mean density rank (7) among the 58 genera for which density estimates were available.

Among the 42 genera for which we had density, diet, and phenology data, neither the duration of the fruiting period nor the fruit availability score (FAI) correlated with the degree of dietary preference (Table 2). This was true both for all food genera and for the five top-ranking genera, the FAI scores of which did not differ from those of other genera (Wilcoxon rank-sum test: $W = 93$, $Z = -0.543$, $P = 0.59$, $N = 42$). Higher preference scores correlated most strongly with the number of months in which food plants contributed to the diet (Table 2). Preferred food genera were used three times as long as non-preferred genera despite the low correlation between preference and fruit availability. Preference scores of the various plant genera did not differ by whether immature fruit, mature fruit, or both were consumed, nor by fruit morphology or the principal habitat type in which each food genus was consumed ($P > 0.10$ in all cases).

Table 2. Spearman rank correlations of genus-specific preference scores by bald-faced sakis, based on the residuals of a regression equation predicting the proportion of each food plant genus in the bald-faced sakis' diet to its density in the study area. Summary characteristics of preferred and non-preferred plant genera (*N* = 58 genera found in both the diet and vegetation plots, 42 of which were also found in phenological study) are also listed.

	Correlation with pref. score	**P**	**Preferred (*N* = 20)**[1]	**Non-preferred (*N* = 38)**
Preference score	n/a	n/a	0.021 (0.002 – 0.074)	–0.008 (–0.055 –0.002)
Prop. of months with fruit (N = 39, mean ± SD)	-0.090	0.571	0.51 ± 0.29	0.45 ± 0.30
No. calendar months with fruit (N = 12, mean ± SD)	0.184	0.170	8.9 ± 2.9	6.2 ± 4.0
Imm. F-score[2]	-0.163	0.301	0.291 (0.03 – 1.71)	0.28 (0.01 – 1.53)
Mat. F-score	-0.053	0.739	0.06 (0 – 0.54)	0.06 (0 – 0.57)
BA (m^2)[3]	0.245	0.064	0.167	0.100
FAI score[4]	-0.092	0.562	717.4 (41 – 3659)	621.9 (0 – 4615)
No. sample months in diet (N = 31)	0.455	<0.001	12 (3 – 31)	4 (1 – 24)
No. calendar months in diet (N = 12, mean ± SD)	0.452	<0.001	8.4 ± 3.0	3.5 ± 2.4
Prop. of diet[5]	0.641	<0.001	0.020 (0.005 – 0.106)	0.001 (0.0001 – 0.036)
Prop. of diet (sum)	n/a	n/a	0.610	0.113
Density[6]	-0.277	0.035	3.0 (0.4 – 29.0)	1.80 (0.4 – 39.6)

[1] Preferred genera = residuals > 0, Non-preferred genera = residuals < 0. For phenological data, $N_{(\text{Preferred})}$ = 17, $N_{(\text{Non-preferred})}$ = 25. Median values (plus range) are used except where noted. [2] F-score = mean productivity (phenology) score for all trees in each genus. F-score for immature fruit was used except for genera from which primarily mature fruit was eaten. [3] BA = mean basal area of food trees used by sakis in each genus (N = 793 trees). [4] FAI = Fruit availability index = F-score x BA. Immature and mature fruit FAI-scores were available for 42 and 39 genera, respectively. [5] Prop. of diet = proportion of saki plant feeding time. [6] Density = stems / ha from 4.28 ha of vegetation plots in the study area.

Intergroup interactions

Interactions between saki groups were generally agonistic but infrequent, with only 116 independent intergroup encounters in over 3,000 hours of study. The monthly number of agonistic interactions per hour of observation varied substantially (mean ± SD = 0.04 ± 0.03, range 0 – 0.09) but was not correlated with the number of species bearing immature or mature fruit, the number of species consumed by sakis, or the immature fruit availability score ($P > 0.10$, $N = 29$ in all cases). While more interactions occurred in months with higher mature fruit availability ($r_s = 0.419$, $P = 0.024$, $N = 29$), they did not generally occur around fruiting trees, and fewer than 15% of all interactions were preceded by feeding bouts.

While sakis generally ignored smaller sympatric primate species, they almost invariably gave way to larger (*Ateles*) and more aggressive (*Cebus*) frugivorous primates. Of the 3,000 hours of observation conducted over 31 months, approximately 20 hours were spent interacting, usually avoiding, these two species (Palminteri unpubl. data).

Discussion

Our results support the general hypothesis that small group-living pitheciine primates, such as *Pithecia irrorata*, minimize the potentially detrimental effects of seasonal food scarcity through the flexible exploitation of a relatively aseasonal food supply for which they appear to face little interspecific competition. Our phenology data indicated that immature fruits of food species consumed sakis were on average available for five months longer each year than mature fruits of the same species. Immature fruits were also available in more plant species at any given time and in larger crops per plant than mature fruits. Sakis further extended the resource availability from some food species by continuing to consume seeds once fruits had ripened. Furthermore, supplementing the diet of immature fruit with fruit pulp from a small number of relatively abundant genera, such as *Mauritia* and *Inga*, further reduced the likelihood of food scarcity.

A diet dominated by seeds of unripe fruit has been recorded for all members of the three Pitheciine genera – *Pithecia* (Soini 1987, Peres 1993, Norconk 1996), *Chiropotes* (bearded sakis, Ayres 1989, van Roosmalen et al. 1988, Peetz 2001), and *Cacajao* (uacaris, Ayres 1989, Boubli 1999). While *P. irrorata* in this study consumed primarily immature fruits (79% of genera), some 15% of food plant genera were taken when mature as well as immature, a pattern also seen in *P. albicans* (Peres 1993), *Cacajao melanocephalus* (Boubli 1999), and *Chiropotes satanas* (Norconk 1996). *P. pithecia*, on the other hand, appears to select plant food when either unripe or ripe, but not both, and has displayed greater monthly switching from seeds to alternative foods, primarily leaves and flowers (Kinzey and Norconk 1993, Norconk & Conklin-Brittain 2004, Cunningham and Janson 2006).

Feeding patterns

Our five saki study groups did not show dietary shifts, such as increased consumption of foliage or other fibrous portions of plants that are typically exhibited by midsized to large-bodied Amazonian primates during periods of reduced food supply. In fact, sakis' high fruit intake was stable throughout the year despite the marked community-wide seasonality in fruit production (Figure 2), with fruit comprising at least 82% of their monthly feeding time, well over half of which consisted of seeds. In May, the only month in which immature fruit comprised less than 50% of the sakis' diet, their primary "alternative" food was ripe fruit pulp, primarily from *Mauritia flexuosa* palms (28% of diet), while flowers and leaves combined represented only 15% of sakis' diet. Moreover, the overall proportion of time spent feeding changed seasonally, but not with respect to fruit availability, as the monthly maximum and minimum amounts of time allocated to feeding did not occur during months of highest or lowest fruit availability. Overall, we can conclude that the sakis maintained a diet dominated by seeds and fruit pulp across the year and consumed flowers as a preferred, rather than a fallback, food source and leaves as a minor portion of the diet, even during months of lowest fruit availability.

The ability of sakis to consume fruits at both immature and mature stages expanded the number of species available to them at any given time, thereby potentially increasing dietary diversity. At the same time, the extended availability of immature fruit potentially allowed sakis to specialise on a smaller number of consistently available species. Our results indicate that sakis maintained a high taxonomic richness in their diet throughout the year. Despite the increased use by sakis of *Mauritia* in April and May, dietary diversity did not decrease during times of lower production of immature fruits. The fact that numbers of both food species and genera were strongly correlated with observation effort suggests that our data are conservative with respect to dietary diversity and that, while sakis act as dietary specialists in largely restricting their foraging behaviour to young seeds (Kinzey and Norconk 1993, Peres 1993, Norconk 1996), they have apparently adopted a generalist strategy within that guild.

The tendency of bald-faced sakis to forage on a wide array of species, including plant families such as Lecythidaceae and Bignoniaceae, the fruits of which contain favoured seeds but lack fleshy pulp, reduces their dependence on species that are heavily exploited by generalist frugivores. For example, figs (Moraceae), a heavily-used staple or “keystone” species for other frugivores (e.g. Terborgh 1983, Felton et al. 2008), were taken very infrequently and by only one of the five saki groups. Palm fruits, which are similarly considered to be a keystone food for several vertebrates and are heavily consumed by capuchins and spider monkeys (Terborgh 1983, Stevenson et al. 2000), were used variably by sakis (see below).

Dietary preference

In general, sakis fed upon fruits of most plant genera according to their abundance, as indicated by a positive relationship between the density of each of the 58 food genera occurring in the floristic plots and their respective dietary contribution, though clearly certain genera were taken preferentially. Even among the five highest-ranking food genera in the diet, four were both widespread and relatively abundant. That preference was more strongly correlated with months in the diet than months available may imply that sakis seek out favoured foods throughout their fruiting cycles, even as they become less available, a pattern also seen in *P. pithecia* (Norconk 1996). Consequently, preferred food genera typically included species exhibiting prolonged fruiting periods (*Mauritia*, *Minquartia*, *Iryanthera*) or genera represented by multiple species but sharing a similar fruit morphology (*Inga*, *Brosimum*). Sakis did not change their overall feeding patterns according to either the temporal availability or fruit crop sizes of these genera, probably because at least some trees were available for most of the year. The trees of food plant genera most preferred by sakis were not larger or more productive than those of other plant genera in their diet, suggesting that sakis were not seeking out particularly large food patches. This is in contrast with preferences shown for tree genera with abundant food crops by primates with greater metabolic demands due to either body size (*Ateles*, Felton et al. 2008) or group size (*Saimiri*, Terborgh 1983; *Cacajao*, Boubli 1999).

Fruits of the three palm species consumed by sakis were among the most consistently available throughout the year in both immature and mature stages; their use by sakis illustrates contrasting levels of preference. Sakis consumed very few fruit of *Iriartea deltoidea*, the most common tree species in our floristic plots and the most negatively selected of all potential food taxa. While *Mauritia flexuosa* accounted for >9% of the sakis' overall feeding time, its consumption was correlated with the availability of alternative foods, rather than its own availability. *Mauritia* fruits were available throughout the year, but their monthly contribution to the diet ranged from 0-3% in June – September to a high of 21-28% in April – May, when community-wide immature fruit availability was lowest. This suggests that sakis switched to *Mauritia* to overcome shortages of alternative food sources. In contrast, although fruits of *Socratea exorrhiza* were only infrequently consumed by sakis, the flowers of this species appeared to be highly sought after, independently of other resources, during the short period they were available. This was the only food resource at which intra-group agonistic interactions were observed during feeding bouts (S. Palminteri, unpubl. data), providing further evidence that *Socratea* flowers were a highly preferred food.

Phenology sampling limitations

Our conclusion that the use by sakis of seeds of immature fruit augmented their potential food supply may be conservative because the small sample sizes of monitored trees did not fully represent community-wide fruit availability. Over two-thirds of the genera used by sakis were consumed during at least one calendar month for which our phenology data recorded no fruit present, clearly indicating that immature fruit were available for longer periods than recorded. In part, this mismatch can be attributed to the once-monthly phenological monitoring of trees, particularly for detecting the initial presence of immature fruits. We suggest however, that a greater part of the mismatch likely resulted from the fact that sakis undoubtedly sampled a far greater number of individuals of each food species within their home ranges than the 4.4 (± 4.8 SD) used in the phenology study. The larger sample would allow them to capitalize on temporal variation in fruit production in even tree populations that largely synchronize their fruiting cycles, which the small phenology sample sizes failed to capture. Conversely, recording the presence of immature fruit does not necessarily mean that they were already palatable to sakis. Either of these cases suggests potential limitations of phenology studies in determining fruit availability for vertebrate consumers, especially granivores.

Effects on saki movement and behaviour

Consistent with our conclusion that sakis have adopted a foraging strategy that minimizes seasonality in food availability, we predicted that saki home range (HR) size and movement patterns would show little or no seasonal changes. In fact, the HRs of three of our five study groups did not change seasonally (see Chapter 4). The HRs of the two smallest groups may have been of low quality or below a size viability threshold, as they expanded considerably in the dry season (May-June and August-September, respectively). These expansions were expressed as short (1-2 day) forays that did not coincide with periods of lowest immature fruit availability (March-April) or with feeding bouts on particularly uncommon food species, and the purpose of these occasional forays remains unclear.

The daily travel paths of our saki groups (see Chapter 4) tended to be longer during wet season months, when a larger number of plant species bore immature ($r_s = 0.546$, $P = 0.067$, $N = 12$) and mature fruit ($r_s = 0.587$, $P = 0.045$, $N = 12$). Day ranges, however, were not correlated with the number of species actually consumed by sakis or the FAI scores of either immature or mature fruit ($P > 0.10$, $N = 12$ in all cases). In addition, while time spent feeding, moving, and resting did not vary significantly by season, social behaviour, including intergroup encounters, comprised a higher proportion (6.0%) of their wet season time, when more food was available, than during dry season (4.6%). Longer wet season travel distances may well be associated with higher investments in intergroup interactions (cf. Stevenson et al. 2000). However, it is unclear whether these longer movements brought neighbouring saki groups into contact more frequently, thereby resulting in more agonistic interactions, or whether increased travel represented an enhanced “patrolling” effort during periods of high fruit availability. The propensity of sakis to approach their HR boundaries during daily movements (Chapter 4) suggests that greater food supplies during the wet season may release time that would otherwise be allocated to foraging to reinforce boundaries with neighbouring groups.

Sakis may avoid direct contests with larger sympatric primates by visiting trees and lianas with unripe fruits, and with neighbouring conspecifics by including a large number of plant food species each month. For example, given that sakis share at least 25 of their food genera with the larger, more aggressive *Cebus* spp. (capuchin monkeys, Terborgh 1983), focusing on immature fruit likely enabled them to avoid interference competition with capuchins, which are relatively abundant at Los Amigos (Chapter 3). Furthermore, focusing on seeds allowed sakis to feed on species bearing sclerocarpic fruits, including *Eschweilera* (Lecythidaceae), *Hevea* (Euphorbiaceae), *Acacia* (Fabaceae), and several Bignoniaceae genera, that were not consumed by either *Cebus* species elsewhere in Madre de Dios (Terborgh 1983). Van Roosmalen et al. (1988) and Kinzey and Norconk (1990) have both suggested that predation by bearded sakis (*Chiropotes satanas*) on seeds of immature fruits, which are eaten by other primates only when mature, evolved to avoid competition with other frugivores. As with *Chiropotes* (van Roosmalen et al. 1988), sakis in this region face potential competition for unripe fruit primarily from macaws (*Ara spp*.) and squirrels (*Sciurus spp*.), the only other arboreal vertebrate seed predators. However, these species are substantially smaller-bodied, and macaws were seen to retreat from a food tree and wait outside it while sakis were present. In any case, dietary overlap between sakis and macaws has been shown to be minimal (Chapter 6).

Our data suggest that by adopting a taxonomically generalist feeding strategy within a relatively specialised dietary niche, arboreal granivores like *Pithecia irrorata* can minimize both the potential effects of seasonal fluctuations in fruit/seed availability and potential interspecific competition for ripe fruit. Nevertheless, sakis occur at low densities or are patchily distributed across much of the largely intact forest landscape of south-western Amazonia (Freese et al. 1982, Peres 1997, Haugaasen and Peres 2005, Endo et al. 2010, Chapter 3), despite their relative immunity to pronounced seasonal changes in food resource availability. In contrast to our finding that sakis were flexible with respect to food resources, for these same saki groups, forest structure was shown to be a powerful indicator of use/occupancy (Chapter 7). This contrast suggests that a well-developed forest structure, rather than food availability, may be limiting saki population density and distribution.

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Appendix. Checklist of 222 food plant species (or morphospecies) in the diet of bald-faced sakis (*Pithecia irrorata*) at Los Amigos, southeastern Peru, describing their life form, plant part consumed, and stage of maturity in which fruits were taken. S = Seed, P = Pulp, Fl = Flower, Fr = Whole fruit, L = Leaf, A = Aril. Maturity levels: 1 = Immature only, 2 = Mature only, 3 = Immature + Mature stages, 4 = Leaves only. Life forms: T = Tree, L = Liana, Ep = Epiphyte, Hep = Hemi-epiphyte.

Sample	Family	Genus	Species	Part eaten	Maturity	Life form
S193	ACHARIACEAE	Lindakeria	paludosa	S	2	T
S31	ANNONACEAE	Guatteria	acutissima	S	3	T
S62	ANNONACEAE	Oxandra	xylopioides	S	1	T
S97	APOCYNACEAE	Odontadenia	puncticulosa	S	1	L
S40	ARACEAE	Heteropsis	flexuosa	S/P	2	Ep
S68	ARACEAE	Philodendron	sp 1	Fl/Fr	2	Ep
S116	ARACEAE	Philodendron	sp 2	Fl/Fr	2	Ep
S96	ARACEAE	Sp	sp	L	4	Ep/L
S130	ARALIACEAE	Schefflera	morototoni	S	1	T
S99	ARECACEAE	Iriartea	deltoidea	P	2	T
S25	ARECACEAE	Mauritia	flexuosa	P	2	T
S03	ARECACEAE	Socratea	exorrhiza	Fl/P	2	T
S129	ARISTOLOCHIACEAE	Aristolochia	rumicifolia	S	1	L
S04	BIGNONIACEAE	Adenocalymma	sp	S	1	L
S126	BIGNONIACEAE	Adenocalymma	sp	S	1	L
S15	BIGNONIACEAE	Adenocalymma	subincanum	S	1	L
S07	BIGNONIACEAE	Arrabidaea	japurensis	S	1	L
S208	BIGNONIACEAE	Arrabidaea	prancei	S	2	L
S18	BIGNONIACEAE	Arrabidaea	sp 1	S	1	L
S148	BIGNONIACEAE	Arrabidaea	sp 2	S	1	L
S150	BIGNONIACEAE	Arrabidaea	sp 3	S	3	L
S33	BIGNONIACEAE	Callichlamys	latifolia	S	1	L
S90	BIGNONIACEAE	Clytostoma	sciuripabulum cf	S	1	L
S202	BIGNONIACEAE	Jacaranda ?	sp 2	S	2	L
S136	BIGNONIACEAE	Macfadyena cf	sp	S	1	L
S121	BIGNONIACEAE	Sp	sp 1	L	4	L
S210	BIGNONIACEAE	Sp	sp 3	S	2	L
S213	BIGNONIACEAE	Sp	sp 4	S	3	L
S88	BIGNONIACEAE	Tynanthus	aff panamensis	S	1	L
S57	BURSERACEAE	Protium	sp 1	S	1	T
S222	BURSERACEAE	Protium	sp 2	S	1	T
S180	BURSERACEAE	Tetragastris	sp 1	S/A	3	T
S144	BURSERACEAE	Tetragastris	sp 2	S/A	1	T
S149	CAPARIDACEAE	Capparis	sp	S	1	L
S84	CELASTRACEAE	Peritassa	sp	S	1	L
S159	CELASTRACEAE	Salacia	impressifolia cf	S	1	L
S119	CELASTRACEAE	Salacia	insignis cf	S/P	3	T
S11	CELASTRACEAE	Salacia	multiflora	S	1	L
S196	CELASTRACEAE	Salacia	sp	S/P	3	T
S199	CELASTRACEAE	Salacia	sp 2	S/P	1	T
S171	CELASTRACEAE	Sp	sp	S	1	T
S45	CHRYSOBALANACEAE	Couepia	sp 1	S	1	T
S189	CHRYSOBALANACEAE	Couepia	sp 2	S	1	T
S60	CHRYSOBALANACEAE	Sp	sp	S	1	T
S91	CLUSIACEAE	Caraipa	sp	S	1	T

