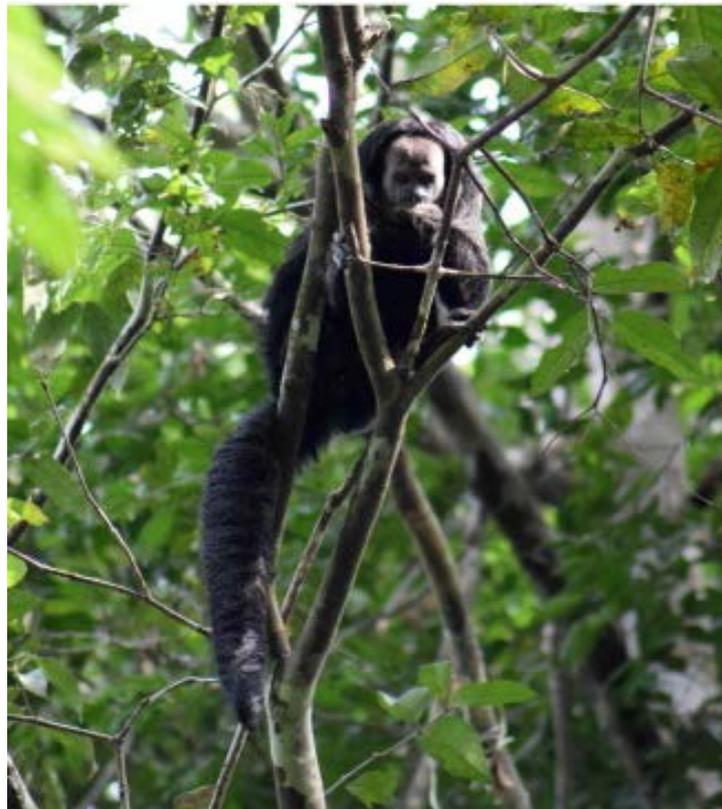




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The behavioural ecology of a potentially undescribed morph of Saki Monkey (genus *Pithecia*) in a highly diverse primate community



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Table of Contents

Abstract	2
Key Words.....	2
Introduction	3
Project Aims and Questions	5
Methods	6
Field Observations of Sakis	6
Analysis of Saki Behavioural Patterns.....	7
Primate Inventory.....	8
Analysis of Primate Vertical Distributions	9
Results	10
Saki Behavioural Patterns.....	10
Saki Use of Forest Strata.....	14
Saki Feeding Habits.....	14
<i>Ad Libitum</i> Observations of Saki Behaviour	15
Primate Inventory.....	16
Interspecific Associations between Primates.....	17
Primate Encounter Frequencies	17
Primate Vertical Distributions	18
Discussion	21
Saki Behavioural Patterns.....	21
Primate Inventory.....	23
Conclusion	26
Acknowledgements	26
References	27
Appendices	32

Abstract

The importance of tropical forests for global diversity and ecosystem function is well established in scientific literature, but is undermined by gaps in our knowledge of tropical ecosystems and species. Primates play important functional roles in these ecosystems, and despite constituting one of the most well-recognised taxa in the world, many species remain poorly studied. The Area de Conservación Regional Communal Tamshiyacu-Tahuayo (ACRCTT), located in the northeastern Peruvian Amazon, harbours one of the most diverse primate assemblages in the world and presents an ideal opportunity for the study of primate communities and mechanisms of their coexistence. Previous research has recorded the presence of an atypically coloured morph of monk saki monkeys (*Pithecia monachus*, *sensu* Marsh 2014) living in sympatry with a population of burnished sakis (*Pithecia inusta*, *sensu* Marsh 2014) in the reserve. In this study, the behavioural ecology of this potentially undescribed morph of saki monkey is described, using continuous focal data collected during the early wet season in the ACRCTT. The sakis were most often encountered in multi-adult groups and in the upper forest strata. The observed feeding strategies suggest that fruits and/or seeds constitute the sakis' primary food source in the wet season, although arthropods were also ingested during a large proportion of feeding records. Sex differences in behavioural patterns provide support for a difference in male and female investment in group defence. As only the monk saki morph was encountered during the study, the potential for seasonal habitat differentiation between the saki populations at the ACRCTT is discussed. A survey of primates in flooded and non-flooded forest areas at the ACRCTT was also conducted, in which nine of the 14 primate species recorded at the ACRCTT were encountered. Significant differences in the vertical distribution of primate groups provide evidence for vertical stratification in the ACRCTT primate community. This study contributes to previous research on the poorly-studied *Pithecia* genus, and provides insights into the mechanisms of niche differentiation between *Pithecia* and other primates.