Sample	Family	Genus	Species	Part eaten	Maturity	Life form
S66	CLUSIACEAE	Clusia	sp 1	S	1	T/Hep
S73	CLUSIACEAE	Clusia	sp 2	S	1	T/Hep
S183	CLUSIACEAE	Clusia	sp 3	S	1	T/Hep
S103	CLUSIACEAE	Mirtiania	sp	S	1	T
S182	CLUSIACEAE	Sp	sp	S	1	T/Hep
S108	CLUSIACEAE	Tovomita	sp	S	1	T
S140	COMBRETACEAE	Buchenavia	sp	S	1	T
S197	COMBRETACEAE	Combretum	sp	S	2	T
S75	CONNARACEAE	Connarus	sp	S	1	L
S14	CUCURBITACEAE	Cayaponia	sp 1	S	1	T
S83	CUCURBITACEAE	Cayaponia	sp 2	S	1	L
S138	CUCURBITACEAE	Cayaponia	sp 3	S	1	L
S19	CUCURBITACEAE	Gurania	insolita	S	1	L
S61	CUCURBITACEAE	Sp	sp	S	1	L
S111	DIOSCOREACEAE	Dioscorea	spicata	S	1	L
S147	EBENACEAE	Diospyros	sp	S/P	1	T
S184	ELAEOCARPACEAE	Sloanea	excelsa	S	3	T
S34	ELAEOCARPACEAE	Sloanea	fragrans	S	1	T
S186	ELAEOCARPACEAE	Sloanea	guianensis cf	S	1	T
S100	ELAEOCARPACEAE	Sloanea	sp 1	S	1	T
S172	ELAEOCARPACEAE	Sloanea	sp 2	S	1	T
S50	EUPHORBIACEAE	Alchornea	glandulosa	S	3	T
S22	EUPHORBIACEAE	Hevea	guianansis	S	1	T
S110	EUPHORBIACEAE	Hura	crepitans	S	1	T
S179	EUPHORBIACEAE	Mabea	sp	S	1	T
S78	EUPHORBIACEAE	Nealchornea	yapurensis_cf	S/P	1	T
S187	EUPHORBIACEAE	Omphalea	sp	P	2	L
S200	EUPHORBIACEAE	Omphalea	diandra	S	1	T
S24	EUPHORBIACEAE	Pausandra	trianea	S	3	T
S128	EUPHORBIACEAE	Plukenetia	brachybrotrya	S/L	1	L
S13	FABACEAE	Acacia	altiscandens	S	3	T
S141	FABACEAE	Acacia	sp 1	S/P	3	T
S157	FABACEAE	Acacia	sp 2	S	3	T
S48	FABACEAE	Andira	sp 1	S	1	T
S214	FABACEAE	Brownea	disepala	S	3	T
S211	FABACEAE	Copaifera?	sp	S	1	T
S165	FABACEAE	Dussia	sp	S	1	T
S115	FABACEAE	Enterolobium	barnebianum	S	1	T
S217	FABACEAE	Inga	alba	L	4	T
S218	FABACEAE	Inga	auristellae	P	2	T
S69	FABACEAE	Inga	capitata	P	2	T
S79	FABACEAE	Inga	edulis	P	2	T
S20	FABACEAE	Inga	sp 1	P	2	T
S30	FABACEAE	Inga	sp 2	P	2	T
S46	FABACEAE	Inga	sp 3	P	2	T
S51	FABACEAE	Inga	sp 4	P	2	T
S81	FABACEAE	Inga	sp 5	P	2	T
S82	FABACEAE	Inga	sp 6	P	2	T
S94	FABACEAE	Inga	sp 7	P	2	T
S118	FABACEAE	Inga	sp 8	P	2	T
S122	FABACEAE	Inga	sp 9	P	2	T
S134	FABACEAE	Inga	sp 10	P	2	T
S139	FABACEAE	Inga	sp 11	P	2	T
S162	FABACEAE	Inga	sp 12	P	2	T
S163	FABACEAE	Inga	sp 13	P	2	T

Sample	Family	Genus	Species	Part eaten	Maturity	Life form
S170	FABACEAE	Inga	sp 14	P	2	T
S174	FABACEAE	Inga	sp 15	P	2	T
S176	FABACEAE	Inga	sp 16	S	2	T
S177	FABACEAE	Inga	sp 17	P	2	T
S178	FABACEAE	Inga	sp 18	S/P	3	T
S190	FABACEAE	Inga	sp 19	L	4	T
S201	FABACEAE	Inga	sp 20	P	2	T
S203	FABACEAE	Inga	sp 21	P	2	T
S212	FABACEAE	Inga	sp 22	P/L	2	T
S02	FABACEAE	Lecointea	amazonica	P/L	2	T
S86	FABACEAE	Mucuna	sp	S/P	3	L
S143	FABACEAE	Pterocarpus	sp	S	1	T
S113	FABACEAE	Sp	sp	S/P	2	T
S220	LAURACEAE	Sp	sp	S	1	T
S38	LECYTHIDACEAE	Eschweilera	sp 1	S	1	T
S58	LECYTHIDACEAE	Eschweilera	sp 2	S	1	T
S154	LECYTHIDACEAE	Eschweilera	sp 3	S	1	T
S169	LECYTHIDACEAE	Eschweilera	sp 4	S	1	T
S192	LINACEAE	Roucheria	punctata	S	2	T
S37	LOGANIACEAE	Strychnos	lobertiana	S/P	2	L
S124	LOGANIACEAE	Strychnos	sp	S	3	L
S142	LORANTHACEAE	Oryctanthus cf	sp	S	1	L
S109	MALPIGHIACEAE	Byrsonima	sp	S	1	T
S120	MALPIGHIACEAE	Sp	sp 1	S	1	L
S161	MALPIGHIACEAE	Sp	sp 2	S	3	L
S219	MALPIGHIACEAE	Sp	sp 3	S	3	T
S93	MALVACEAE	Matisia	malacocalyx	S	1	T
S98	MARCGRAVIACEAE	Marcgraviastrum	sp	S	1	T
S151	MELASTOMATACEAE	Bellucia	sp	S/P	1	T
S207	MELIACEAE	Trichilia	micrantha	S	2	T
S167	MELIACEAE	Trichilia	quadrijuga	S	1	T
S117	MEMECYLACEAE	Mouriri	nervosa	S	1	T
S206	MENISPERMACEAE	Abuta	sp	S	3	T
S123	MENISPERMACEAE	Sp	sp	S	1	T
S16	MORACEAE	Brosimum	acutifolium	S	1	T
S43	MORACEAE	Brosimum	lactescens	S	1	T
S92	MORACEAE	Brosimum	parinarioides	S	1	T
S125	MORACEAE	Brosimum	potabile	S	1	T
S41	MORACEAE	Brosimum	rubescens	S	1	T
S59	MORACEAE	Brosimum	sp	S	1	T
S10	MORACEAE	Clarisia	racemosa	S/Fl	1	T
S54	MORACEAE	Ficus	aff maxima	S	1	T
S56	MORACEAE	Helicostylis	scabra	S	1	T
S23	MORACEAE	Naucleopsis	naga	S	1	T
S63	MORACEAE	Perebea	mollis	S	1	T
S09	MORACEAE	Perebea	tessmannii	S	1	T
S32	MORACEAE	Pseudolmedia	laevigata	S/P	3	T
S32b	MORACEAE	Pseudolmedia	laevis	S	1	T
S39	MORACEAE	Pseudolmedia	macrophylla	S	1	T
S156	MYRISTICACEAE	Iryanthera	juruensis	S	1	T
S21	MYRISTICACEAE	Iryanthera	ulei	S	1	T
S53	MYRISTICACEAE	Otoba	parvifolia	S/P	3	T
S127	MYRTACEAE	Calycolpus	sp	S	1	T
S191	MYRTACEAE	Eugenia	sp	S	3	T
S01	OLACACEAE	Minquartia	guianensis cf	S/P	3	T

Sample	Family	Genus	Species	Part eaten	Maturity	Life form
S216	OLACACEAE	Sp	sp	L	4	T
S112	PASSIFLORACEAE	Dilkea	sp	S	1	L
S173	PASSIFLORACEAE	Passiflora	sp 1	S	1	L
S146	PASSIFLORACEAE	Passiflora	sp 2	S	1	L
S105	PASSIFLORACEAE	Sp	sp 1	S	1	L
S27	QUIINACEAE	Quiina	amazonica	S	1	T
S89	RHIZOPHORACEAE	Cassipourea	peruviana	S	1	T
S131	RUBIACEAE	Sp	sp 1	S	1	T
S137	RUBIACEAE	Sp	sp 2	S	1	T
S158	SALICACEAE	Lunania	sp	S	3	T
S198	SAPINDACEAE	Matayba	sp	S	1	L
S209	SAPINDACEAE	Paullinia	histrix	S	3	T
S36	SAPINDACEAE	Paullinia	sp 1	S	1	L
S80	SAPINDACEAE	Paullinia	sp 2	S/P	2	L
S101	SAPINDACEAE	Paullinia	sp 3	S/A	3	L
S107	SAPINDACEAE	Paullinia	sp 4	S	1	L
S145	SAPINDACEAE	Sp	sp 1	S	3	L
S204	SAPINDACEAE	Sp	sp 2	S	2	L
S102	SAPOTACEAE	Manilkara	sp	S	1	T
S06	SAPOTACEAE	Micropholis	guyanensis	S	1	T
S135	SAPOTACEAE	Micropholis	sp	S	1	T
S17	SAPOTACEAE	Pouteria	caimito	S/P	3	T
S05	SAPOTACEAE	Pouteria	laevigata	S	1	T
S29	SAPOTACEAE	Pouteria	sp 1	S	3	T
S35	SAPOTACEAE	Pouteria	sp 2	S	1	T
S44	SAPOTACEAE	Pouteria	sp 3	S	1	T
S71	SAPOTACEAE	Pouteria	sp 4	S	1	T
S72	SAPOTACEAE	Pouteria	sp 5	S	1	T
S106	SAPOTACEAE	Pouteria	sp 6	S	2	T
S133	SAPOTACEAE	Pouteria	sp 7	S	1	T
S155	SAPOTACEAE	Pouteria	sp 8	S	1	T
S160	SAPOTACEAE	Pouteria	sp 9	S	1	T
S164	SAPOTACEAE	Pouteria	sp 10	S	1	T
S185	SAPOTACEAE	Pouteria	sp 11	S	3	T
S188	SAPOTACEAE	Pouteria	sp 12	S/P	3	T
S194	SAPOTACEAE	Pouteria	sp 13	S	2	T
S195	SAPOTACEAE	Pouteria	sp 14	S	2	T
S47	SAPOTACEAE	Pouteria	torta	S	1	T
S08	SAPOTACEAE	Sp	sp 1	S	1	T
S42	SAPOTACEAE	Sp	sp 2	S	1	T
S76	SAPOTACEAE	Sp	sp 3	S	1	T
S77	SAPOTACEAE	Sp	sp 4	S	1	T
S85	SAPOTACEAE	Sp	sp 5	S	1	T
S104	SAPOTACEAE	Sp	sp 6	S	1	T
S215	SAPOTACEAE	Sp	sp 7	S	1	T
S49	SAPOTACEAE	Sp	sp 8	S	1	T
S52	SIMAROUBACEAE	Simarouba	amara	S	1	T
S152	SIMAROUBACEAE	Simaba	sp	S	1	T
S87	SIPARUNACEAE	Siparuna	dicipiens	S	1	T
S70	SIPARUNACEAE	Siparuna	monogyna cf	S	1	T
S67	SP (unidentified)	S67	sp 1	S	1	T
S205	SP (unidentified)	S205	sp 2	S	3	L
S221	SP (unidentified)	S221	sp 3	S	1	T
S28	STERCULEACEAE	Byttneria	asterotricha	S	3	L
S26	STERCULEACEAE	Byttneria	cordifolia	S	1	L

Sample	Family	Genus	Species	Part eaten	Maturity	Life form
S74	ULMACEAE	Celtis	schippii	S	1	T
S181	ULMACEAE	Ampelocera	sp	L	4	T
S55	URTICACEAE	Pourouma	minor	S	1	T
S166	URTICACEAE	Pourouma	mollis	S	1	T
S12	URTICACEAE	Pourouma	sp 1	S/P	1	T
S132	URTICACEAE	Pourouma	sp 2	S	1	T
S175	URTICACEAE	Pourouma	sp 3	S	1	T
S64	URTICACEAE	Pourouma	tomentoso cf. 1	S	1	T
S114	URTICACEAE	Pourouma	tomentoso cf. 2	S	1	T
S168	URTICACEAE	Pourouma	tomentoso cf. 3	S	1	T
S95	VIOLACEAE	Rinorea	sp	S	1	T
S153	VOCHYSIACEAE	Vochysia	sp	S	1	T

Chapter 6: Competition between Pitheciines and large *Ara* macaws, two specialist seed-eaters

Abstract

The specialisation of Pitheciines and large macaws on hard, unripe seeds encourages the comparison of their diets and the investigation of potential competition between these two groups of seed predators. Using standard indices to compare 1171 feeding observations on five groups of *Pithecia irrorata* and 40-50 radio-tagged and non-tagged large macaws (*Ara spp*.) in southeastern Peru between January 2004 and December 2005, we examined the extent to which the diets of *Pithecia* and large *Ara* macaws overlap and whether the overlap varies by season and food availability. While the diets of both taxa comprised mainly unripe seeds, saki diets were taxonomically more diverse than macaws', and they tended to include multiple species in each food plant genus. Macaws consumed a wider variety of plant parts and plants of more locally monospecific genera. The two consumers shared only 19% of the total 109 food plant genera in the analysis and only 18% of their most important food plant genera. These two consumer groups rarely ate from the same genera at the same time or in the same proportions. Monthly dietary overlap values corresponded to immature fruit production and may also have been determined by consumption of key food species, such as *Bertholletia excelsa* and *Pseudolmedia spp*. Overall dietary overlap values for this study were lower than those in studies among other Neotropical frugivorous primates. Nevertheless, values for three individual months fall within the range of primate-primate comparative studies. This suggests that for certain months of the year, *Pithecia* may face higher dietary overlap and potentially greater competition with non-mammalian frugivores than with other primates.

In press: Palminteri, S., G.V.N Powell, K. Adamek, and R. Tupayachi. Competition between pitheciines and large *Ara* Macaws, two specialist seed-eaters. In Veiga, L.M., A.A. Barnett, S.F. Ferrari, and M.A. Norconk. Evolutionary Biology and Conservation of Titis, Sakis and Uacaris (Book in prep). Cambridge, UK: Cambridge University Press.

Introduction

Interspecific competition may arise from individuals of different species either exhibiting aggressive or other damaging behaviour (interference competition, see Schoener 1983) or sharing the same limited resources (exploitation competition, Connell 1983, Schoener 1983). Interspecific competition among sympatric primates appears to be variable but in general relatively minor, due in part to changes in preferred foods during times of fruit scarcity (Peres 1994, Wahungu 1998, Stevenson *et al.* 2000) or use of different canopy heights (Terborgh 1983, Peres 1991).

Gautier-Hion *et al.* (1985) observed considerable overlap in the fruit diets of taxonomically distinct vertebrate groups in a Gabonese forest community, while Poulsen *et al.* (2002) found that hornbills and primates in Cameroon each showed greater dietary overlap within their respective taxonomic groups than between hornbill-primate pairings.

Pitheciines' specialisation on hard, well-protected, and often immature seeds minimizes dietary competition with other primates (Soini 1987, Ayres 1989, Kinzey and Norconk 1993, Peres 1993, Aquino and Encarnación 1999, Barnett *et al.* 2005). However, the importance of competition with other sympatric seed predators remains largely unexplored. Based on data collected in Venezuela, Norconk *et al.* (1997) suggested that pitheciines may compete with large macaws (*Ara spp.*), another group that specializes on hard, often unripe, seeds (Gilardi *et al.* 1999, Powell *et al.* 1999, Berg *et al.* 2007). More recently, Barnett *et al.* (2005) documented feeding by scarlet macaws (*A. macao*) in Brazil on fruits that were also eaten by black-headed uakaris, *Cacajao melanocephalus.*

Up to three species of large macaws- *Ara chloropterus, A. ararauna, and A. macao*- are sympatric with pitheciines across much of the Amazon biome (Patterson *et al*. 2005, Ridgely *et al*. 2007). We examined the extent to which the diets of *Pithecia* and large *Ara* macaws overlap and whether the overlap varies with respect to availability of preferred foods, to indicate the degree of competition between these bird and primate taxa.

Methods

Study area

Data on diet, behaviour, and habitat use of *Pithecia* and *Ara* were collected concurrently in the Los Amigos Conservation Concession, 140,000 ha of largely intact evergreen seasonal forest (Osher and Buol 1998) at 250 m a.m.s.l in southeastern Peru (Figure 1). Most of the annual 2200mm of rain falls between November and May (Pitman 2005).

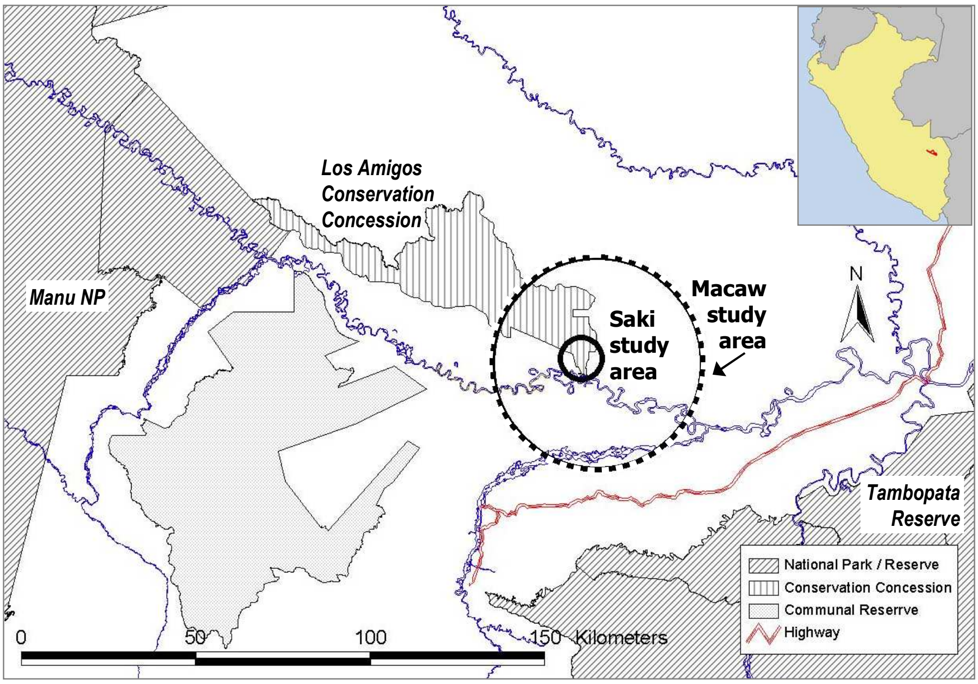

Figure 1. Study area for saki and macaw studies in Madre de Dios, southeastern Peru.

Foraging data collection

Between June 2004 and December 2005, we recorded feeding patterns of five habituated groups of bald-faced sakis (*Pithecia irrorata*) during five-minute instantaneous scans, monitoring each group for approximately five days each month. A separate field team collected macaw feeding data between January 2004 and December 2005 from observations of radio-tagged birds and birds seen on foraging walks each month. Each visit by a group or individual of either species to a food tree, regardless of the number of individuals or length of the observation, was considered one feeding bout. For each feeding bout, we recorded: plant species, plant part consumed (seed, mesocarp, whole fruit, flower, leaf), and maturity of fruits or seeds consumed. Non-plant feeding bouts were ignored.

Diet analysis

Feeding bouts representing 18 months of observations served as the unit of analysis. For this analysis, we grouped the three *Ara* species, considering all as potential competitors to the seed-eating sakis. We compared the richness and diversity of saki and macaw diets using standard indices. We calculated the generic richness of each taxon's diet using the Margalef (1958) index:

$$R' = (G-1)/ln(n)$$

where G is the total number of plant genera consumed by each consumer taxon, and n is the number of feeding records for each genus. We calculated the diversity of food plant genera in each taxon's diet with the Shannon index (Shannon 1948):

$$H' = - \sum (p_i)(lnp_i)$$

where H' is the diversity index and p is proportion of individuals of the sample belonging to the *i*th genus.

To analyse seasonal variation in diet, while correcting for variation in monthly sampling effort, we compared the number of genera consumed per month as a function of the number of feeding observations that month.

Fruit abundance and availability

To determine whether the relative availability of food resources throughout the year influenced seasonal dietary overlap, we recorded the phenology of 839 marked trees, representing 116 plant genera, from February 2005-December 2006. We averaged each month's data to produce a single 12-month cycle. Each month, we estimated the percentage of maximum production of flowers, immature fruits, and mature fruits in up to five individuals of each plant species (Fournier 1974). Based on these percentage values, we assigned each tree a monthly value of 0-5 for each plant reproductive part. We used t-tests to compare monthly fruit production values of immature and mature fruits for all 116 plant genera and to compare immature fruit production among preferred saki and macaw foods.

Dietary overlap

We generated monthly and overall indices of dietary overlap between sakis and macaws using Schoener's (1974) resource overlap index:

$$R_o = 1 - ½ \sum_{i=1}^{n} \left| p_{ij} - p_{ik} \right|$$

where R_o is resource overlap, and p_{ij} and p_{ik} are the proportions of the observations in which species *j* and *k* consume resource *i*. The resulting value ranges from 0 to 1, with 0 representing no overlap and 1 representing complete overlap (Poulsen *et al*. 2002). We also analysed separately the 20 plant genera eaten most frequently by each consumer group to determine whether the species' preferred food items overlapped differently from their overall diets. We analysed monthly dietary overlap values for the plant genera with the greatest overall *Pithecia-Ara* overlap.

To compare our results to those of Stevenson *et al.* (2000) of dietary overlap among four Colombian primates, we also calculated Morisita's overlap index (Morisita 1959, cited in Horn 1966). In Morisita's index:

$$O = 2 \sum(x_i y_i) / (\sum x_i^2 + \sum y_i^2)$$

x_i is the proportion of food genus *i* in the diet of animal species *x*, y_i is the proportion of food genus *i* in the diet of animal species *y*, and the sum includes all fruit genera that are consumed by both *x* and *y*. This value also varies between 0-1, with higher values indicating greater overlap. We compared monthly dietary overlap with immature and mature fruit production values using Pearson's correlations and linear regression.

Results

Dietary characteristics

We analysed 1,171 feeding bouts involving consumption of plant parts by bald-faced sakis (n=585) and macaws (n=586). Together, fruits and seeds comprised 98% (575) and 88% (516) of the feeding bouts of sakis and macaws, respectively (Figure 2). Seeds alone made up 83% of the feeding bouts of sakis and 68% of the feeding bouts of macaws. While seeds played an important role in saki and macaw diets throughout the year, pulp was taken in over 20% of saki feeding bouts in February and March, the time when it was least consumed by macaws. Overall, flowers comprised 5% of macaw diets but just 0.5% of saki diets. Macaws consumed both flowers and leaves in the dry season (primarily April – September); with flowers contributing nearly 30% to their diet in June and leaves comprising 23% of their diet in July.

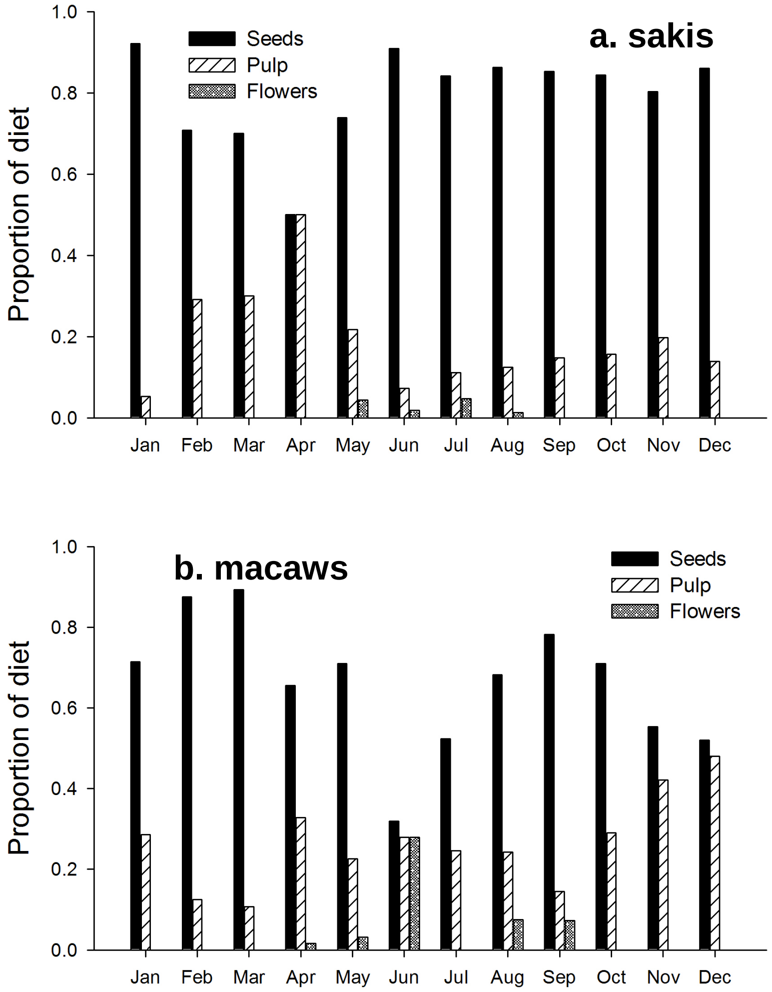

Figure 2. Proportion of seeds, pulp (including whole fruits), and flowers in the monthly diets of *P. irrorata*, 2a, and *Ara* macaws, 2b, 2004-2005. Leaves comprised an additional 5% of macaws' overall diet (not shown).

During the study, we observed sakis and macaws consuming parts of plants of 109 genera in 43 families (Appendix). Saki diets included more plant families (37), genera (66), and morphospecies (at least 118) than those of macaws (27 families, 64 genera, and at least 104 morphospecies), and scores for overall dietary richness (Margalef 1958), diversity, and evenness (Shannon 1948) were all higher for sakis (Table 1).

Table 1. Dietary diversity of sakis (*Pithecia irrorata*) and macaws (*Ara spp.*) in Madre de Dios, Peru, 2004-2005.

	Families (unique to taxon)	Genera (unique to taxon)	Generic Richness[1]	Generic Diversity[2]	Generic Evenness[2]	No. genera in 50% of obs	No. genera in 75% of obs
Sakis	37 (16)	66[b] (45)	10.36	3.36	0.80	6	15
Macaws	27 (6)	64[b] (43)	10.04	3.11	0.75	5	16
Total	43[a]	109[b]					

[a] known families

[b] 109 genera with known families + 1 additional category called "family unknown"

1. Margalef (1958). 2. Shannon (1948).

Fruit abundance and availability

Sakis and macaws typically ate the seeds of immature fruits and the pulp of mature fruits. Immature fruit was most abundant from November through January, the initial months of rainy season, and least abundant in April, at the end of the rainy season (Figure 3). Mature fruit production remained below 4% of maximum potential throughout the year, except for a peak in production in the late rainy season of February and March. Immature fruit abundance was significantly higher than mature fruit abundance in all months ($t = -11.106$, $df=22$, $p<0.0001$). Several important food species of the Euphorbiaceae (*Hevea*), Sapotaceae (*Pouteria*), and Fabaceae (*Inga*) families reach their highest immature fruit production in early rainy season (November-January), while production of several species of Moraceae (*Pseudolmedia, Castilla*) peaked in September and October. Three palm genera (*Mauritia, Iriartea, Socratea*) showed a constant fruit production throughout the year.

The 20 preferred food plant genera of each consumer (32 total genera) accounted for 79% and 76% of all feeding bouts recorded for *Pithecia* and *Ara* (Appendix). Only six (18%) of these genera were preferred foods of both taxa. Mean levels of immature fruit production among preferred saki food plant genera were similar to those among preferred macaw food plant genera ($t=1.750$, $df=38$, $p=0.088$).

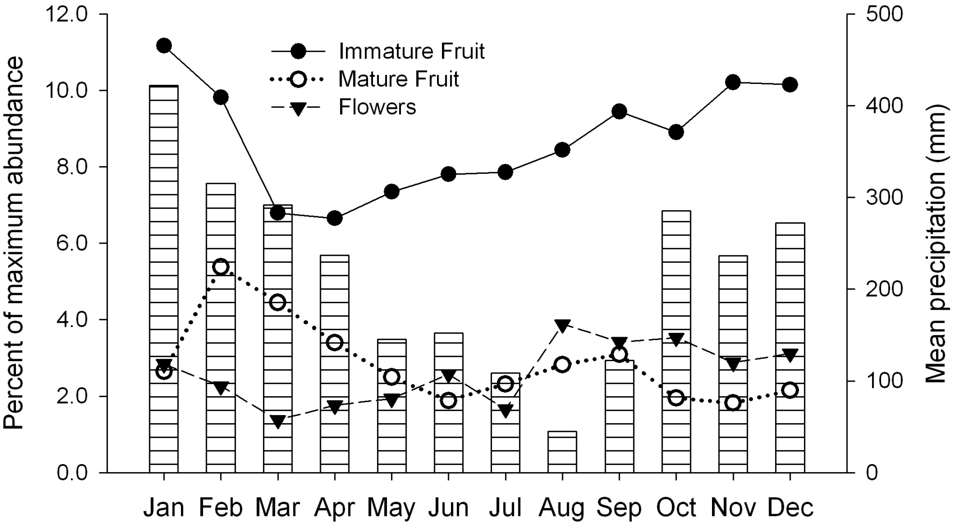

Figure 3. Monthly precipitation and mean phenological cycle for flowers and fruits from 839 marked trees from 116 plant genera in Madre de Dios, southeastern Peru, 2005-2006. Maximum abundance represents the maximum production characteristic of each plant species.

Dietary overlap

At the generic level, the diet of *Pithecia* showed little resemblance to that of *Ara spp.* (Appendix). Of the 109 genera consumed by these two consumers, only 21 (19%), each representing from 1-12 species, were consumed by both (Table 2). Schoener's (1974) resource overlap values of 0.244, calculated for the complete diets, and 0.238, calculated for the 20 genera most frequently consumed by each study animal, indicate a less than 25% dietary overlap between sakis and macaws during this period.

Table 2. Twenty-one food plant genera shared by *Pithecia* and *Ara*, with number of species and months consumed by each animal taxon.

		No. species		Key months consumed	
Family	**Genus**	**Sakis**	**Macaws**	**Sakis**	**Macaws**
Fabaceae	Acacia	2	1	Jun-Aug, Oct	Sept
Combretaceae	Buchenavia	1	1	Aug	Jul
Sterculiaceae	Byttneria	2	2	May, Jul-Sep	Jul-Aug
Cucurbitaceae	Cayaponia	2	3	Jun, Aug-Sep	Jul-Aug
Chrysobalanaceae	Couepia	2	1	Sep-Dec	Oct
Lecythidaceae	Eschweilera	3	5	Aug,Oct-Nov, Jan	Jan-Feb, Apr, Jun-Nov
Euphorbiaceae	Hevea	1	1	Mar, Jul-Aug	May-Aug, Nov-Mar
Euphorbiaceae	Hura	1	1	Jun	Mar, May-Jun
Fabaceae	Inga	12	5	Jun-Apr	Mar-Jan
Arecaceae	Iriartea	1	1	May	Mar-Aug, Nov
Malvaceae	Matisia	1	1	May-Jun	Jul, Oct-Nov
Arecaceae	Mauritia	1	1	Oct-Aug	Feb, Apr, Jun-Aug, Oct-Nov
Cecropiaceae	Pourouma	6	1	Jun-Sep, Dec	Nov
Sapotaceae	Pouteria	9	7	Feb, Jun-Dec	Apr, Jul, Nov-Dec
Moraceae	Pseudolmedia	3	3	May-Dec	Sep, Nov
Celastraceae	Salacia	1	1	Jul-Aug	Nov
Elaeocarpaceae	Sloanea	1	2	May-Jun	Aug, Nov-Dec
Arecaceae	Socratea	1	1	Aug	May
Bignoniaceae	Sp	5*	1	Jun-Oct, Dec	Sep
Fabaceae	Sp	1*	4	Oct-Nov	May, Jul-Sep
Vochysiaceae	Vochysia	1	1	Sep	Jul, Sep

*****Identification to genus level is ongoing in these families.

Individual monthly overlap values ranged from a low of 0.032 in May to a high of 0.253 in September (Figure 4). With the exception of September, all individual monthly overlap values (Schoener 1974), as well as their mean (0.147 ± 0.07 SD), were lower than the annual overlap value of 0.244. Dietary overlap values were lowest during the changeover from wet to dry season (April - June) and highest during the changeover from dry to wet season (Sept-January). Monthly overlap values correlated significantly with mean production values of immature fruit ($r=0.778$, $p=0.003$, $n=12$) but not of mature fruit ($r= -0.200$, $p=0.534$, $n=12$). The pattern of monthly overlap values obtained using Morisita's (1959) index was similar to that obtained using Schoener's index (Figure 4). The overall Morisita index value was 0.195, and the mean monthly dietary overlap measure was 0.152 ± 0.11 SD.

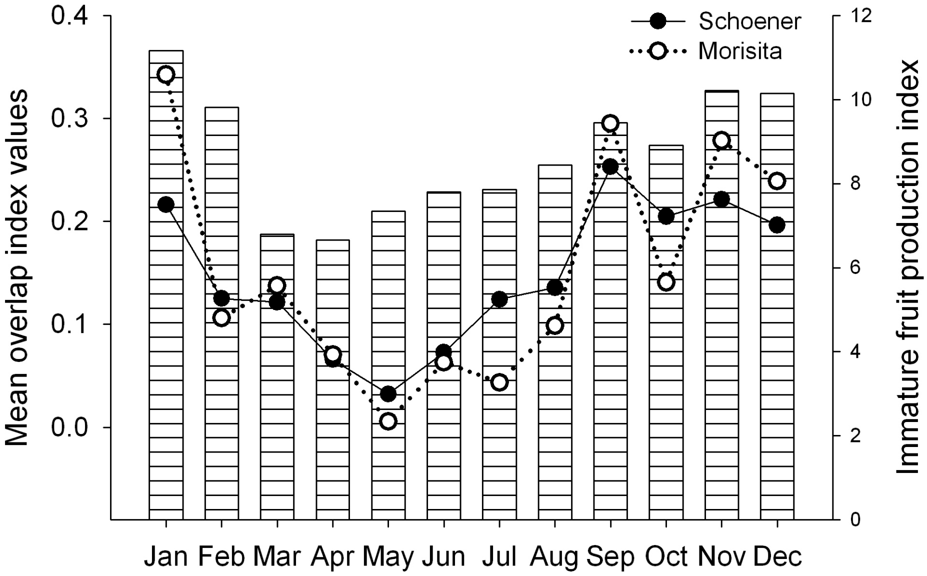

Figure 4. Mean monthly dietary overlap values (Schoener 1974; Morisita, cited in Horn, 1966) between sakis and macaws, 2004-2005. 0.0= no overlap, 1.0=complete overlap for both indices. Immature fruit production index is shown for comparison.

Sakis consumed foods of more plant genera in April and May (Figure 5), when dietary overlap with macaws was lowest, than at the end of the dry season (September-November), when overlap was highest. The higher dietary diversity in April and May explains part of the decrease in dietary overlap in that period (r^2=0.692, p=0.0008 df=11). Macaw dietary diversity did not correlate with overlap value (r= −0.283, p=0.372, n=12). Use of particular genera may have contributed to lower overlap values in certain months. Species of four genera− *Mauritia*, *Sloanea*, *Matisia*, and Sapotaceae *sp.*− made up over 60% of sakis' diet in May. These same genera were absent from the diet of macaws in May, but present during other months. Conversely, *Bertholletia* and *Euterpe* contributed 58% and 12%, respectively, to the macaw diet in May, while neither genus contained foods eaten by sakis. Even in September, the month with highest overlap, 30% of macaw feeding observations were of a genus of Fabaceae (*Parkia*) not eaten by sakis.

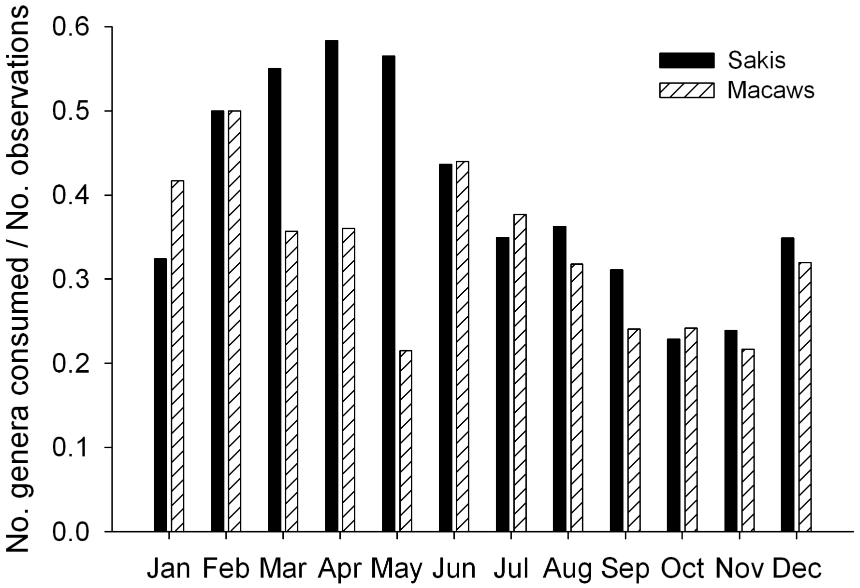

Figure 5. Number of food plant genera consumed monthly by sakis and macaws in 2004-2005, standardized by number of feeding observations per month.

The six genera that showed the greatest average overlap values (Schoener 1974, Figure 6) were consumed at different times of the year and in different amounts by *Pithecia* and *Ara*. For example, in September, *Pseudolmedia* represented over 36% of the diet of *Pithecia*, but just 7% of that of *Ara* (Figure 6a). Levels of *Inga* consumption by macaws and sakis were similar from June to September but diverged over the rest of the year (Figure 6b) as production of immature and mature *Inga* fruit increased. Consumption of three genera- *Mauritia*, *Pouteria*, and *Eschweilera*- was concentrated in key months for one consumer and spread across the year by the other (Figures 6c, 6d, and 6e). Finally, *Pithecia* and *Ara* ate *Sloanea* in different months, with no temporal overlap (Figure 6f).

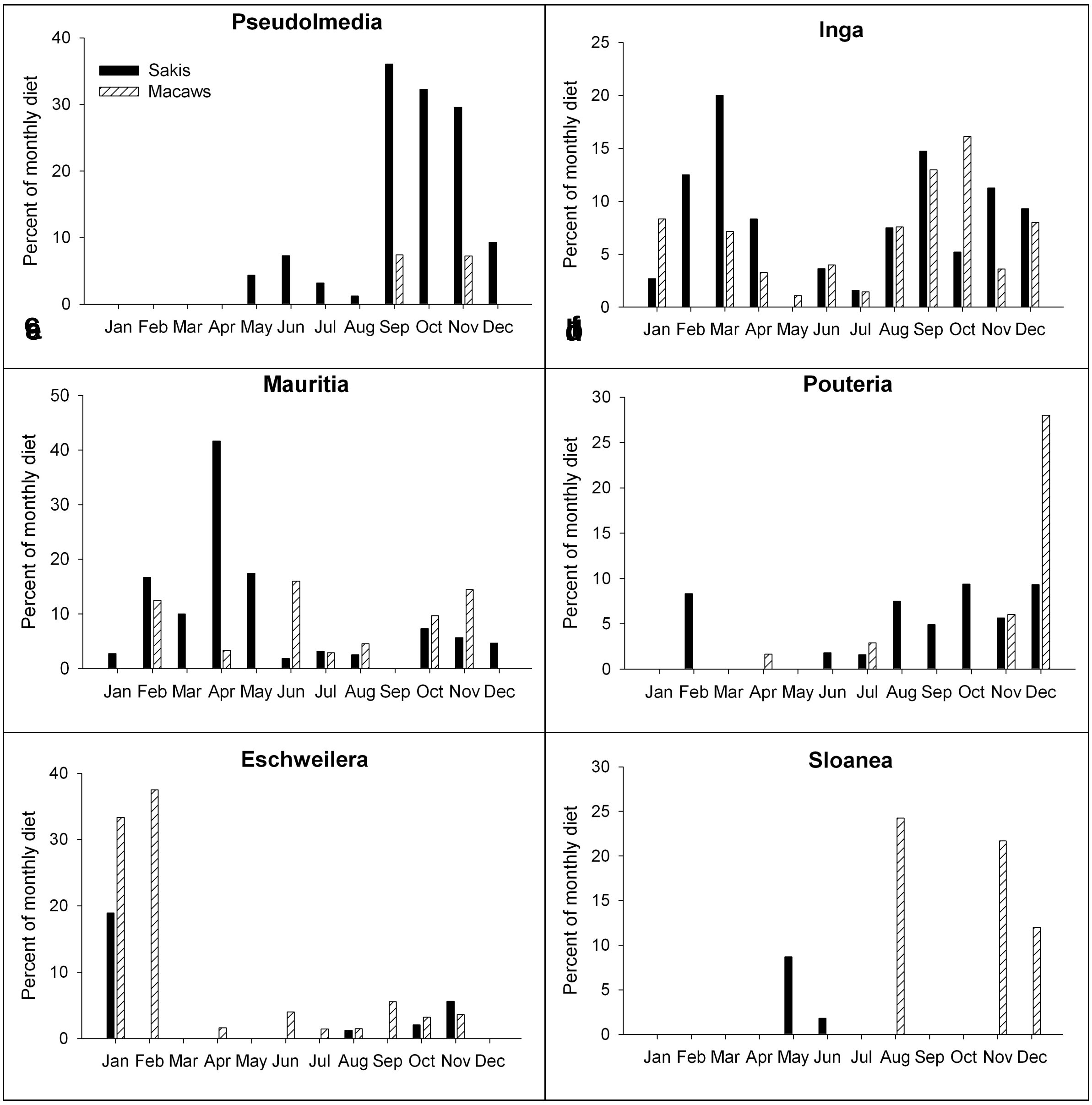

Figure 6. Percent contribution to monthly diets of sakis and macaws for the six genera (6a-6f) of greatest dietary overlap, 2004-2005.

Interspecific interactions

During over 1800 hours of following sakis, we never recorded their feeding in the same tree with macaws. On two occasions, we watched macaws either leave a feeding tree or wait nearby until a saki group finished feeding and left the tree, implying avoidance of interference competition (*sensu* Case and Gilpin 1974, Schoener 1983). During this same period, the team studying macaws recorded one incidence of *Pithecia* and *A. ararauna* feeding interspersed in the same tree. Thus, in almost 2000 combined hours of observation, we have observed only three potential incidences of interference competition between *Pithecia* and *Ara*.