Key words: Amazon, behavioural ecology, niche differentiation, Peru, *Pithecia*, primates, saki monkey.

Introduction

Although tropical forests cover only 15 % of the world's land area (Taylor 2011), they hold a disproportionately high importance for sustaining the world's biodiversity, ecosystem services, and our living environment. Tropical forests harbour at least 50% of the world's species (Gardner et al. 2010, Harding et al. 2014), including a majority of the world's endemic species (Myers et al. 2000, Dirzo and Raven 2003), provide a vast diversity of timber and non-timber forest products used worldwide (Montagnini and Jordan 2005, Foley et al. 2007), store a majority of the world's vegetation carbon stock (Baccini et al. 2012), regulate regional climatic patterns and temperatures (Montagnini and Jordan 2005, Foley et al. 2007), and provide resources and ecosystem services for the 40 % of the world population living in the tropics (Harding et al. 2014). The Amazon rainforest, as the world's largest intact forest (Foley et al. 2007), and home to the most species-rich communities of plants, mammals, birds, amphibians, and many invertebrate groups, ever recorded (Dirzo and Raven 2003, Vié et al. 2009, Peres et al. 2010), performs a large proportion of these functions. However, these functions grow increasingly threatened with continuing deforestation and degradation of tropical forests. Approximately 7 million hectares of the world's tropical forest cover were lost between 2000 – 2010 (FAO 2016), of which a majority was lost in the Neotropics (Hansen et al. 2013), primarily due to land conversion for agriculture and urban development (Geist and Lambin 2002, Gardner et al. 2010, FAO 2016). In addition, the remaining tropical forests are becoming increasingly degraded through unsustainable practices in forestry, hunting, and other forms of resource exploitation (Dirzo and Raven 2003, Foley et al. 2007, Gardner et al. 2010). The consequences of this exploitation on tropical forest ecosystem services and function are already being observed (Baccini et al. 2012, Hooper et al. 2012), most prominently through rapid population declines in many tropical species: an estimated 41 % of tropical forest species have been lost between 1970 – 2009 (WWF 2016). Given the current rate of exploitation, these consequences are expected to grow in magnitude, particularly alongside the growing threats of climate change to the world's ecosystems (Gardner et al. 2009, Peres et al. 2010, Stork 2010). In light of these eventualities, there is a clear and imminent need for effective management and conservation of the biodiversity and ecosystem function in tropical forests.

One of the challenges in conserving tropical forests lies in filling the gaps in our knowledge of tropical ecosystems and the biodiversity within them. Not only is a significantly lower proportion of data available for tropical species than for species in other biomes (Collen et al. 2008, Zuidema et al. 2013), but a majority of undiscovered species in the world are also thought to be associated with tropical forests (Giam et al. 2012). These data deficiencies can be attributed to a myriad of factors: firstly, since developing countries tend to be centered in the tropics (Harding et al. 2014), the financial resources for tropical research are limited, and a significant proportion of available funding is contributed by foreign and international scientific bodies (Romero and Andrade 2004). As a result, long-term research in the tropics is also severely lacking (Collen et al. 2008, Gardner et al. 2010). Secondly, the necessary infrastructure, workforce, and equipment for *in situ* research are often unavailable or difficult to acquire in tropical forests (Collen et al. 2008), many of which remain uninhabited by humans and are yet to be studied (Gardner et al. 2009, Peres et al. 2010). Finally, the high biodiversity and ecosystem productivity in tropical forests are likely to be driven by a complex network of ecological dynamics, and understanding these dynamics requires significantly more long-term, large-scale research than other, more species-poor areas (Gardner et al. 2009, Giam et al. 2012, Zuidema et al. 2013). Both despite and in light of these limitations, tropical forests have received substantial attention from public and scientific communities in recent decades (Gardner et al. 2010), resulting in a greater interest for research in tropical ecology, a greater investment into conservation and development in tropical regions, including