Discussion

Dietary characteristics

The contribution of seeds (83% of feeding bouts) to the diet of *P. irrorata* in southeastern Peru was higher than that of *P. pithecia* (61%) and *Chiropotes satanas* (75%) in Venezuela (Kinzey & Norconk, 1993), *P. albicans* (45%) in Brazil (Peres, 1993), and *P. monachus* in northern Peru (3%, Happel, 1982 and 40%, Soini, 1987).

Our results in southeastern Peru indicate that while macaws generally ate more different parts of plants, sakis maintained a taxonomically more varied diet than the macaws, particularly during the period of lowest immature fruit production. They fed on more plant families, genera, and species than did the macaws, and their scores for richness, diversity, and evenness were all higher than corresponding indices for macaws.

Dietary overlap

Dietary overlap: interference competition

Our observations suggest that interference competition is virtually non-existent between the two study taxa, with three interactions seen in over 2000 hours of observation.

Dietary overlap: exploitation competition in southeastern Peru

While months of higher dietary overlap tended to be those with greater production of immature fruit, months with lower overlap tended to be those with high production of fruit of a few preferred plant genera. Quantities of fruit production among the preferred saki food plant genera and the preferred macaw food plant genera were similar, suggesting that differences in diet between sakis and macaws were not a function of relative availability of immature fruit.

The use of food plant genera, rather than species, in the analysis may overestimate potential competition. In some cases, it is possible that the two consumers were eating different species of the same genus in a given time period. Monthly variation in dietary overlap and the variable relationship between overlap and fruit production further complicate evaluation of the level of exploitation competition between these two taxa.

Dietary overlap: regional exploitation competition

In their three-month study of dietary overlap between a Pitheciine, *Chiropotes satanas*, and an *Ara, A. chloropterus*, Norconk *et al* (1997) provide qualitative data from a forest remnant in Venezuela's recently-flooded Guri Lake. While six of the seven food plant species recorded in the diet of *A. chloropterus* were also eaten by *C. satanas*, over half of the 17 species of plants consumed by *C. satanas* were not consumed by *A. chloropterus*. While sharing of food species in a short period suggests competition, the extent and seasonality of dietary overlap were not quantified, due the limited number of observations of *Ara*.

Despite the substantial shift in plant species composition across the Amazon basin (ter Steege *et al.*, 2006) and the resulting divergence in food plants consumed, Pitheciine monkeys and *Ara* macaws in Venezuela and Peru both focus their feeding on hard, unripe seeds. Calculation and comparison of dietary overlap for *C. satanas* (or *P. pithecia*) and *A. chloropterus* in Venezuela at geographically opposite ends of the Amazon basin would provide an interesting look at how a foraging guild adapts to variations in food resources.

Bearing in mind possible overestimation from generic-level plant identification, our overlap value was intermediate when compared with those of sympatric primates in Colombia. Our overall value for Morisita's overlap index (0.195) was greater than those for pairings of *Alouatta seniculus* with *Cebus apella*, *Lagothrix lagotricha*, or *Ateles belzebuth* (all less than 0.15, Stevenson *et al.*, 2000) but less than those between pairings of species with more frugivorous diets: *C. apella*, *L. lagotricha*, and *A. belzebuth* (each overlap >0.20). Our overlap values for three individual months (January, September, and November) fell within the average range of overlap among even these more frugivorous primates, though during certain biweekly periods, Stevenson et al. (2000) reported primate-primate overlap values almost three times greater than the highest saki/macaw values we observed. Interspecific competition among sympatric primates may be both more variable and potentially much greater than that across vertebrate orders.

Monthly overlap values (after Schoener 1974) between primates and hornbills in Cameroon ranged from 0.025 to 0.350 (Poulsen *et al.* 2002). The mean monthly primate-hornbill overlap value of 0.159 is not significantly different from the 0.147 mean monthly overlap value obtained with the same index for sakis and macaws in our study (t= −0.297, p=0.769, df=221). Poulsen *et al* (2002) concluded that, despite some 36 plant species consumed by both hornbills and primates in Cameroon, actual dietary overlap between these groups was low due to differences in fruit characteristics, proportion of food plants in each consumer’s diet, and canopy height frequented by each group. While we could not obtain precise foraging height data for the macaws, we observed that they tended to feed on the outside of the canopy at the ends of branches (G. Powell pers. obs), while *Pithecia* tended to feed within the canopy (S. Palminteri pers. obs.).

Poulsen *et al.* (2002) suggested that primates are more limited in their mobility than frugivorous birds and thus may be under greater pressure to diversify their diet. In south-eastern Peru, sakis did maintain a taxonomically more diverse diet than macaws. Radio-tagged macaws had far larger home ranges, travelling up to 50 km from their nest site, including a region devoid of sakis (G. Powell *et al*. unpublished data), demonstrating their ability to track the location and production of fruit over far greater distances than *Pithecia*.

We have found that these two seed predators, *P. irrorata* and *Ara* macaws, live sympatrically with limited dietary overlap. Evidence that their respective diets are influenced by competition is equivocal. They rarely ate fruit and seeds from trees of the same genera at the same time, in the same proportions. At the generic level, the availability of fruits and seeds was not the main source of this variation in consumption patterns. Plant identification to species level will improve this analysis; additional research on the density and/or population size of sakis and macaws in this region, and their seasonal changes due to macaw migrations, will also help to determine the extent to which consumption of food resources by one taxon affects their availability to the other.

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Appendix

Number of feeding bout records in 109 plant genera (plus unidentified samples) in the diets of *Pithecia irrorata* and *Ara spp.* in SE Peru in 2004-2005.

			No. of species used in genus		**Item consumed**		**Number of feeding bout records**	
Plant Family	**Plant Genus**		***P. irrorata***	***Ara spp.***	***P. irrorata***	***Ara spp.***	***P. irrorata***	***Ara spp.***
Annonaceae	***Guatteria***	***P***	**1**		**S**		**7**	
Annonaceae	*Sp*			1		S		1
Araceae	*Heteropsis*		1		S		3	
Araceae	*Philodendron*		1		S		1	
Arecaceae	*Attalea*			1		P		3
Arecaceae	***Euterpe***	***P***		**1**		**F**		**16**
Arecaceae	***Iriartea***	***P***	1	**1**	P	**L,S**	1	**33**
Arecaceae	***Mauritia***	***P***	**1**	**1**	**P**	**P**	**34**	**30**
Arecaceae	*Oenocarpus*			1		P		1
Arecaceae	*Socratea*		1	1	F,P	?	1	1
Arecaceae	*Sp*			1		F		3
Aristolochiaceae	*Aristolochia*		1		S		1	
Bignoniaceae	***Jacaranda***	***P***		**1**		**S**		**9**
Bignoniaceae	*Adenocalymma*		1		S		3	
Bignoniaceae	***Sp***		**5**	1	**S**	S	**19**	1
Bixaceae	*Bixa*			1		S		1
Boraginaceae	*Cordia*			1		S		2
Boraginaceae	*Sp*			1		F		1
Caryocaraceae	*Anthodiscus*			1		S		1
Caryocaraceae	*Caryocar*			1		S		2
Cecropiaceae	***Cecropia***	***P***		**2**		**F**		**15**
Cecropiaceae	***Pourouma***	***P***	**6**	1	**S**	S	**28**	1
Celastraceae	*Sp Pith11*		1		S		1	
Celastraceae	*Salacia*		1	1	P,S	S	4	1
Chrysobalanaceae	***Sp Pith60***		**1**		**S**		**16**	
Chrysobalanaceae	*Sp Pith95*		1		S		2	
Chrysobalanaceae	***Couepia***		**2**	1	**S**	S	**16**	3
Clusiaceae	*Clusia*	*P*	3		S		4	
Clusiaceae	*Caraipa*		1		S		3	
Clusiaceae	*Symphonia*	*P*		1		FL		6
Combretaceae	*Buchenavia*		1	1	S	S	1	1
Combretaceae	*Combretum*		1		S		3	
Connaraceae	*Connarus*		1		S		1	
Cucurbitaceae	***Cayaponia***	***P***	**2**	**3**	**S**	**S**	**5**	**8**
Cucurbitaceae	*Gurania*	*P*		1		F		5
Cucurbitaceae	*Helmontia*		1		S		1	
Cucurbitaceae	*Sp*		1		S		5	
Elaeocarpaceae	***Sloanea***	***P***	1	**2**	S	**S**	3	**37**
Euphorbiaceae	***Alchornea***	***P***	**1**		**S**		**7**	
Euphorbiaceae	*Dysidendrum*			1		F		1
Euphorbiaceae	*Nealchornea cf*		1		S		1	
Euphorbiaceae	***Hevea***	***P***	1	**1**	S	**S**	4	**28**
Euphorbiaceae	*Hura*	*P*	1	1	S	S	1	5
Euphorbiaceae	*Maniot*	*P*		1		S		4
Euphorbiaceae	*Pausandra*		1		S		2	

			No. of species used in genus		Item consumed		Number of feeding bout records	
Euphorbiaceae	*Plukenetia*		1		S		2	
Euphorbiaceae	*Sapium*	*P*		1		F		4
Fabaceae	***Acacia***	***P***	**1**	1	**S**	S	**6**	1
Fabaceae	*Apuleia*			1		S		2
Fabaceae	*Cedrelinga*			1		F		3
Fabaceae	*Ducia*			1		S		1
Fabaceae	***Dipteryx***	***P***		**1**		**S**		**7**
Fabaceae	*Enterolobium*	*P*		1		S		4
Fabaceae	***Erythrina***	***P***		**1**		**?**		**9**
Fabaceae	***Inga***	***P***	**12**	**5**	**P,S**	**S**	**44**	**24**
Fabaceae	*Lecointea*		1		P			
Fabaceae	*Parkia*	*P*		2		S		6
Fabaceae	*Phyllocarpus*			1		FL		3
Fabaceae	*Pterocarpus*		1		S		1	
Fabaceae	***Sp Ara39***			**1**		**S**		**27**
Fabaceae	*Sp*		1	3	P	S	4	5
Lecythidaceae	***Bertholletia***	***P***		**1**		**S**		**135**
Lecythidaceae	*Cariniana*	*P*		1		S		6
Lecythidaceae	***Couratari***	***P***		**2**		**S**		**7**
Lecythidaceae	***Eschweilera***	***P***	**3**	**5**	**S**	**S**	**14**	**19**
Lecythidaceae	*Sp*			1		S		3
Loganiaceae	*Strychnos*		2		P		5	
Malpighiaceae	*Byrsonima cf*			1		F		1
Malpighiaceae	*Sp*		2		S		3	
Malvaceae	*Apeiba*	*P*		1		A,S		6
Malvaceae	*Ceiba*	*P*		2		F,FL		5
Malvaceae	*Huberodendron*			2		S		3
Malvaceae	***Matisia***	***P***	1	**1**	S	**S**	3	**8**
Melastomaceae	*Bellucia*		1		S		1	
Meliaceae	*Cedrela*			1		S		1
Meliaceae	*Trichilia*		1		S		1	
Memecylaceae	*Mouriri*		1		S		2	
Menispermaceae	*Anomospermun*			1		F		1
Moraceae	***Brosimum***	***P***	**5**		**S**		**34**	
Moraceae	***Castilla***	***P***		**1**		**P,S**		**7**
Moraceae	*Clarisia*	*P*	1		S,F		6	
Moraceae	*Ficus*		1		S		2	
Moraceae	*Naucleopsis*	*P*	1		S		5	
Moraceae	***Pseudolmedia***	***P***	**3**	**3**	**S,P**	**P,S**	**86**	**10**
Myristicaceae	***Iryanthera***	***P***	**2**		**S**		**22**	
Myristicaceae	***Otoba***	***P***	**1**		**S**		**10**	
Myrtaceae	*Calycolpus*		1		S		1	
Olacaceae	***Minquartia***	***P***	**1**		**S**		**10**	
Passifloriaceae	*Dilkea*		1		S		1	
Phytolacaceae	*Gallesia*			1		FL		1
Quiinaceae	*Quiina*		1		S		3	
Rhizophoraceae	*Cassipourea*		1		S		1	
Rubiaceae	*Cinchona*			1		S		1
Rubiaceae	*Sp*		2		S		3	
Sabiaceae	*Meliosma*			1		S		2
Sapindaceae	*Paullinia*		2		S		3	
Sapotaceae	*Micropholis*		1		S		1	

			No. of species used in genus		Item consumed		Number of feeding bout records	
Sapotaceae	***Pouteria***	***P***	**9**	**7**	**S**	**P,S**	**30**	**15**
Sapotaceae	***Sp***		**5**		**S**		**64**	
Simaroubaceae	*Simarouba*	*P*	1		S		5	
Siparunaceae	*Siparuna*		1		S		1	
SP	*Euphonia?*			1		F		2
SP	*Gabaretia?*			1		?		1
SP	*Sp Pith152*		1		S		4	
SP	*Sp Pith67*		1		S		1	
SP	*Ochroma*			1		FL		3
Sterculiaceae	***Byttneria***	***P***	**2**	2	**S**	S	**11**	5
Ulmaceae	*Celtis*		1		S		3	
Vochysiaceae	*Vochysia*		1	1	S	S	1	3
Unidentified	*Sp*		2	14			12	25

A=Aril, FL=Flower, F=Fruit, L=Leaf, P=Pulp, S=Seed**,** ?=Unknown

32 items in **bold** represent the 20 food plant genera most frequently consumed each by sakis and macaws.

P = Forty-one of the 109 genera, denoted with a "P", were represented in the phenology study. Plant species collection and identification are ongoing.

Chapter 7: Remotely-sensed canopy structure as a determinant of habitat quality for arboreal mammals in tropical forests

Abstract

The three-dimensional spatial configuration of forest habitats affects the capacity of non-volant arboreal vertebrates to move, access food, and avoid predation. However, sampling vegetation structure over large areas from a sufficient density of field plots to incorporate fine-grained heterogeneity at the landscape scale is logistically difficult, labour-intensive, time-consuming and costly, particularly in remote areas of tropical forests. We used airborne waveform light detection and ranging (LiDAR) data acquired over the south-eastern Peruvian Amazon in combination with field data on a population of bald-faced saki monkeys (*Pithecia irrorata*) to assess the utility of LiDAR-derived indices of canopy structure in describing parameters of preferred forest types for this arboreal primate. Forest structure parameters represented by LiDAR measurements were significantly different between home range areas used by sakis and those that were not used. Both overall and within each of four main forest types, areas used by sakis, particularly core home range areas, represented a predictable subset of available forest areas, generally those containing the tallest and most uniform canopies. Differences observed within a focal area occupied by five habituated study groups were consistent across the wider landscape; groups of sakis were missing from areas of shorter, heterogeneous canopies but occupied adjacent areas with taller and less variable canopies, demonstrating that high-resolution remote sensing can uncover key insights into the relationship between habitat structure and habitat use by arboreal vertebrates in tropical forests. The nonlinear relationship between canopy structure values and the intensity of use by sakis within their home ranges suggests that while forest structure indices derived from LiDAR may help determine minimum structural characteristics of suitable habitat for bald-faced sakis in this region, other factors likely contribute to their fine-scale use of space.

Introduction

Animals rarely use space uniformly. Not only do population densities vary considerably across most landscapes, but space is typically used unequally within fixed home range boundaries. While the abundance and distribution of food resources have been repeatedly shown to affect the use of space by vertebrates, particularly frugivores (e.g. Garber 1987, Van Schaik 1993, Peres 1994, Saracco et al. 2004), patterns of space use may also be driven in part by habitat structure itself (e.g. MacArthur and MacArthur 1961, Warner 2002). Habitat structure has been shown to influence hunting site selection by large carnivores (Loarie et al. in press) and movement patterns of prey species (Schultz and Noë 2002, Fortin et al. 2005). Three-dimensional spatial configuration of forest habitat may function as a major determinant of habitat suitability for arboreal vertebrates (Emmons and Gentry 1983, Lefsky et al. 2002, Warner 2002, Clawges et al. 2008), affecting their capacity to move through the habitat (Williams-Guilen et al. 2006), their access to food, and their vulnerability to attack by aerial predators (e.g. Terborgh 1983, Lemos de Sá and Strier 1992, Youlatos 1999, Raboy et al. 2004, da Silva et al. 2009). In particular, habitat structure may play a critical anti-predation role for small-bodied solitary or small-group living non-volant species (Terborgh 1983, Boinski et al 2003, Vidal and Cintra 2006, Crompton and Sellers 2007).

An example is the genus *Pithecia* (saki monkeys), which are medium-bodied, small-group living high-forest specialists typically found at low densities or variable rates of local habitat occupancy across the Amazon basin (Peres and Janson 1999, Heymann et al. 2002, Youlatos 2004, Sheth et al. 2009). The four *Pithecia* species occurring south of the Amazon River spend most of their time in the mid- to upper portions of the canopy of tall forests (Happel 1982, Soini 1986, Peres 1993, S. Palminteri, pers. obs.). They live in groups of 2-8 individuals (Soini 1988, Peres 1993) and are seed predators, thereby benefitting from a relatively aseasonal food supply (Chapter 5). The breadth and consistency of saki diets (Norconk 1996, Soini 1987, Peres 1993a, Chapter 5) suggest that their patterns of home range use and movements may be influenced by factors other than food availability. Unlike the relatively well-studied Guianan saki (*P. pithecia*), occurring north of the Amazon River, which are more committed leapers between high-angled supports and tree trunks in the forest understorey and midstorey (Fleagle and Meldrum 1988, Walker 2005), it has been hypothesized that the four larger-bodied southern Amazonian congeners (*Pithecia irrorata, P. monachus, P. albicans and P. aequatorialis*) move cryptically, primarily by quadrupedal walking and leaping between relatively large-diameter low-angled subcanopy and canopy branches (Peres 1993a). This is consistent with the widespread vernacular name of these relatively secretive species (often meaning the "flying monkey") and observations during short-term field studies (Happel 1982, Setz 1994, Walker 1996, Buchanan-Smith et al. 2000). Southern Amazonian sakis may therefore be limited to areas with sufficiently high-statured forest structure that provides adequate primary and secondary branching for their positional and locomotor repertoire.

Consistent with the hypothesis that saki movements require structurally well-developed habitats, a recent long-term systematic study of bald-faced sakis (*Pithecia irrorata*) in southeastern Peru demonstrated that they showed a strong preference for mature unflooded terra firme and floodplain forest types over low-phytomass forest habitats such as bamboo and palm-dominated stands (Chapter 4), which would be expected to have minimal branching structure (Kalliola et al. 1991, Smith and Nelson submitted/in press). If sakis specialize in higher forest strata of tall forest with well-developed low-angled branching, then patterns of habitat use could be expected to reflect measurable variability in forest canopy structure, both in terms of wood/foliage density and aboveground height. Consistent with this hypothesis, spatial variation in home range use intensity should be correlated with physical characteristics of the forest canopy.

Despite the importance of vertical vegetation structure in shaping use of space and three-dimensional kinetics of arboreal vertebrates, quantitative data describing the physical structure of arboreal habitats remain largely lacking. In particular, fine-scale structural characteristics that define habitat suitability are poorly known for most tropical forest vertebrates, in part because generating unbiased high-resolution data, often through floristic plots, at appropriate spatial scales required for these analyses has proven exceptionally difficult (Bradbury et al. 2005, Hudak et al. 2009). Field assessments generally rely on vegetation plots that sample only a tiny fraction of the study area and produce relatively coarse-scale analyses (Clawges et al. 2008, Falkowski et al. 2009), such as those measuring impacts of logging on vertebrate densities (Felton et al. 2003, Hamard et al. 2010). In the humid tropics, generating canopy data from the ground is particularly challenging due to high habitat complexity and poor canopy access in relatively remote sites. Consequently, hypotheses relating habitat use of arboreal mammals to fine-scale habitat structure remain largely untested.

Airborne LiDAR (Light Detection And Ranging) generates high-resolution canopy data, including height and the fine-scale roughness, or variability in height. Critical for forest studies, mean canopy vertical height profiles derived from LiDAR measurements have been shown to correlate strongly with field-based estimates of the volume (Clawges et al. 2008, Flaspohler et al. 2008), density (Bradbury et al. 2005), and structure (Lefsky et al. 2002) of vegetation, as well as tree stem density (Clawges et al. 2008). LiDAR data affords the advantage of rapid acquisition at fine scale over large areas, and with a high level of accuracy. We therefore use LiDAR-generated data to test the hypothesis that bald-faced sakis should show habitat preference for areas within their home ranges with more developed vegetation structure, as indicated by measures of canopy height and variability of canopy height. Canopy height in this study represented the total volume of woody structures, whereas the standard deviation (SD) of canopy height represented canopy “roughness”, or fine-scale variability in height (as reviewed in Vierling et al. 2008). We quantified patterns of space use by five habituated groups of bald-faced sakis over a three-year period and analyzed the patterns of home range use and habitat preference with respect to the physical structure of the canopy as measured by LiDAR. We also tested the relationship between canopy and use intensity by comparing canopy characteristics of both foraging and non-foraging sites. Finally, we compared the LiDAR-derived canopy structure indices to two independent measures of saki food tree distribution to examine whether food availability was correlated with a well-developed canopy. Finally, drawing upon the relationships we established between canopy physiognomy and fine-scale use of space across the focal area, we further investigated habitat occupancy at a coarser scale across a much larger surrounding area where LiDAR data were also available.

Methods

Study area

The study took place in the Madre de Dios region of southeastern Peru, in the lower Los Amigos watershed within the 145,000-hectare Los Amigos Conservation Concession (12°34’07”S 70°05’57”W), ~270 meters above sea level (Figure 1). Four main forest types characterize the area: upland terra firme forest, upland bamboo-dominated (*Guadua spp.*) stands, mature floodplain forest, and palm swamp dominated by a large arborescent palm (*Mauritia flexuosa*). Terra firme and mature floodplain forests were primarily species-rich, closed-canopy vegetation, while bamboo stands and palm swamps occurred in discrete enclaves, 1−78 ha each, dominated by a few canopy species and a more open canopy. Annual rainfall across the study area averaged ~2,700 mm yr^{-1}, between 2001 and 2007 (range = 2,250 – 3,500 mm yr^{-1}, http://atrium.andesamazon.org, BRIT 2009) and was highly seasonal, with over 70% falling between October and March.

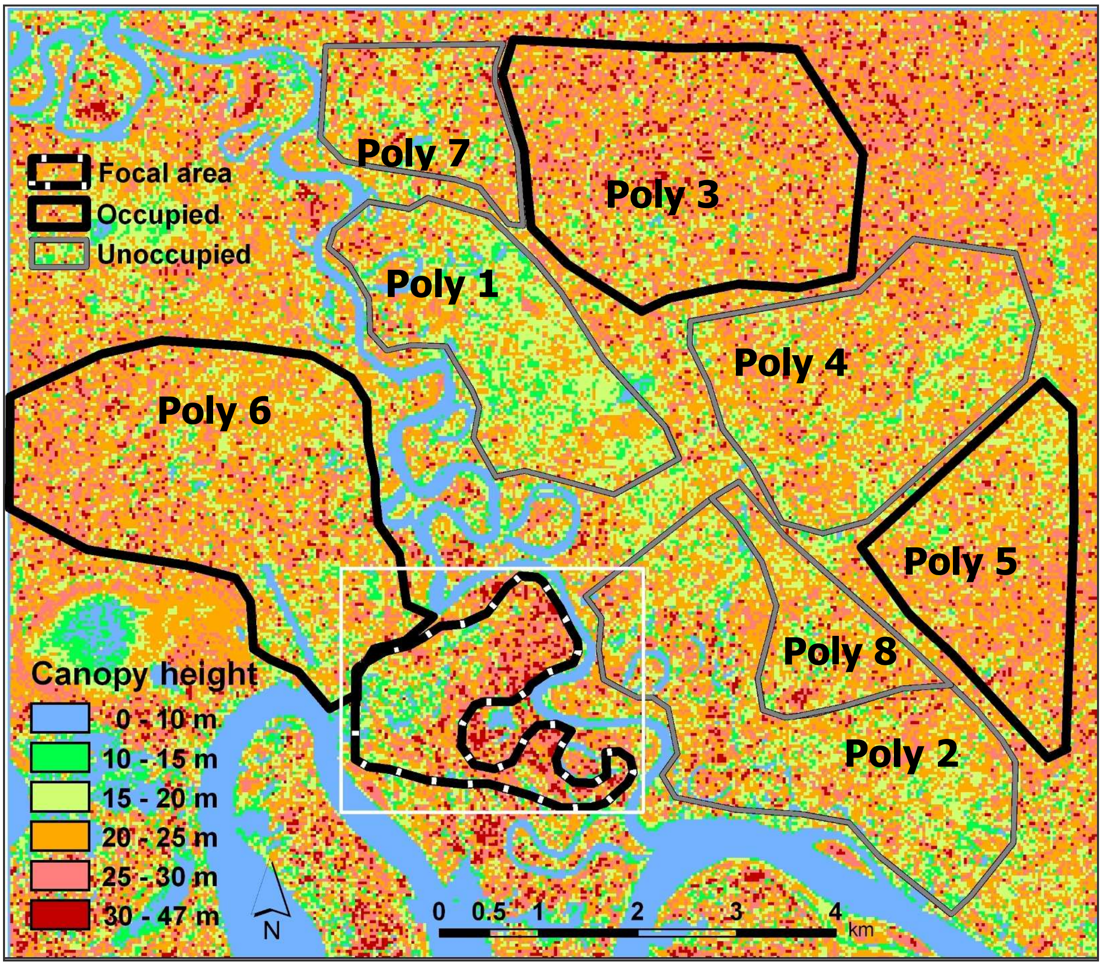

Figure 1: The study area showing LiDAR values for mean canopy height of 30 m x 30 m quadrats overlaid by the focal area and eight additional survey polygons (see text). During the 3-year study period, sakis were recorded throughout the occupied polygons, but not within the unoccupied polygons, according to both systematic acoustic censuses based on playbacks and the cumulative observation effort from many *ad hoc* researchers (see text). The white box around the focal area corresponds to the area detailed in Figure 2.

The study area consisted of approximately 6,400 ha covering most of the trail systems of two field stations: CICRA on the south-western bank and CM1 on the north-eastern bank of the Los Amigos River (Figure 1). At the southern end of the study area, we selected a 335-ha zone (hereafter, focal area) to intensively monitor five study groups of *Pithecia irrorata*. This focal area was defined as the area within the minimum convex polygon (MCP) surrounding all point locations of the five groups, adjusted to exclude both unsuitable habitats (e.g. lakes and clearings) and known territories of groups that we did not study (for further details, see Chapters 4 and 5). All points within the focal area, which consisted of 39% upland terra firme forest, 8% upland bamboo stands, 45% mature floodplain forest, and 8% palm swamp, were potentially accessible to at least one of the five study groups.

Monitoring in the focal area

Five adjacent groups of *Pithecia irrorata* were habituated and followed between January 2005 and December 2007, for a total of approximately 3,000 hours of observation. Groups consisted of a single adult male, one to three adult females, and associated immature individuals, averaging 4.7 (± 1.5 SD, range = 2 – 8) individuals over the study period, and maintained home ranges (HRs) of between 16 and 60 ha (see Chapter 4). We quantified habitat use through instantaneous group scan samples obtained every 15 minutes (Altmann 1974) during which we recorded the behaviour, location, habitat type, and vertical position (3 levels – canopy, sub-canopy and understory) of all visible animals. We also recorded the most prevalent activity pattern and the location of the geographic centre of the group (Terborgh 1983, Stoner 1996, Matthews 2009), either with a handheld Garmin 12XL GPS (typical reported error 8−10 m) or calculated locations in ArcView 3.3 GIS (ESRI, Redlands California) using recorded distances and angles from known coordinates within a georeferenced trail system. A 30 x 30 m grid was subsequently overlaid upon the entire study area, and all *Pithecia* positional records (15-min scan locations, N = 9,119) were assigned to the appropriate grid cell (hereafter, quadrat).

To correct for uneven monitoring effort among study groups, the sum of all scans in each quadrat was expressed as a proportion of the total number of 15-min scans recorded for each study group (e.g. Dietz et al. 1997, Buzzard 2006). For quadrats within home range overlap areas used by more than one group, we calculated the proportion of total scans recorded for the two groups using that quadrat. The resulting values for each quadrat defined its use intensity by sakis during this study. We identified as "preferred" those quadrats with use intensity values higher than the median value. Feeding quadrats were those in which we recorded at least one feeding bout on plant dietary items, including fruits/seeds, flowers, or leaves.

Occupancy in the wider study area

We investigated occupancy at a coarse scale across the larger study area, which was ~20 times the size of the focal area, by accumulating *Pithecia* presence-absence data based on two main sources. We used playbacks of saki territorial calls to stimulate responses from groups while walking an extensive trail grid during 52 days over a 34-month period. Initial tests with focal groups watched by an observer revealed that playbacks elicited consistent counter-calls detectable from a distance of up to ~100m. Playback walks were therefore conducted along research trails, with vocalizations played every 200 m. Each detection was then located as the distance and direction from either a GPS location or a trail marker. We also plotted the approximate locations of *Pithecia* groups systematically reported from *ad hoc* observations in 2006 and 2007 by other researchers at the two stations who had been solicited to report all *Pithecia* sightings. We were unable to quantify the number of hours during which participating researchers and field assistants were present in each quadrat potentially collecting saki presence-absence data. As a very conservative estimate, however, the annual number of visits to each research trail paid by this steady stream of observers (mean ≈ 27 per day at the CICRA station at any given time during the 2006-2007 period; http://cicra.acca.org.pe/english/cicra_60_segundos.html) far exceeded 30 and for some trails exceeded 5,000 visits. In addition, between 12 and 20 field observers studying other species, as part of our greater research programme, were present in the study area throughout the study period, with instructions to locate and report any *Pithecia* sighting.

LiDAR acquisition of forest structure data

We extracted a section of airborne LiDAR-generated data for the study area that had been collected in September/October 2009 using the Carnegie Airborne Observatory (CAO) scanning-waveform LiDAR system (Asner et al. 2007), as part of a larger research project aiming to estimate forest carbon stocks (Asner et al. 2010). The flights were conducted from 2,000 m above ground level, 1.1-m LiDAR spot spacing, 34° field of view, 50-kHz pulse repetition frequency.

The LiDAR collection system combines highly accurate GPS, Inertial Measurement Unit, and laser transmitter and receiver sensor that together record the location and orientation of an aircraft and the time it takes for light to travel from the aircraft to the forest/ground and back. The sensors are thus able to measure the three-dimensional distribution of vegetation structure, providing highly accurate estimates of vegetation density and height with a 1-m resolution and <1% error (Asner et al 2010). The 1-m resolution canopy height data generated by the LiDAR system were convolved to the 30 m x 30 m-resolution quadrats that were used to aggregate the movement data from the five saki study groups (detailed above). Thus, two metrics of forest canopy structure for each quadrat — the mean and the standard deviation (SD) of canopy height — were generated from 900 values representing each 1-m^2 LiDAR cell and used to examine quadrat-level habitat use by sakis in relation to canopy structure. In total, this study is based on the quantitative description of canopy structure in 48,195,200 LiDAR cells across the entire study area.

Data analysis: forest structure and use at the fine scale

Canopy structure and use by Pithecia

We used binary logistic regression to determine whether there was a threshold level of canopy height or variability in height that could explain whether or not quadrats in the focal area were used by our five study groups. We used a response variable (0 = never visited, 1 = visited) to examine the probability of saki use of a given quadrat based on values of each canopy structure parameter. We repeated the logistic regression within each of the four main habitat types.

We tested whether the two within-quadrat canopy structure metrics — mean canopy height and SD of canopy height (hereafter roughness) — differed between used and unused quadrats, preferred and non-preferred quadrats, and feeding and non-feeding quadrats using independent t-tests. Pairwise differences in the distributions of these variables were tested using two-sample Kolmogorov-Smirnov (K-S) tests. These comparisons were repeated for quadrats within each of the four forest types and within the home ranges of each of the five saki study groups. We also tested for variation in the overall canopy index values among the forest types and saki group home range areas using one-way ANOVA with Tukey post hoc comparisons.

We used two-sample K-S tests to further compare the distribution of mean quadrat heights to that of the heights and diameter at breast height (DBH) of 793 saki food trees. Tree heights were either measured in the field using a laser rangefinder or estimated using a DBH-to-height allometric equation generated in the same region (Asner et al. 2010).

Relating use to forest canopy structure

We used quantile regression (Koenker and Bassett 1978) to assess the relationship between the intensity of quadrat use by sakis and mean canopy height because of unequal variance in use intensity along the height gradient. Quantile regression estimates the rates of change (slopes) for specified quantiles of the dependent variable distribution rather than just changes in the mean (Cade and Noon 2003), thereby providing a more complete view of the relationship between the two variables than those captured by least squares regression (Knight and Ackerly 2002). We estimated a complete series of quantile regression functions from the 10th to the 90th quantile, plus the 99th quantile, for the relationship between mean quadrat canopy height and use by sakis. Analyses were carried out in R, using the '*quantreg*' package (Koenker 2009).

Forest structure and use at the coarse scale

Within the wider Los Amigos study area, we examined site occupancy of unhabituated saki groups as a function of forest canopy structure by comparing the distributions of canopy structure metrics in occupied and unoccupied areas with those of used and unused quadrats in the focal area, which we assumed to represent characteristics of suitable and less suitable habitat, respectively. We predicted that the canopy structure [distributions of mean height and roughness (N = 900 1-m^2 values) of 30 x 30m quadrats] of areas occupied by sakis would be similar to those of used quadrats in the focal area, whereas the distributions of these variables in unoccupied areas would be more similar to those of unused quadrats. We first delineated eight large neighbouring polygons, covering >4,500 ha of forest (Figure 1), on the basis of their known levels of *Pithecia* occupancy, derived from the coarse, presence-absence data generated through both systematic playback censuses and the cumulative observation effort of over 100 investigators and field assistants over a 24-month period. The eight polygons ranged from 200-900 ha, though polygon size was independent of both mean canopy height and canopy roughness ($r^2 = 0.02 – 0.06$, $F = 0.002 – 0.0008$, $P > 0.50$ for both metrics). We used t-tests to compare the mean and SD of canopy height of all quadrats within polygons for which *Pithecia* had been reported (“occupied”) to those where they had never been reported (“unoccupied”), and to compare the height distributions of each of these polygons with those of the focal area. We further used K-S tests to compare the respective distributions of mean height and roughness of occupied and unoccupied polygons with those of used quadrats (representing adequate canopy structure for saki occupancy), unused quadrats (representing sub-optimal canopy structure), and all quadrats of the focal area. Unless otherwise stated, data were analyzed using JMP and SPSS statistical software; statistical significance was set at the α=0.05 level (two-tailed tests).

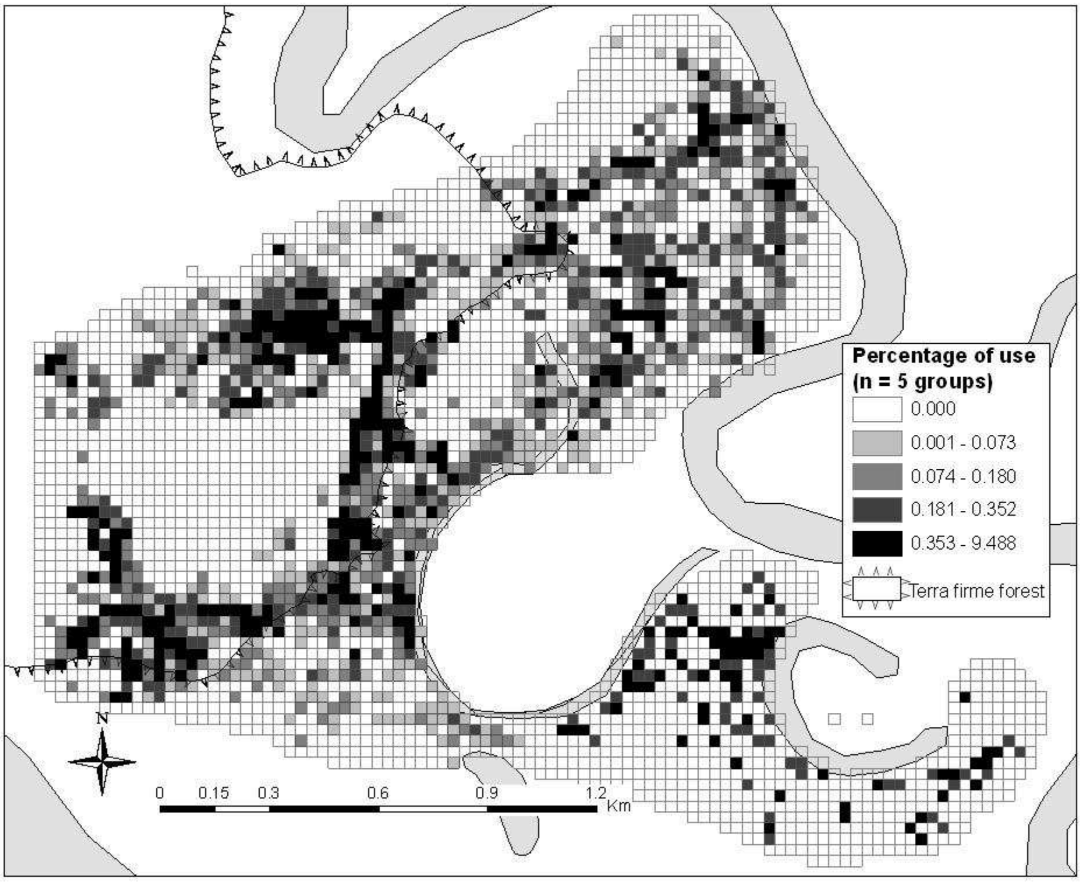

Figure 2: Focal area comprised of 3,418 quadrats of 30m x 30m covering the home ranges of five saki study groups. The proportion of total 15-min scans recorded for a given group in any of its home range quadrats varied from 0 to >9.5%. Quadrats are coded by their overall use intensity, defined as the proportion of total scans of the relevant group(s) in each. Blank squares represent quadrats that were accessible to one or more groups but had no record of ever being used.

Results

Use of space in the focal area

The five study groups were recorded at least once in a total of 1,378 of the 3,418 quadrats within the focal area (Figure 2, Table 1). Quadrat use ranged from 1 – 113 visits (15-min locations), and the proportion of total time that a given group spent in any of its quadrats varied from 0 to >9.5% (median = 0.18%). Saki groups primarily used the lower to sub-canopy, using somewhat higher portions of the canopy when in quadrats containing higher-statured forests, as well as when feeding (χ^2= 296.6, df = 2, p<0.0001, Figure 3).

Table 1. Forest structure characteristics derived from LiDAR data for 30m x 30m quadrats that were used and unused by bald-faced sakis (*Pithecia irrorata*) within a focal area of 3,418 quadrats in southeastern Peru. Mean and standard deviation of canopy height values for each quadrat were derived from 900 values corresponding to individual 1m^2 cells within each quadrat. Values are presented for quadrats grouped by presence vs. absence of sakis (use) and preference (preferred vs. used but non-preferred) for the entire focal area and for quadrats within the home ranges of each of five study groups (A – E). The total numbers of quadrats within each category are indicated in parentheses.

Cell Grouping	Mean Canopy height (m)	SD Canopy height
Used (1378)	25.0 ± 5.1 *†	6.7 ± 1.9 *†
Unused (2040)	20.6 ± 7.2	7.2 ± 2.2
Preferred (671)	25.9 ± 4.7 *†	6.7 ± 1.9
Non-preferred (707)	24.1 ± 5.4	6.8 ± 1.9
A – Used (430)	24.9 ± 4.9 *†	6.8 ± 1.8 *†
A – Unused (190)	19.6 ± 7.4	7.5 ± 2.1
A – All (620)	23.3 ± 6.3	7.0 ± 1.9
B – Used (340)	23.0 ± 4.7 *†	6.8 ± 2.0
B – Unused (148)	18.7 ± 5.9	7.2 ± 2.3
B – All (488)	21.7 ± 5.5	6.9 ± 2.1
C – Used (117)	28.1 ± 4.1 *†	6.7 ± 2.0 *†
C – Unused (349)	23.6 ± 7.6	7.4 ± 2.5
C – All (466)	24.7 ± 7.2	7.2 ± 2.4
D – Used (480)	26.8 ± 4.4 *†	6.55 ± 1.8 *
D – Unused (318)	24.2 ± 6.1	7.02 ± 1.8
D – All (798)	25.8 ± 5.3	6.74 ± 1.8
E – Used (169)	21.6 ± 5.3 *†	7.04 ± 1.9
E – Unused (84)	18.0 ± 5.1	6.58 ± 1.9
E – All (253)	20.4 ± 5.5	6.88 ± 1.9

* For Used sub-groups, denotes significantly different mean values from Unused.

† For Used sub-groups, denotes significantly different distributions from Unused (two-sample Kolmogorov-Smirnov tests).

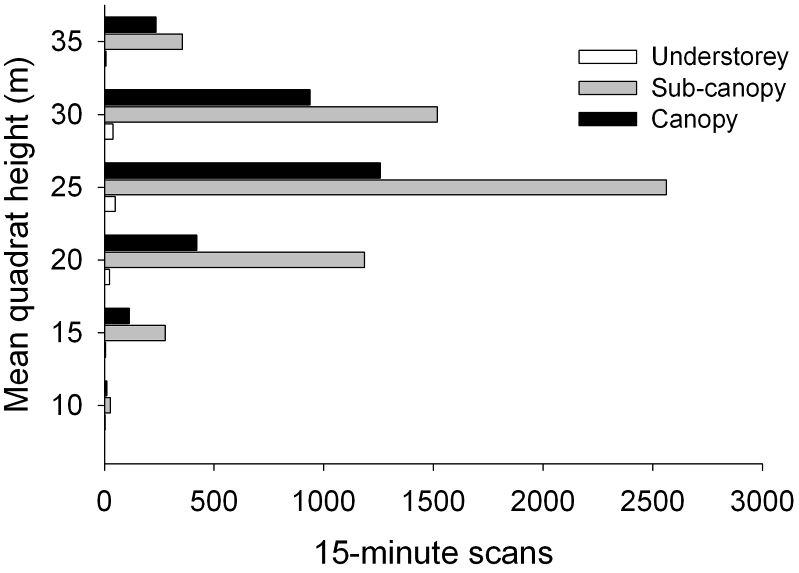

Figure 3. Vertical position of sakis in the canopy at different mean quadrat heights during 9,042 observational (15-min) scans of saki groups across 31 months of study between 2005 and 2007. The y-axis designates the midpoint of quadrat height categories. Subcanopy (≈12–25 m) comprised over 59% of scans in each quadrat height category. While the forest understory (≈ 5–12 m) was virtually never used (N = 127, 1.4% of all scans), the subcanopy forest stratum was consistently the most heavily used (65% of all scans), even in taller quadrats. Sakis used the tallest portions of the canopy during 33% of scans.