the development of the eco-tourism industry, and an array of campaigns conveying the importance of tropical conservation to the public (Romero and Andrade 2004, Kull et al. 2007). As a result of these efforts and the increasing rate of development in tropical countries (Harding et al. 2014), these knowledge gaps are steadily becoming smaller.

Primates constitute a diverse assemblage of species spread across all the major tropical regions (Wich and Marshall 2016), and are arguably the most well-recognised animal group in the world (Mittermeier 1988, Marshall and Wich 2016). The negative effects of tropical forest degradation on primates are also well documented (Wich and Marshall 2016), with over half of all known primate species currently red-listed in the global Red List of Threatened Species (Vié et al. 2009). As such, primates are commonly showcased as flagship species for increasing public awareness and support for tropical forest conservation (Mittermeier 1988, Marshall and Wich 2016). In addition, primates play key functional roles in tropical ecosystems. Primates account for 25 – 40 % of the frugivorous animal biomass in the tropics (Chapman 1995), and studies across the tropics have documented significantly lower plant species diversity, particularly of large-seeded tree species, and significantly lower seed dispersal rates in regions with low primate abundance (Bourlière 1985, Nunez-Iturri et al. 2008, Calle-Rendón et al. 2016). Furthermore, research suggests that primates indirectly contribute to maintaining the animal diversity of tropical ecosystems, as changes in primate abundance has been linked to changes in the abundances of other species, including plants (Chapman et al. 2013), birds (Feeley and Terborgh 2006), and other mammals (Peres and Dolman 2000, Effiom et al. 2013). In addition to their ecological importance, the wide diversity of morphological, behavioural and social adaptations in primates, including their remarkably complex and diverse social structures (Bourlière 1985, Marshall and Wich 2016), provides important opportunities for research in evolution and the development of our own societies.

As for tropical forests overall, a lack of knowledge about the diversity and ecology of primates limits our ability to effectively conserve their habitats. 82 new species of primates, including five new primate genera, have been described since 2000 alone; of these, 18 species were described in the Neotropics (Mittermeier and Rylands 2016). Five of these 18 species belonged to the genus *Pithecia*, or saki monkeys, which is commonly regarded as one of the most poorly-studied primate genera in the world (Peres 1993, Marsh 2014). Not only are saki monkeys, like other pitheciine primates, shy and difficult to observe in the wild (Pinto et al. 2013), but a high variation in pelage colouration between sex and age classes within the genus has also complicated the identification and taxonomic classification of *Pithecia* species (Hershkovitz 1987). In particular, the clade of western Amazonian saki species have proved difficult to classify. All five of the abovementioned new *Pithecia* species belong to this clade, and were described in one recent comprehensive taxonomic review of the genus (Marsh 2014), through which the number of recognised *Pithecia* species was doubled from 8 (Hershkovitz 1987) to 16. This review was based on the examination of hundreds of live and museum specimens and photographs (Marsh 2014); however, information on the distribution and ecology of these species remains fragmented. Previous field studies of *Pithecia* species are few, and often restricted to a small number of populations that live in more easily accessible areas (Norconk 1996, Norconk and Conklin-Brittain 2004, Norconk 2006, Thompson et al. 2012). Given that saki monkeys are found across the majority of the Amazon (Marsh 2014), these knowledge gaps considerably limit our understanding of Amazonian primates, their role in Amazonian forest ecosystems, and how they are affected by anthropogenic disturbance.