Forest structure and use at the fine scale

Canopy characteristics and use

Simple dichotomous logistic regressions of canopy structure metrics versus saki presence within the focal area showed that structure parameters significantly explained saki quadrat occupancy (Table 2). Mean canopy height significantly predicted saki quadrat occupancy within each of the four main forest types, while canopy roughness (SD height) predicted occupancy only within floodplain forest.

Table 2. Parameter estimates from logistic regression models describing the probability of saki visitation to a given 30 x 30 m quadrat (*N* = 3,418), based on its mean canopy height and mean canopy roughness (here represented by standard deviation of canopy height). Values are presented for the entire focal area and for quadrats within each of its four main forest types.

Forest type	**Predictor**	**Constant ± SE**	**β ± SE**	**LL**	**L-R χ^2**	**Exp(β)**	**R^2**	**df**	**p-value**
All	Mean Height	−2.93 ± 0.15	0.11 ± 0.01	2115.92	377.47	1.12	0.14	1	<0.001
All	SD_Height	0.36 ± 0.13	−0.11 ± 0.02	2285.07	39.17	0.90	0.02	1	<0.001
TF	Mean Height	−3.06 ± 0.35	0.17 ± 0.02	444.83	141.16	1.19	0.23	1	<0.001
TF	SD_Height	0.96 ± 0.27	−0.06 ± 0.04	514.15	2.52	0.94	0.004	1	0.11
FL	Mean Height	−2.98 ± 0.24	0.10 ± 0.01	1183.89	150.19	1.11	0.10	1	<0.001
FL	SD_Height	0.52 ± 0.17	−0.14 ± 0.02	1241.46	35.04	0.87	0.03	1	<0.001
BA	Mean Height	−5.27 ± 0.54	0.21 ± 0.03	185.23	69.94	1.23	0.22	1	<0.001
BA	SD_Height	−2.11 ± 0.44	0.05 ± 0.05	219.72	0.97	1.06	0.003	1	0.32
PS	Mean Height	−2.41 ± 0.83	0.06 ± 0.04	138.54	3.27	1.06	0.02	1	0.07
PS	SD_Height	−0.86 ± 0.55	−0.02 ± 0.08	140.15	0.06	0.97	0.001	1	0.81

SE = Standard error, LL = Log-Likelihood, L-R, χ^2 = Likelihood-ratio chi-square for model; R^2 = Nagelkerke R^2. All = Quadrats within all forest types of the focal area. TF = terra firme forest; FL = mature floodplain forest; BA = bamboo forest; PS = palm swamp forest.

Canopy characteristics and use intensity

Patterns of quadrat use intensity by *Pithecia* in the focal area (Figure 2) demonstrated a strong preference for quadrats with taller, more homogeneous canopies. Canopies of quadrats that were visited by sakis at least once (*N* = 1,378) were substantially taller (t = 21.02, df = 3408, P < 0.0001) and had a more homogeneous topology (t = –6.41, df = 3208, P < 0.0001) than those of unvisited quadrats (Table 1). These features indicate forest areas with complex canopy, tall trees, and more uniform crown structure. The differences between used and unused quadrats were also reflected in more kurtotic distributions of both forest structure variables (two-sample Kolmogorov-Smirnov tests; mean height: Z = 8.70, roughness (SD height): Z = 2.70, *N* = 3418, P< 0.0001 in both cases, Figure 4) in used quadrats, indicating preference for a certain structural environment. Preferred quadrats were characterized by even taller canopies with more kurtotic distributions of quadrat height values than non-preferred quadrats (mean difference = 1.8 m, t = 6.48, df = 1367, P < 0.0001, K-S test: Z = 3.06, *N* = 1378, P<=

0.001, Table 1). Canopy roughness did not differ between these two groups (t= −0.62, df = 1371, P = 0.54; K-S test: Z = 0.79, P=0.57).

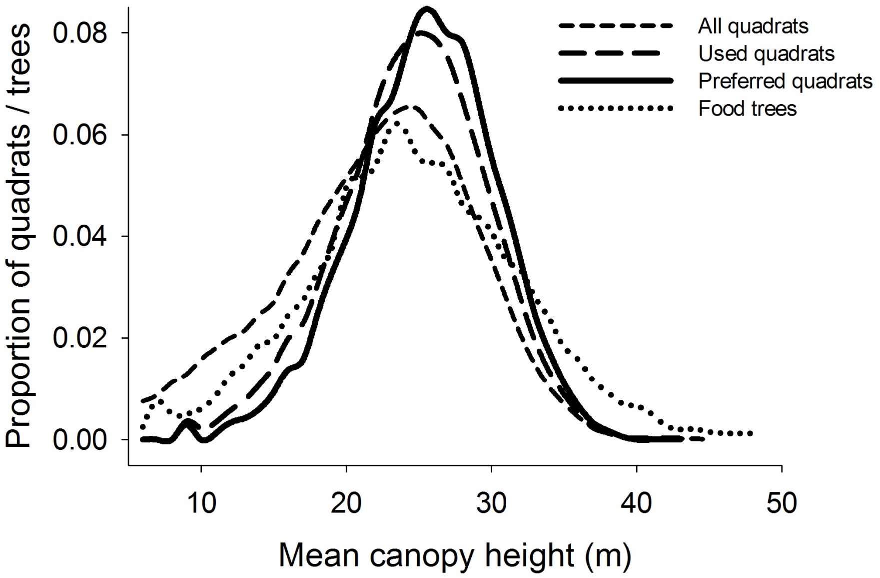

Figure 4. Proportional distributions of mean canopy heights of focal area quadrats (N = 3418) and food trees (N = 793) of five saki study groups. Used quadrats (N = 1378) were visited at least once by a study group, and preferred quadrats (N = 671) received more than the median proportion of total visits (15-min scans). The higher heterogeneity of food tree heights, compared to used and preferred quadrat heights, suggests that saki plant feeding bouts often targeted relatively short trees but rarely low-canopy quadrats, and that sakis used particularly tall food trees even as the availability of high-canopy quadrats declined.

The unequal variance in the distribution of use intensity with respect to canopy height (Figure 5a) indicated not only that more than one slope describes the relationship between height and use intensity, but that variance increased as a function of height. Sakis avoided quadrats with canopies shorter than 15m and spent most of their time in quadrats with canopies of 25 – 35 m (Figure 5a-b). The canopy height-use relationship was, however, non-linear, as many quadrats associated with extremely tall canopies had low or no recorded use. Nevertheless, while sakis infrequently visited quadrats of all heights, quadrats with the highest frequencies of use (90-99% quantiles) were almost always taller.

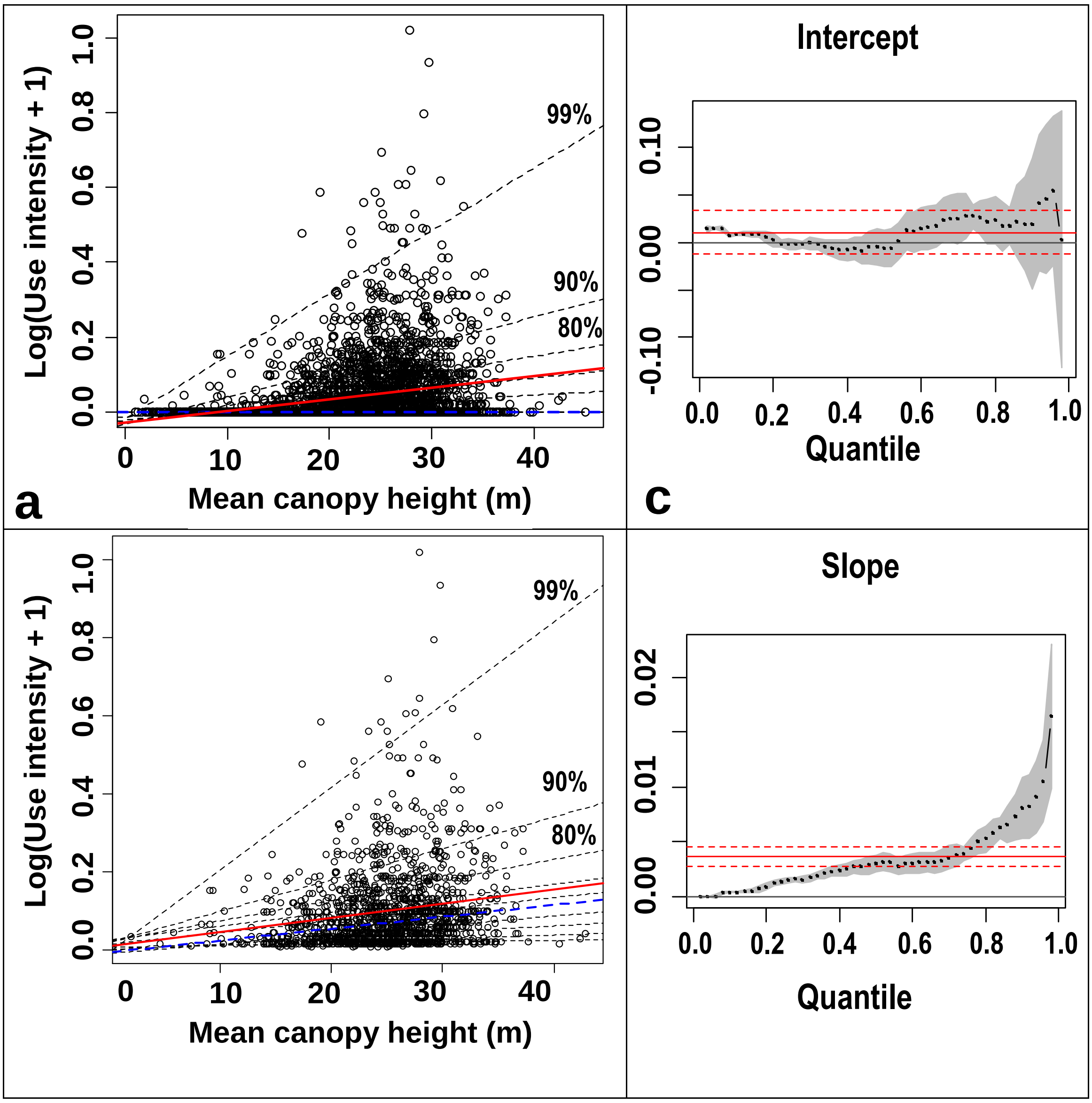

Figure 5. Quantile regression plots showing linear relationships between 10 different quantiles of the distribution of intensity of quadrat use by bald-faced sakis as a function of canopy height. Points represent individual quadrats, and linear relationships are shown for 10 different quantiles of the distribution including (a) all quadrats in the focal area (n = 3418) and (b) excluding all unused quadrats (n = 2040). The distribution of the intercept values for all percentiles for used quadrats (n = 1378, c) indicates that almost all begin at zero, indicating lack of use in very short canopies. The higher quantile estimates had greater positive slopes (d), and they increase abruptly above the 0.8 percentile. The single standard linear regression (red solid line) produced an $r^2 = 0.07$, F = 241.72, $P < 0.0001$, N = 3418.

Individually, each of the five study groups preferentially used the taller portions of its respective home range (Figure 6, Table 1). In each case, canopy height values were more narrowly distributed in used than unused quadrats (K-S tests for mean height: Z range = 2.16 – 4.47, P < 0.0001 for all groups), though the distributions of canopy roughness differed significantly for only two of the five groups (SD height: Z range = 1.22 – 1.99, Figure 7). Forest canopy in preferred quadrats was even taller than that in other used quadrats (Z range = 1.60 – 2.29, P < 0.01 for all groups), whereas canopy roughness of preferred quadrats was narrower than that of other used quadrats for only one of the groups (Z range = 0.64 – 1.59).

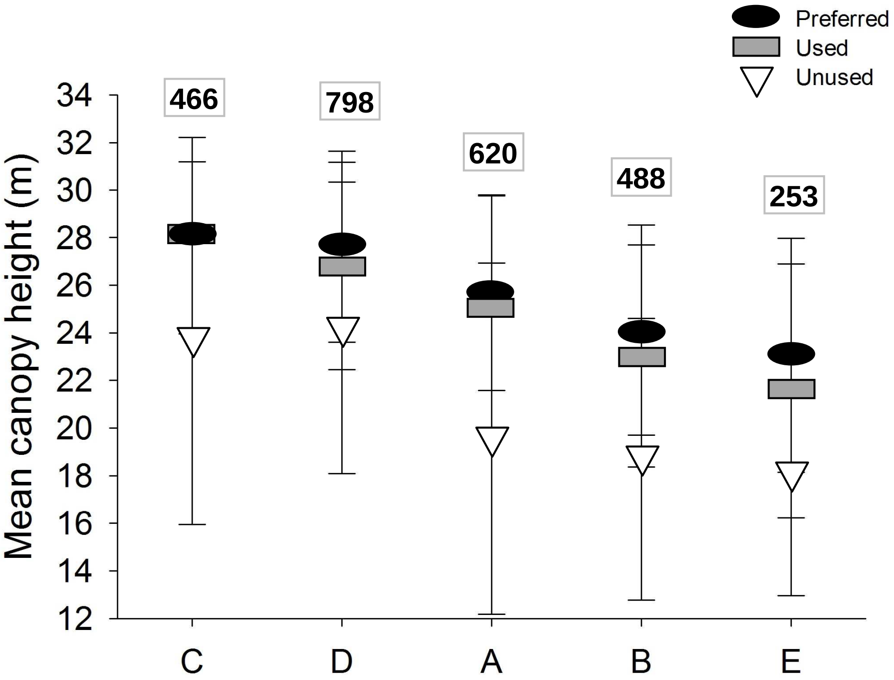

Figure 6. Mean ± SD canopy height in preferred quadrats (proportion of use > median value), used, and unused quadrats of the home ranges of each of five study groups. Home ranges (HRs) of groups C and D were predominantly floodplain forest, while those of groups B and E were predominantly terra firme forest. Used and preferred quadrats for group C were the same, due to a smaller sample size for this group. Numbers represent the number of 30 x 30m quadrats within the 95% kernel HR polygon of each study group (Chapter 4). Areas of HR overlap were counted for each group; 984 quadrats in the focal area were outside the 95% kernel HR polygons of any of the five groups.

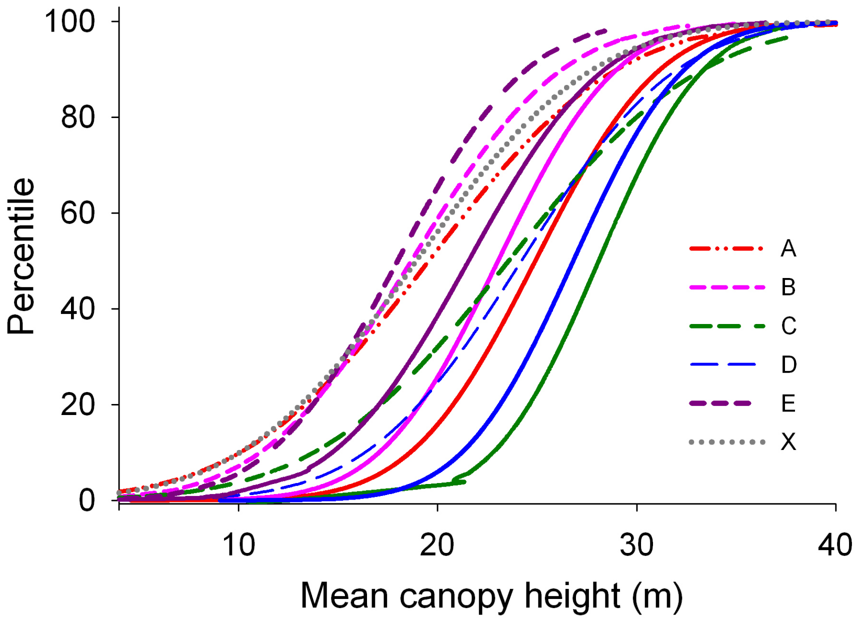

Figure 7. Cumulative Distribution Function (CDF) plots of distributions of mean canopy height in 30 x 30 m quadrats in areas used and unused by five saki groups within their respective home ranges. The five groups (A – E) are shown in colour, with solid lines representing used quadrats, and broken lines representing unused quadrats. X = quadrats in the focal area accessible to at least one group but with no recorded use and outside all home range polygons.

Canopy characteristics and feeding

Canopies of quadrats in which at least one plant feeding bout on fruits, seeds, flowers, or leaves was recorded ("feeding quadrats", mean height = 25.3 ± 4.7 m) were taller than those in other used quadrats (24.6 ± 5.5 m, t = 2.79, df = 1422, P = 0.005), suggesting that food availability partly explains saki preference for taller forest. However, this 3% height difference was minor compared with that between used and unused quadrats (≈18%), and canopy roughness did not differ between feeding quadrats (6.8 ± 1.9 m) and those used only during other activities (6.7 ± 1.9 m, t = –1.72, df = 1497, P = 0.09). Furthermore, when this is weighted by use intensity (number of scans per quadrat), mean canopy height of quadrats used for activities other than feeding (25.8 ± 4.6 m) was slightly greater than that of quadrats with feeding scans (25.5 ± 4.5 m, t = –3.15, df = 6123, P = 0.002).

Two measures of food resource use suggested that saki preference for tall canopies was not exclusively tied to food resource density. Mean height of feeding quadrats (25.0 ±

4.9 m) was significantly lower than that of preferred quadrats (25.9 ± 4.7 m, $t = -3.55$, $df = 183$, $P = 0.0004$). Moreover, saki food trees themselves (mean tree height 24.7 ± 7.1 m, $N = 793$) were shorter than the mean height of preferred quadrats ($t = -3.93$, $df = 1387$, $P < 0.0001$) but not that of quadrats used to a lesser extent (25.0 ± 5.12 m, $t = -1.10$, $df = 1275$, $P = 0.27$). The heights of food trees were also more variable than those of used, preferred or feeding quadrats (K-S tests: $Z = 2.82$, 3.60, and 3.14, respectively, $P < 0.0001$ in all cases; Figure 4), suggesting that sakis selected areas with taller, more uniform canopy within which they fed in trees of a variety of sizes.

Canopy characteristics of different habitat types

Among the four forest types, mature floodplain forest had the tallest canopy, whereas *Mauritia flexuosa*-dominated palm swamp was the least variable forest type in terms of canopy height (Table 3). Bamboo-dominated forest had both the shortest and the most variable canopy, ranging between 6.3 m and 9.1 m shorter than other forest types. Within palm swamp, canopy structure values did not differ between used and unused areas. The overall patterns of taller and more uniform canopies in both preferred and less intensively used quadrats versus unused quadrats were consistent across the other three forest types (Table 3). The distributions of height values across the used quadrats within terra firme, floodplain, and bamboo forest were more kurtotic than those of unused quadrats, although canopy roughness differed only in floodplain forest (K-S: $Z = 2.76$, $P < 0.0001$).

Table 3. Mean LiDAR-derived values of forest structure characteristics of used and unused 30 x 30m quadrats and Kolmogorov-Smirnov test results within each of four main forest types within the focal area. Mean and SD of canopy height values for each quadrat were derived from 900 values per quadrat, corresponding to individual 1m^2 LiDAR cells.

Forest type	**Variable**	**Overall (mean ± SD)**	**Used (mean ± SD)**	**Unused (mean ± SD)**	**K-S Z-value**	**P**
TF	Mean height	21.7 ± 5.9	23.6 ± 5.1	18.6 ± 5.9	5.43	<0.0001
N = 785	SD height	6.8 ± 2.0	6.6 ± 1.9	7.0 ± 2.1	1.08	0.19
FL	Mean height	24.5 ± 6.4	26.6 ± 4.6	23.1 ± 7.0	5.29	<0.0001
N = 1881	SD height	7.0 ± 2.1	6.7 ± 1.9	7.2 ± 2.2	2.76	<0.0001
BA	Mean height	15.4 ± 5.5	20.0 ± 4.6	14.5 ± 5.2	3.68	<0.0001
N = 512	SD height	7.6 ± 2.2	7.8 ± 1.9	7.5 ± 2.3	1.02	0.25
PS	Mean height	22.4 ± 4.4	23.3 ± 3.7	22.1 ± 4.6	1.02	0.25
N = 240	SD height	6.4 ± 1.8	6.4 ± 1.8	6.4 ± 1.7	0.45	0.99
ALL	Mean height	22.3 ± 6.8	25.0 ± 5.1	20.6 ± 7.2	8.70	<0.0001
N = 3418	SD height	7.0 ± 2.1	6.7 ± 1.9	7.2 ± 2.2	2.70	<0.0001

Forest structure and use at the coarse scale

Pithecia *occurrence across the wider study area*

In the analysis of occupancy across the wider study area, we found a similar pattern of use with respect to canopy height values. The three polygons occupied by sakis had canopies that were taller (mean canopy height ± SD = 22.96 ± 0.82 m) than those in which sakis were not detected (20.98 ± 1.18 m, t-test: t = 2.79, df = 5.69, P = 0.03), and they were characterized by a considerably higher proportion of tall quadrats than were the unoccupied polygons (K-S test: Z = 21.2, P < 0.0001, Figure 8). Canopy roughness did not differ between the occupied (6.5 ± 0.3 m) and unoccupied (6.6 ± 0.5 m, t = −0.343, df = 6.0, P = 0.74) polygons.

Canopy characteristics and use by Pithecia

Occupied polygons had canopy height profile values (mean quadrat canopy height across all three polygons = 23.0 ± 4.7 m) that were similar to but more homogeneous than those of the focal area (K-S tests for mean canopy height: Z = 6.4, P < 0.0001; roughness: Z = 5.2, P < 0.0001, Figure 9). The distributions of mean canopy height values in occupied polygons were intermediate between those of the used focal area quadrats, representing characteristics of acceptable habitat for sakis (K-S test: Z = 7.3, P < 0.0001), and unused quadrats, representing unacceptable saki habitat (Z = 9.6, P < 0.0001). Canopy roughness, the fine-scale variability in height within a single quadrat, was lower in quadrats of occupied polygons than in those of either used focal area quadrats (K-S test: Z = 2.0, P= 0.001) or unused focal area quadrats (Z = 5.6, P < 0.0001).

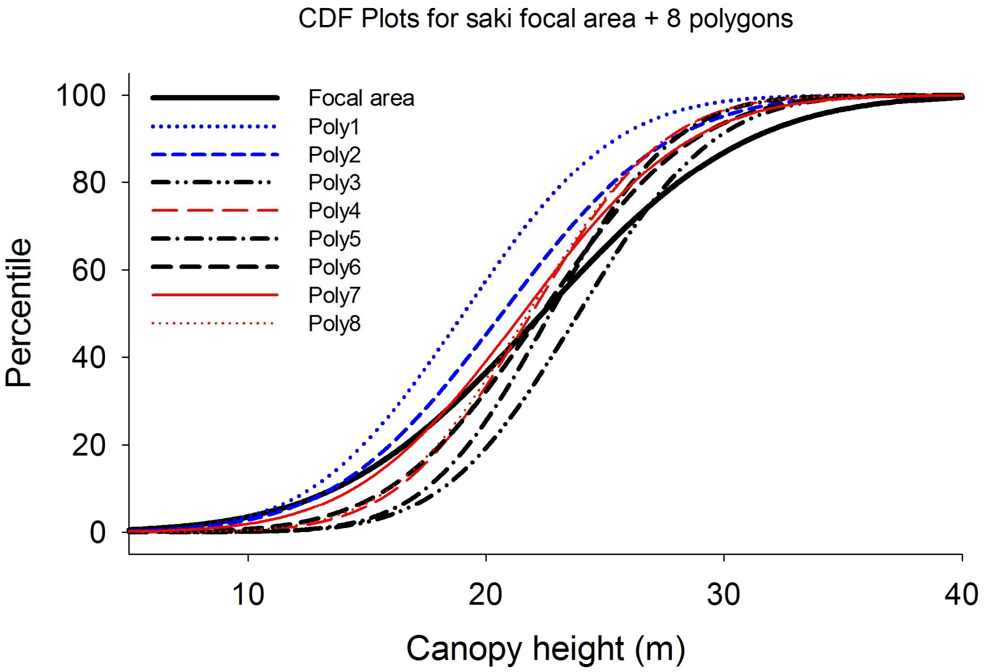

Figure 8. Cumulative Distribution Function (CDF) plots of the distribution of canopy height of 30 x 30 m quadrats within the focal area (solid line, 335 ha) and 8 surrounding polygons (210 – 910 ha). Polygons 3, 5, and 6 (black broken lines) were occupied by sakis and display distributions of height values in which 20-35% of quadrats were <20 m tall, while the 35-60% of the quadrats of polygons 1,2,4,7, and 8, which were effectively unoccupied by sakis, were < 20 m tall. Unoccupied floodplain polygons are shown as blue lines, while unoccupied terra firme polygons are shown as red lines.

While the mean canopy height value of quadrats within the five unoccupied polygons (20.8 ± 5.2 m) more closely resembled that of unused focal area quadrats, their distribution was far less variable (K-S mean canopy height: Z = 5.2, P < 0.0001, canopy roughness: Z = 5.7, P < 0.0001, Figure 9). Unoccupied polygons supported shorter but less heterogeneous canopies than the focal area overall (K-S test mean canopy height: Z = 10.6, P < 0.0001; roughness: Z = 5.3, P < 0.0001) and both far shorter and more variable than used focal area quadrats (K-S mean canopy height Z = 12.7, P < 0.0001, roughness: Z = 2.0, P = 0.001). Overall, the canopy height profiles of quadrats comprising the three occupied polygons were more similar to those of the used focal area quadrats (indicator of acceptable habitat), while the distribution of canopy height of quadrats in the five unoccupied polygons was strongly shifted towards the distribution of the unused quadrats.

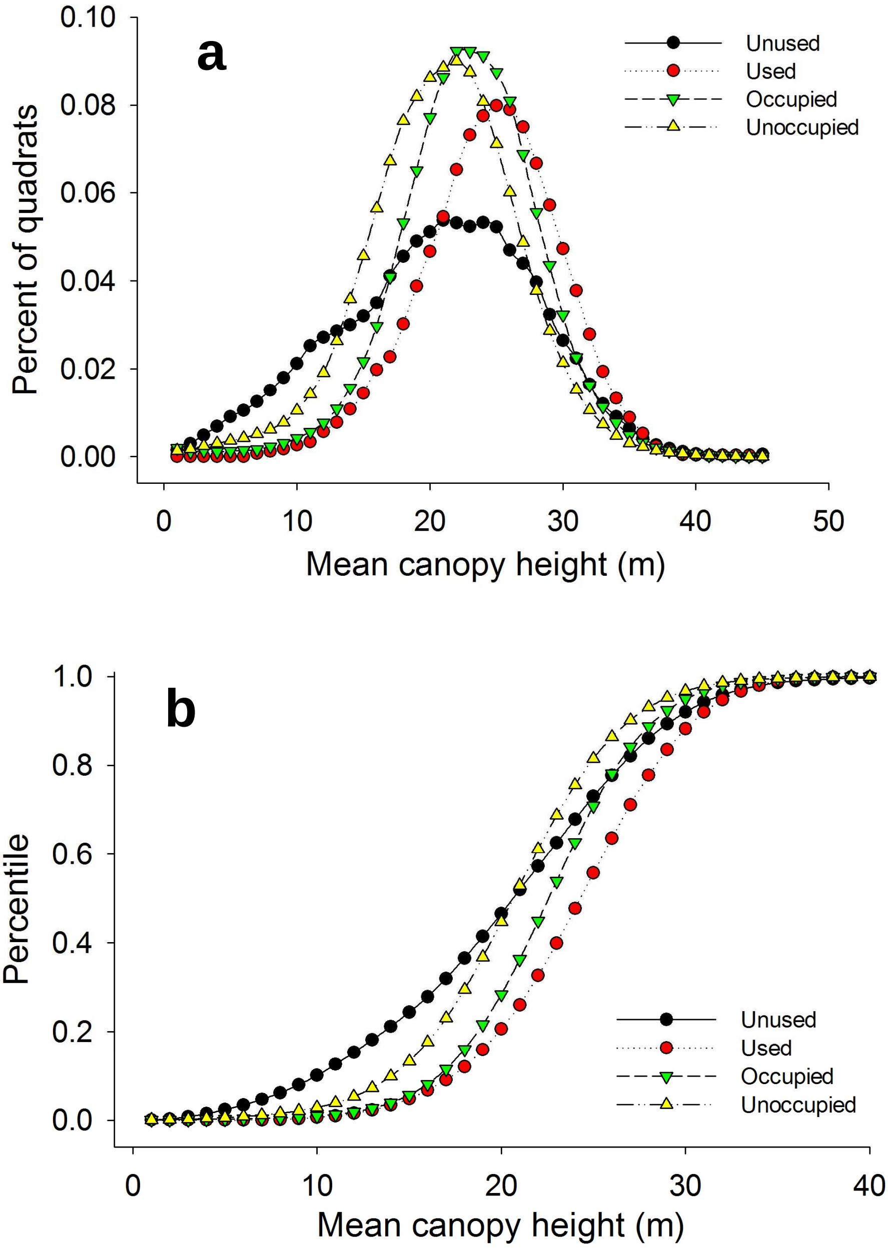

Figure 9. Proportion distributions (a) and Cumulative Distribution Function (CDF) plots (b) of the distribution of mean canopy height values of quadrats in polygons occupied (N = 3) and unoccupied (N = 5) by bald-faced sakis, compared to corresponding values in used and unused quadrats within the focal area.

Discussion

Home range use and canopy structure

To our knowledge, this is the first study relating forest canopy structure independently quantified over large spatial scales to use of horizontal and vertical space in a tropical arboreal vertebrate. We found that, within their home ranges, bald-faced saki groups tended to use more well-developed forest areas containing a taller and more uniform canopy structure, as consistently illustrated by comparisons of used versus unused and preferred versus lesser-used quadrats (Figure 9). However while quadrats used by sakis tended to be taller, the effect of height on saki use intensity was variable (Figure 5). Regression slopes for different portions (quantiles) of the distribution of quadrat use as a function of height provided a better, though still incomplete, picture of the relationship than a single least-squares regression. Quadrats with taller forest were clearly the most preferred in terms of use frequency (highest quantiles), while lower quantile estimates, representing low-use quadrats, indicated that sakis also used a wide range of canopy heights. While quadrats used most frequently were uniformly tall, some use might be allocated to quadrats that were shorter and more open if they had other features important to sakis. The differential in canopy height effect size suggests that interactions between canopy structure and other unmeasured factors — such as the distribution of food resources, territorial disputes and patrolling of range boundaries, movements through less preferred quadrats to reach optimal foraging sites, and movements along natural internal corridors — were likely greater in areas of low or moderate use (Cade et al. 1999, Planque and Buffaz 2008).

Movements through the home range matrix

While all saki study groups showed preference for a taller, more uniform canopy topology, each of their home ranges contained a variable matrix of microhabitats with a gradient of preference to sakis (Figure 2). A visit to a preferred quadrat inevitably involves travel through less preferable quadrats, which may be visited briefly regardless of their physical and plant species composition attributes (e.g. Albernaz 1997). Likewise, isolated tall trees would likely be visited less frequently than those embedded within a tall canopy matrix. A typical saki group daily travel path of ≈1,000 meters in length (see Chapter 4) usually included visits to some 50 quadrats. While quadrats used for feeding were slightly taller than those used for other activities, time spent feeding on plant material made up just 30% of our total saki observation time of 3050 h. Another

20% of their time was allocated to moving through their home ranges (Chapter 4); consequently, over the course of a monthly sampling period, a saki group ranged over its entire home range (Chapter 4), including low-preference quadrats with suboptimal structural attributes.

Territorial disputes and patrolling

Sakis defend their territories primarily through long-range calls, counter-calls and approaches to range boundaries in response to vocalizations of other groups (Norconk et al. 2003, S. Palminteri unpubl. data). Movements mediated by intergroup spacing were rapid and likely to be less sensitive to forest structure. Furthermore, the saki groups demonstrated a propensity to visit areas of their home ranges overlapping those of neighbouring groups (Chapter 4). Quadrats in overlap areas had taller forest ($t = 3.40$, $df = 228$, $P = 0.0008$) and contained more saki food trees than those in non-overlap areas (Wilcoxon rank-sum test: $W = 487377$, $Z = 15.3$, $P < 0.0001$), suggesting that territorial defence may be related to both food patch density in high-quality forest habitat.

Habitat type

The positive relationship between canopy structure and use by sakis was observed for three of the four forest types in our focal area. This relationship was strongest in bamboo-dominated forest, which had the shortest and most variable canopy and was clearly avoided by sakis. While sakis did not venture far into bamboo stands, they did use the few tall peripheral trees within the short canopy matrix of this habitat type. Use of bamboo-dominated forest, therefore, did not decrease in areas of greater heterogeneity in canopy height. Use of palm swamp, which was dominated by a single arborescent palm species, was particularly unrelated to the LiDAR-derived canopy metrics. The strong positive relationship between forest canopy height and vegetation volume and structure does not appear to apply to a palm-dominated forest (Asner et al. 2010). Despite the tall canopy of this habitat type, it lacks the associated low-angled branch structure used by sakis. Sakis spent just 2.8% of their time in this habitat, primarily while feeding on fruits of *Mauritia flexuosa*, a palm with minimum crown volume despite its relatively tall, radially-symmetric fanlike fronds.

In contrast to the bamboo-dominated habitat, floodplain forest in the focal area was taller overall than other forest types, yet sakis consistently selected the portions of this habitat with the tallest canopy. While overall canopy roughness did not differ between terra firme and floodplain forests, roughness in floodplain forest quadrats used by sakis was significantly lower than that of unused quadrats. This tendency by sakis to select areas with greater canopy structure within floodplain forest, which has a more well-developed canopy overall, suggests that the standards for canopy structure used by sakis may be more exacting for floodplain forest than for terra firme forest. Sakis may occupy floodplain forest only when it is of particularly high quality, in terms of overall structure and composition. The finding by Haugaasen and Peres (2005) that sakis would only use flooded várzea forest when it was immediately adjacent to terra firme forest further demonstrates their more stringent selectivity of floodplain forest. That terra firme did not have the tallest or least variable forest and yet was preferred relative to floodplain forest (Chapter 4) further suggests that forest structure, as measured by canopy height profiles, is important but that other factors affect use of space.

Drivers of habitat selection

The clear relationship between canopy structure and saki home range use raises the question of what driver(s) might be ultimately responsible. Here we consider two possible factors, food resource distribution and predation risk.

Food resource distribution

The extent to which food resources may be responsible for the observed preference for canopy structure should be influenced by a possible relationship between canopy height and food availability. It is widely recognized that habitat use by primates is influenced by food availability (e.g. Peres 1994, Dietz et al. 1997, Stevenson et al. 2000). However, *Pithecia irrorata* is a small-group living midsized primate capable of exploiting a wide array of food patch sizes, and groups consequently have low metabolic requirements and should be less constrained by food distribution. In addition, their diet consists primarily of unripe seeds of over 200 species showing a broad spatio-temporal distribution of food that is available throughout the year in a relatively uniform fashion across their home ranges (Chapter 5, S. Palminteri, unpubl. data).

Canopies of quadrats used at least once during plant feeding bouts were on average slightly taller (0.7m) than those used during activities other than feeding, and feeding quadrats had a similar canopy height to those of food trees, suggesting that the distribution of food is a driver for selection of quadrats with tall canopies. However, several measures associated with food resources suggested that quadrat selection may also be influenced by other drivers. Food trees were on average considerably shorter than the forest canopy in preferred quadrats, and tree heights were more variable than the mean heights of used and preferred quadrats, and even feeding quadrats. Sakis showed a greater propensity to use short food trees than to use quadrats associated with short, less structured canopy, and the shorter stature of both food trees and feeding quadrats, compared to preferred quadrats, suggests that forest structure itself affects use of space independently of food resources.

Motion capacity and predation risk

While sakis clearly demonstrated a preference for tall canopies, they were primarily found in the lower parts of canopy and emergent tree crowns, and their use of this forest stratum was largely independent of changes in canopy height (Figure 3). The subcanopy layer may provide maximum access to the large and medium sized primary and secondary low-angled tree branches and large high-climbing woody lianas over which they exercise much of their positional repertoires, while minimizing detectability. Indeed, the consistent tendency of sakis to maximize foraging time while minimizing locomotion within palm swamps, where horizontal connectivity through major branches is minimal, supports this conclusion.

Smaller-bodied forest primates often attempt to avoid predation risk by remaining lower in the forest (Terborgh 1983, Peres 1993c, Boinski et al. 2003), forming larger conspecific (e.g. *Saimiri* spp.: Terborgh 1983, Boinski) or heterospecific groups (e.g. mixed-species groups of *Saguinus* spp.: Peres 1993c, Terborgh 1983) or behaving cryptically, such as *Cebuella* spp., *Callimico goeldii* (Porter and Garber 2007) or *Callicebus* spp. (Terborgh 1983). Larger-bodied platyrrhine primates, on the other hand, are relatively immune to aerial predation and have been shown to use higher forest strata than smaller-bodied species (Bobadilla & Ferrari 2000, Buchanan-Smith *et al*. 2000, Heymann *et al*. 2002, Peres 1993b, Sheth et al. 2009). This positive relationship may be partly linked to the degree of per capita vulnerability to aerial predator attacks (Terborgh 1983, Youlatos 2004).

Sakis are an exception to these trends, maintaining small groups that rarely join other primate species in mixed troops (Peres 1993a, S. Palminteri unpubl. data) and remaining higher in the canopy than expected for their size (Peres 1993b, Youlatos 2004). In contrast, they appear to have adopted both physical and behavioural crypticity to minimize detectability. Their locomotion and feeding behaviour are exceptionally quiet (Peres 1993b, Kinzey 1986, Palminteri pers. obs.), as they generally leap from and land onto relatively large-diameter supports, rather than use far noisier small branches and terminal foliage (S. Palminteri and C. Peres, unpublished data). Their quadrupedal and saltatorial modes of locomotion, supported by relatively heavy branches, reduce background noise but restrict sakis to the main low-angled scaffold framework of the forest coinciding with the primary branching region of large canopy trees. As committed leapers, they also reduce propulsion loss of energy by using large woody substrates during takeoff. Moreover, the *Pithecia* call design further fits a behaviourally cryptic template in that their vocalizations are infrequent and contact calls used during intragroup communication are usually soft twitters resembling birds. Their very long, coarse, black-and-white mottled pelage and unusually bushy tail enhance their shaggy body plan and apparent size, as well as their chromatically camouflaged appearance in resembling the colour and texture of the major tree branches upon which they sit, walk, and rest. As an anti-predation strategy, the strong preference for areas with more developed canopy structure exhibited by sakis therefore complements their ecomorphology, general appearance and locomotor behaviour. It is not surprising, therefore, that southern Amazonian sakis are often referred to in many indigenous languages as the “silent” or the “flying” monkey (C.A. Peres, pers. obs). Nevertheless, as midsized primates exposed within lofty tree crowns, sakis remain highly vulnerable to aerial predation, which is consistent with dozens of locals reports of southern Amazonian *Pithecia* spp. falling prey to harpy eagles *Harpia harpija* and Guianan crested eagles *Morphnus guianensis* across the geographic range of these species (C.A. Peres, unpubl. data).

LiDAR as a tool for measuring tropical forest habitat suitability

The clear relationships between LiDAR-generated forest structure data and forest use intensity by five independent groups of sakis, and the congruent extension of those relationships to habitat occupancy across a much larger surrounding study area point to the value of airborne LiDAR as an emerging tool for ecologists and conservation planners. The collection of vegetation structure data by LiDAR provided a unique opportunity to study ecological relationships at three spatial scales. Our data were sufficiently precise to enable examination of heterogeneity of forest canopy structure at the scale of home ranges, 10 to 60 ha in the case of sakis, which permitted analyses of habitat preference by the individual groups. Such analyses would be difficult or impossible to achieve through either ground-based approaches or satellite imagery (Bradbury et al 2005, Lefsky et al. 2002).

Species presence-absence data across the surrounding Los Amigos landscape allowed us to assess habitat suitability at a far larger scale. The substantial difference in canopy height and roughness between occupied floodplain forest in the focal area and unoccupied floodplain polygons 1 and 2 in the wider study area provided insights into habitat preference that may help to explain patterns of floodplain forest use that have heretofore eluded us. Occupied floodplain forest in the focal area was taller than the other habitat types, though less intensively and more selectively used than the surrounding terra firme forest. If floodplain forest structure throughout south-western Amazonia more closely resembles that of our wider study area, its less-developed canopy structure can help explain the lower *Pithecia* abundances that are frequently reported for these floodplain sites (Chapter 3), Sheth et al. 2009).