The rise of eco-tourism in tropical forests has seen the establishment of a number of sustainably run eco-tourism lodges that, in addition to contributing with conservation and economic opportunities for local

communities, provide means for tropical forest research in remote, protected forest areas (Stronza and Pêgas 2008). Such areas of pristine forest are particularly important for conserving the diverse species assemblages of the tropics as the surrounding landscapes become increasingly modified (Barlow et al. 2007, Gardner et al. 2009, Anand et al. 2010, Gibson et al. 2011). The Tahuayo lodge, built and run by Amazonia Expeditions, is the only eco-tourism lodge with access to the Area de Conservación Regional Communal Tamshiyacu-Tahuayo (ACRCTT); a 4,200.8 km² protected reserve of pristine forest area that harbours some of the highest recorded biodiversities of trees and mammals, including primates, in the world (Puertas and Bodmer 1993). 14 species of primates have been recorded in the ACRCTT, among them the red-listed species black spider monkey (*Ateles paniscus*), red bald-headed uakari monkey (*Cacajao calvus ssp. rubicundus*), and Poepig's woolly monkey (*Lagothrix poeppigii*) (Puertas and Bodmer 1993). The presence of burnished saki monkeys (*Pithecia inusta*, *sensu* Marsh 2014) has also been confirmed (Fleck et al. 1999, Chism et al. (in review)), although recent research has revealed the presence of a second, distinct saki population occurring in sympatry with the burnished sakis in the reserve (Chism et al. (in review)). Unlike the burnished sakis, this latter population shows a sexually dichromatic facial colouration, whereby the males have reddish-brown fur from the crown to the cheeks, and the females have pale, grey-white facial fur (Chism et al. (in review))(Appendices 1 - 2). Morphologically, individuals of the latter population fit with descriptions of monk sakis (*Pithecia monachus*, *sensu* Marsh 2014) (Appendix 3); however, observations of individuals with atypical facial fur colouration suggest that the ACRCTT population may represent a yet undescribed morph of saki monkey (Chism et al. (in review)). Furthermore, observations of syntopy between monk and equatorial sakis, both in the ACRCTT (Chism et al. (in review)) and within the region (Aquino et al. 2009a) suggest that these atypically coloured individuals could also be the result of hybridisation. Until genetic analyses can be conducted on these groups, the evolutionary history of these sakis may be studied via their behaviour and the dimensions that make up their ecological niche. Since competitive exclusion theory states that the niches of any two species must differ in some way for them to coexist (Hardin 1960), an understanding of the existing primate community and niche differentiation between primate species at the reserve is also needed.

Project Aims and Questions

This project aims to gather information on primates in the ACRCTT in two parts: (1) by investigating the behavioural ecology of the potentially undescribed saki morph, and (2) by presenting a primate inventory, with an analysis of their use of habitat types and forest strata – both of which are well documented forms of niche differentiation in primate communities (Mittermeier and van Roosmalen 1981, Terborgh 1983, Peres 1993b, Schreier et al. 2009, Sheth et al. 2009). Fieldwork was conducted during the early wet season, and as such, complements previous primate inventories conducted in the dry season at the reserve (Dosantos Santillán and Tegnér 2015). The questions this research seeks to answer are:

- 1.1. What behavioural patterns do the undescribed saki species display?
- 1.2. Do the behavioural patterns, use of forest strata, or feeding habits of the sakis differ depending on the sex or age of the individual?
- 1.3. Do the sakis display different behavioural patterns in different forest strata?

- 2.1. Which primate species are encountered during the wet season in the ACRCTT?
- 2.2. Are there differences in the species richness and encounter frequencies of primates between flooded and non-flooded forests?
- 2.3. Does the vertical distribution of primate groups differ by species or by forest type?