Finally, the potential to acquire high-resolution forest structure data from an airborne platform, such as LiDAR, over vast tracts of otherwise inaccessible areas and yet with no change in precision — such as the 0.5 million ha of forest coverage over a 4 million ha section of the south-western Amazon (Asner et al. 2010) — will allow ecologists to scale up habitat analyses to map meso-scale patterns of vegetation biomass, as accomplished by Asner et al. (2010). Analyses of fine-scale vegetation structure data, with respect to regional-scale patterns of animal occupancy and habitat use will help to elucidate relationships between forest physiognomy and animal distribution patterns. In the case of sakis, for example, this sheds light on the enigmatic pattern of patchy distribution (Chapter 3) or variable population densities at which these arboreal seed-predators are typically reported in primate surveys (Branch 1983, Johns 1986, Haugaasen and Peres 2005, Sheth et al. 2009). Identifying the drivers of, and ultimately predicting, these spatial patterns across complex environmental gradients is critical to informed, meso-scale conservation planning for the lowland Amazon and other tropical forest regions.

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Chapter 8: Concluding remarks

Primate assemblage heterogeneity

The aim of this thesis has been to contribute to our ecological understanding of the factors that affect the use of space and consequent meso-scale distribution of animal communities of tropical moist forest ecosystems through complementary research on relatively complex primate assemblages of south-western Amazonia and the basic ecology of its most poorly-known species, the bald-faced saki. The ultimate aim is to apply this understanding to help strengthen the process of science-based conservation planning for the south-western Amazon and Amazonia in general.

The findings shed light on primate distributions and use of space at various spatial scales. Contrary to expectations that primate communities of the Madre de Dios (MDD) watershed of southeastern Peru should be relatively homogeneous, given the lack of species turnover and the relatively minor changes in habitat type and level of human disturbance, my colleagues and I found substantial natural heterogeneity in the assemblage structure across the basin (Chapter 3). The variable primate community structure across MDD reflects large-scale species patchiness, rather than species turnover, even for some relatively common species (e.g. *Cebus albifrons*, *Saimiri boliviensis*).

Of the 13+ resident primate species, three were found in fewer than half of the 37 survey sites compiled in this study, while two others were not detected at all. The ranges of the first three species – emperor tamarin (*S. imperator*), woolly monkey (*Lagothrix cana*), and bald-faced saki (*P. irrorata*) – did not extend south of the Madre de Dios River to the Tambopata watershed. *S. imperator*, which has the most restricted geographic range of the region's primates (IUCN 2008), was present at eight of 10 sites in the Los Amigos watershed, but only three of 10 sites in Manu National Park, some 100 km upstream, and missing from sites in the middle Las Piedras basin, all north of the Madre de Dios River. Like *S. imperator*, Goeldi's marmoset (*Callimico goeldii*), a species undetected in all 37 primate surveys, favours disturbed habitats, such as bamboo or early successional forests (Terborgh 1983, Buchanan-Smith et al. 2000, Porter et al. 2007). Despite the presence of both vegetation types in the region, *C. goeldii* is rarely sighted throughout MDD (Terborgh 1983, Chapter 3) and only slightly more regularly during primate surveys in adjacent Pando, Bolivia (Christen and Geissman 1994, Buchanan-Smith et al. 2000). While its large home range and short day path may account in part for low detectability (Porter et al. 2007), the complete absence of this species from all regional primate surveys remains poorly explained.

At the other end of the scale, large-bodied frugivores, such as woolly monkey, are heavily hunted (Peres 1990) and are consequently less abundant at hunted sites (Kirkby 2004, Chapter 3). However, the absence of this species from historically nonhunted sites (e.g. Cocha Cashu, Terborgh 1983) across much of the MDD basin, including nonhunted survey sites in the Tambopata watershed (Nuñez-Iturri and Howe 2007, Chapter 3), occurred independently of hunting pressure. The extensive seasonal home range shifts exhibited by woolly monkeys in the central Amazon (Peres 1994) suggest that seasonal fruit scarcity may alter the ranging behaviour and, thus, patterns of occupancy of this genus in nutrient-poor forests; however, contrasting findings by DiFiore (2003) in the upper Amazon (Ecuador) point to seasonal changes in the *Lagothrix* diet, rather than ranging patterns, as a response to ripe fruit scarcity, which would not be reflected in changes in local density.

Natural and anthropogenic drivers of primate community structure

Multiple factors appear to contribute to primate community heterogeneity, which affect the ability of coarse-scale range maps to depict fine-scale distributions of all but the most ubiquitous species. Rivers serve as potential barriers to species dispersal (Ayres and Clutton-Brock 1992), sources of varying levels of soil nutrients (Kalliola et al. 1993), and physical drivers of succession and habitat structure (Prance 1979, Salo et al. 1986, Puhakka et al. 1992), all of which affect the structure and composition not only of vegetation (Ruokolainen et al. 1997) but also of primary consumers like primates (e.g. Peres 1997). Regional floristic distribution patterns of trees and understory plants have been shown to vary according to changes in microhabitats, such as edaphic gradients, within broad forest types (i.e. Tuomisto *et al*. 1995, Phillips *et al*. 2003). The patterns of primate species occupancy, including unexplained absences, observed in this study were consistent with such fine-scale variation in soil and vegetation. The differences among species assemblages of primates in the largely undisturbed forests of a single watershed of south-western Amazonia imply that community heterogeneity may be even greater in more species-rich taxa, as well as in regions of greater habitat diversity.

In MDD, hunting pressure is focused along a centralized development corridor that historically included the Madre de Dios River and its major tributaries and has now expanded to include the newly upgraded highway that connects western Brazilian Amazonia to the Peruvian coast. My analyses of primate communities at 37 sites along that corridor demonstrated that the loss of larger-bodied primate species due to hunting pressure was not compensated for by a corresponding increase in smaller species, resulting in novel primate communities at more heavily-hunted sites, ironically augmenting the natural variability in primate community structure (Chapter 3). The impacts of hunting have not yet extirpated any species from most of the MDD region as they have elsewhere (Freese et al. 1982, Peres 1990, Heymann et al. 2002). Nevertheless, the changes detected in primate communities among hunted areas highlight the importance of protected areas in maintaining robust primate populations both by restricting the direct loss of individuals from hunting and by maintaining source populations of larger-bodied species that may mitigate the impact of hunting pressure at unprotected sites. Such areas will be critical to maintaining ecosystem processes, such as seed dispersal, that primates and other forest vertebrates provide (Knogge et al. 2003, Link and DiFiore 2006, Nuñez-Iturri and Howe 2007).

Fine-scale habitat selection and resource use by a naturally rare primate

Like *S. imperator*, *P. irrorata*, a medium-sized seed predator, was also more abundant outside of protected areas, and its abundance was variable throughout the MDD basin. With so little information available on bald-faced sakis before this study, a major aim of this thesis was to identify features of its basic ecology that would help to explain its apparently patchy distribution across the region. *Pithecia* populations across MDD face little or no hunting pressure or habitat disturbance from forest fragmentation and logging (Chapter 6). Thus, the observed meso-scale patchiness is likely independent of human disturbance and reflects true species/habitat relationships that heretofore remain largely unexplained.

Habitat selection

In this study, saki groups showed a strong preference for mature unflooded (terra firme) forest with a high degree of canopy structure and complexity (Chapter 7). Groups in terra firme forest showed larger group size, smaller home range size, and greater home range overlap than groups in floodplain forest, and all groups demonstrated longer travel distances in and greater than expected use of terra firme forest. These combined findings suggest that saki densities in south-western Amazonia will likely be higher in areas of terra firme forest than in other habitat types, such as relatively low-phytomass forests with large patches of bamboo-dominated habitat or monodominant palm forests. In my study area, for example, use of bamboo-dominated *Guadua* stands was generally limited to edges adjacent to terra firme forest. Similarly, visits to *Mauritia*-dominated palm swamps tended to be brief and primarily for feeding. The ripe *Mauritia* fruits consumed by sakis reached their highest year-round availability in January-February but were consumed most heavily in April and May, when community-wide fruit availability was low, suggesting that it might be an important fallback food for sakis. *Mauritia* palm is tall and forms monodominant stands in low-lying permanently water-logged portions of the floodplain. While these large arborescent palms are of relatively even height and so presented the most uniform canopy height profiles of all the forest types (Chapter 7), their branching structure is highly reduced and the typical spacing between conspecific trees requires the sakis to leap between trees. Leaping between palms is especially risky not only because the trees are tall with no lower branching as a safety-net against free-fall following a bad landing, but also because leaping across palm fronds increases the likelihood of acoustic detection by and accessibility to aerial predators (Terborgh 1983, pers. obs.).

Dietary flexibility

The data I have presented in this thesis suggest that by adopting a taxonomically generalist feeding pattern within a relatively specialized niche (granivory/frugivory), sakis minimize the potential effects of seasonal decreases in fruit availability that are routinely experienced by pulp-eating frugivores. Analyses showed that unripe fruit consumed by sakis tends to be available for much longer periods, on more species, and in greater quantities than ripe fruit of the same species (Chapter 5). Thus, by specializing on the seeds of unripe fruit, sakis benefit from their greater temporal and spatial availability, compared to ripe fruit pulp.

As small-group-living primates, sakis can feed successfully in food patches of variable sizes, as reflected in the size heterogeneity of their food trees (Chapter 7). Top food plant genera of the five saki groups systematically followed in this study were among the most abundant in vegetation plots and were found in both flooded and unflooded forests across the focal study area. Feeding time allocation to most food tree species was not significantly different from that expected on the basis of their abundance.

While many were large canopy trees, such as the genera *Brosimum*, *Pouteria*, *Eschweilera*, others, including *Inga* and *Pseudolmedia*, were relatively small. Furthermore, no significant difference was detected between the fruit availability index scores or basal areas of the five top-ranking food plant genera and those of all other food plant genera (Chapter 6). These findings suggest that sakis were relatively generalist in their selection of immature fruit sources and did not specialize in large food patches, a finding that is consistent with the fact that the relatively low saki group biomass places relatively small metabolic demands on a given food patch, compared to those of most (sub)canopy foraging primates, primarily the Atelines and other Pitheciines, that tend to be larger-bodied or travel in larger groups.

The specialised teeth and jaws of pitheciines, including sakis (Martin et al. 2003) ensures that they can feed efficiently on immature fruit, thereby reducing the need to compete with larger sympatric primates, such as *Ateles chamek* and *Cebus apella*, that typically avoid unripe fruit (Zhang 1995, Suarez 2006). Their specialised dentition allows them to consume non-fleshy or sclerocarpic fruits, such as *Eschweilera* and several Bignoniaceae genera, further broadening the array of plant taxa available as food. Sympatric arboreal seed predators, such as macaws and squirrels, appear to present little dietary competition to sakis (Chapter 6).

With regards to intraspecific competition, observations of interference competition with conspecifics were rare. While groups used their areas of home range overlap preferentially, direct intergroup interactions were infrequent. Nevertheless, the higher than expected use of overlap areas, and the tendency of sakis to travel to their home range boundaries during daily movements (Chapter 4) suggests that sakis regularly reinforce intergroup spacing and allocated time and energy to home range defence. Contrary to much of interspecific competition theory (e.g. Stevenson et al. 2000), intergroup interactions were actually more frequent in the wet season, when more food was available, though it is unclear whether longer day paths, typical during the wet season, brought neighbouring saki groups into contact more frequently, thereby resulting in more agonistic interactions, or whether increased travel represented an enhanced "patrolling" effort during periods of high fruit availability.

Relative importance of forest structure

Given the relative spatiotemporal abundance of the saki food supply, combined with the associated saki movement and behavioural patterns, the observed landscape-scale patchiness in saki distributions may not derive from a corresponding patchiness of food resources. In contrast to our finding that sakis were flexible with respect to food resources, for these same saki groups, forest structure was shown to be a powerful indicator of use (Chapter 7). Canopy structure in saki home ranges within quadrats that were used and preferred was significantly taller and less variable than that in unused or less preferred areas. Across the wider landscape, sakis also tended to occur in areas with a taller, more highly-structured forest canopy. This contrast suggests that a well-developed forest structure, rather than food availability per se, may limit the population density and distribution of sakis.

The small body size and group size that enables sakis to be relatively insensitive to food patch size is likely to increase their vulnerability to predation (Terborgh 1983, Boinski et al 2003), particularly because they spend most of their time in the canopy, rather than the more sheltered forest understory. Sakis appear to specialise on forests with mature canopy structure, which tends to be tall with large primary and secondary branches, upon which they sit, feed, and walk relatively noiselessly. In both appearance and behaviour, sakis are particularly cryptic monkeys, so dense canopy may be especially important for them. As Warren Kinzey (1986) noted "…The most difficult species to study seem to be members of the Subtribe Pitheciina, especially *Pithecia* which moves extremely fast, high in the canopy, and completely silently...". This cryptic behaviour likely reflects a predation evasion strategy associated with a small-group-living canopy lifestyle. Large raptors are frequently reported to take midsized primates, including sakis, as prey (Terborgh 1983, C. Peres, unpubl. data, T. Sanaiotti, personal communication), further indicating their vulnerability to predation and their need to rely on stealth, in the absence of either large body size or large group size as mechanisms for evading predation (see review in Caro 2005) . *P. irrorata* rarely joins mixed species groups, like *Saguinus* spp. or *Cebus* and *Saimiri*; rather, it behaves more like *Callicebus brunneus* (brown titi), another small-bodied, small-group living primate in our study area that behaves cryptically but occupies a shorter, more open habitat type characterised by tangles of dead leaves.

Given the habitat preferences of *P. irrorata* (Chapter 4), I expected that terra firme forest would have the tallest, most well-connected canopy of the four main forest types in the focal area. That the canopy structure of terra firme forest was neither the tallest nor the most uniform and that canopy structure affected saki home range use patterns nonlinearly together suggest that other factors contribute to daily ranging patterns. The apparently greater tolerance shown by sakis for shorter canopy in terra firme, versus floodplain forest, in the study area further suggests that the relative benefits of terra firme forest are sufficient for groups to occupy areas of this habitat type even when they present slightly lower, less structured canopies. In fact, my results suggest that sakis may occupy floodplain forest only when it is of particularly high quality, in terms of structure and composition, or when it is embedded in an appropriate landscape context within the matrix of terra firme forest (Haugaasen and Peres 2005; Chapter 7).

Variability among study groups

One of the key findings in this thesis was the different patterns of resource and habitat use among adjacent saki study groups, a pattern observed in other platyrrhine studies in which more than one habituated group was studied (e.g. Stoner 1996, Dietz et al. 1997). In part the differences in day path length, home range size, frequency of intergroup interactions, and food species preferences among saki groups were due to the distinct configuration of forest types within their home ranges. Of particular interest were differences observed between groups with predominantly floodplain forest and those with mainly terra firme forest in their home range, though this pronounced variability in home range use may also have been due to other factors, such food species availability or group size and composition.

The monitoring of several saki groups at once allowed the analysis of variability, albeit limited due to small sample size, in the use of forest types, canopy structure, and behavioural patterns. Consistent among the five saki study groups were: predominance of seeds of unripe fruit in the diet, a preference for terra firme forest and tall canopy, and regular travel to peripheral areas of the home range. There was also pronounced variability in individual group use of food plant taxa, tolerance of canopy roughness, concentration of use of portions of their home range, and allocation of time to specific habitats, such as palm swamp.

In addition to enabling among-group comparisons of space use within a single saki population, the monitoring of multiple groups over a three-year period in a naturally heterogeneous landscape also helped to minimize potential sources of bias inherent in studying a single group, within a single home range locality, or during a single season. Furthermore, it also allowed us to measure home range overlap among the five adjacent groups to test whether overlap is positively associated with home range size (Nunn and Barton 2000) or forest type, and thus whether overlap estimates can be used to refine primate density estimates.

Working with adjacent groups necessarily concentrated sampling effort in a small area, which, in this case, was also the westernmost portion of the geographic range of this species. Despite the peripheral location of our study area in relation to *Pithecia* populations in core parts of Amazonia, there is no particular reason to suspect that the ecology of the five study groups considered here is inherently atypical or unrepresentative of broad ecological patterns found for all *Pithecia* species south of the Amazon. Future research to determine variability in resource use and ecological requirements of conspecifics in different habitats and areas of their geographic ranges would complement this study. For example, the location of this study in the upper Amazon basin meant that floodplain forest was tall and highly structured, with far less frequent and prolonged flooding than elsewhere in the Amazon basin. The year-round use by sakis of this highly-structured floodplain forest might not have been possible in regions with more pronounced flooding regimes (Haugaasen and Peres 2005). The disparity between the structural characteristics of the floodplain forest in the focal area used by the saki study groups and those of the floodplain forest in the wider landscape (polygons 1 and 2, Figure 7.1), which was not known to be occupied by sakis, supports this hypothesis. The relatively small differences in primate community composition and structure between flooded and unflooded forests in Madre de Dios, compared to those recorded in the central Amazon (e.g. Peres 1997, Haugaasen and Peres 2005), suggest that floodplain forest use varies geographically for other primate species as well.

Applications and future directions

While knowledge of key ecological requirements of sakis and other forest canopy species will help to improve density estimations within the relatively intact south-western Amazon, I suggest that combined findings of this study point to sakis being sensitive to changes that are projected to occur in this region in response to the combined effects of climate change and the documented impacts of human activity.

Amazon forest dieback is projected by most climate change models (Malhi et al. 2009), and in south-western Amazonia, climatic changes are projected to effect shifts in the dominant vegetation type from broadleaf evergreen to a more deciduous vegetation type (Asner et al. 2010). The region already contains large expanses of bamboo-dominated forests that are expected to expand significantly in response to climate change and associated increases in forest fires (Nelson 1994, Smith and Nelson in press). Bamboo-dominated forest occurs naturally on the region’s old, poorly-drained soils and supports lower aboveground phytomass and fewer tree species than better-drained soils (Osher and Buol 1998). Stands of bamboo (*Guadua* spp.) maintain their open structure by damaging branches of small-diameter trees (Griscom and Ashton 2006, Smith and Nelson in press), and bamboo benefits from disturbance, including human-caused fire and drying from fragmentation and climate change (Smith and Nelson in press, Aragão et al. 2008, Phillips et al. 2009), and likely by recurrent microbursts generated by convective windstorms (J. Terborgh, pers. comm.).

At the same time, mature terra firme forest in the basin is increasingly threatened by an expanding human footprint (Nepstad et al. 1999, Asner et al. 2010). Human activities in the region, including selective logging, promote forest desiccation and associated subsequent fires and land conversion (Aragão et al. 2008, Asner et al. 2010), as well as hunting of large seed-dispersing birds and mammals (Nuñez-Iturri and Howe 2007, Endo et al. 2010). Drying, fire, and loss of seed dispersers such as large primates, in turn, cause impoverishment of the plant community (Nepstad et al. 1999, Barlos and Peres 2008, Terborgh et al. 2008). Together, these trends potentially threaten the long-term viability of specialists of mature terra firme forest, such as sakis. Special attention will need to be given by regional conservationists to ensuring that extensive blocks of terra firme forest are protected in areas that remain relatively free of bamboo.

While expanding bamboo-dominated forest might actually benefit disturbance specialists, such as Goeldi’s marmoset and emperor tamarins, it will presumably be a detriment to canopy residents, including sakis, woolly monkeys and other species favouring mature terra firme forest. Although sakis are primarily seed predators, their consumption of relatively large-seeded fruits and strong preference for tall, verticallystratified and structurally complex forest canopy renders them, in the long run, vulnerable to the loss of sympatric seed dispersers from hunting and forest fragmentation (Link and DiFiore 2006, Nuñez-Iturri and Howe 2007, Terborgh et al. 2008, Peres and Palacios 2007). Despite the potential seed dispersal services of birds and small primates (Holbrook and Loiselle 2009, Culot et al. 2009), the higher proportion of small and wind-dispersed seeds found in secondary forests relative to primary forests, may render them suboptimal to sakis. The coincidence of most of the geographic range boundaries of saki species with major rivers indicates the limited dispersal ability of this specialist on highly structured forest canopy (e.g. Branch 1983, Heymann et al 2002, Aquino et al. 2009, Chapter 2). The preference of sakis for terra firme forest and their avoidance of bamboo, seasonally flooded várzea, and successional forests, in both the central and western Amazon (Peres 1997, Haugaasen and Peres 2005, Chapter 4) may further limit the potential ability of sakis to shift their areas of occupancy along with projected disturbance-mediated shifts in dominant vegetation type (Asner et al. 2010, Wright et al. 2009).

Our ability as scientists and conservationists to identify the areas of highest diversity, gaps in species' distributions, or likely impacts of climate change on their future survival, even for a taxonomic group that is as well-known as diurnal primates, is currently limited by, among other things, the coarseness of available data on species distributions, an area of potential future research. Ranging data and knowledge of a species' habitat preferences help to explain the determinants of population densities, and, consequently, distribution patterns within the geographic ranges of organisms. LiDAR and other remotely-sensed data are already contributing to studies of forest succession, species richness, distribution, and survival, and they hold great potential for improving animal-habitat association analyses that will, in turn, improve estimations of species distributions and habitat requirements. Nevertheless, habitat preferences must be considered together with other biotic and abiotic factors in determining species densities at the landscape level. Being able to identify the drivers of, and ultimately predict, patterns of species occupancy and abundance is critical to informed, regional-scale conservation planning for the Amazon and other tropical moist forests.

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