Methods

Fieldwork in the ACRCTT was conducted between 21st of February – 14th April 2016. This time constitutes part of the early wet season in the Peruvian Amazon, characterised by rising water levels and frequent rain showers (Kvist and Nebel 2001). The average temperatures and precipitation in the region during this period are 26.8°C and 271.8 mm, in comparison to annual averages of 26.6°C and 239.7 mm (ClimaTemps 2015). Field surveys were typically conducted twice a day, between 5:30 am – 12:00 pm and 14:30 pm – 17:30 pm. The surveys were divided into two types: flooded forest surveys conducted by canoe, and non-flooded forest surveys conducted by foot. Flooded forest surveys extended both up- and downriver of the Amazonia Research Center (ARC; UTM coordinates: 18M 693853m E, 9517976m N). Occasionally, a motorboat was used to travel further along the river than by canoe, and surveys were conducted while silently floating downriver. Non-flooded forest surveys were conducted within a 2 km x 2 km trail grid, located approximately 100 m southeast of the ARC. The trail grid was accessed either by foot, or by canoe along a tributary of the Tahuayo river that runs through the trail grid. As some forest areas began to flood through March, a canoe was occasionally used to access flooded areas in the trail grid. During the wet season, fruiting trees tend to be concentrated in flooded forests (Haugaasen and Peres 2009), attracting primate groups to such areas (Neville et al. 1976); as such, survey effort was focused on flooded forests to increase the likelihood of locating saki groups.

The paths taken in riverside and trail grid surveys were not standardised, as the primary purpose of the surveys was to locate saki populations. Rather, surveys were concentrated on areas where sakis had previously been encountered, or recently been observed. Survey effort was quantified as the total time spent in each forest type. Manuel Huayllahua Silva acted as a field guide during all surveys, assisting in maneuvering the boat and canoe, as well as locating and counting primates. Between 5th – 14th April, Anthony Turgeon assisted in surveys, with Dik Rengifo acting as an additional field guide. The date, weather, and time spent in the field were recorded for each survey.

Field Observations of Sakis

When saki groups were encountered during surveys, the time of encounter and the forest type that the encounter occurred in were recorded. Photographs were taken of all visible individuals to aid in identifying the species, age and sex of individuals in later analysis. The vertical distribution of the group was recorded by counting the number of individuals present in each of three levels in the forest: high, mid-level and low, corresponding to equal thirds of the length between the ground or water level and the treetops. This distribution was recorded at the time of first encounter to get a representative snapshot of the vertical distribution of sakis with as little human disturbance as possible.

Encountered saki groups were followed for observation until all individuals remained out of sight or inactive for over an hour, or until all individuals moved to an inaccessible area. Observations were also concluded by 5:30 pm, as sakis are unlikely to be active after sunset (Pinto et al. 2013). If observations were concluded for this reason, the site of the encounter was returned to at sunrise the following morning (between 5:30 – 6:30 am).

The behaviour of individual sakis was recorded through 10 minute continuous focal samples, during which all behaviours performed by the individual, along with the times (to the nearest second) that the individual switched behaviours, over a 10 minute period were recorded (Altmann 1974). No samples were recorded within 10 minutes of the first encounter as a means of habituating the group to the presence of the observers.

Sampling was terminated if the focal individual remained out of sight for over 30 seconds. Samples were recorded for as many individuals in the group as possible, and if all visible individuals had been sampled, these individuals were resampled to obtain as much behavioural data as possible. The recorded behaviours were grouped under seven categories: “Aggression”, “Feeding”, “Resting”, “Self-grooming”, “Social interaction”, “Travelling”, and “Vigilance”, described in Table 1. When feeding was observed, the food item being fed on was recorded as “Arthropods”, “Fruits”, or “Leaves”, also described in Table 1. If sakis were observed ingesting any other food items, these were noted separately. In addition to behaviours, the forest levels (categorised as high, mid-level, or low in the forest as described above) at which the focal individual was present, and the times at which the individual switched between forest levels, were recorded for the duration of each focal sample. Observations of uncommon or otherwise relevant behaviours were recorded *ad libitum*.

Table 1: Descriptions of each behaviour and food item recorded in continuous focal samples of sakis.

Behaviour	Description
Aggression	Antagonistic behaviours, directed at individuals both within or outside of the group
Feeding	Feeding and/or foraging for food
Resting	Individual sitting or lying down, not displaying behaviours from other categories simultaneously
Self-grooming	Individual grooming itself, e.g. brushing dirt out of its fur
Social	Non-antagonistic interactions between individuals in the group, including calling, playing, grooming
Travelling	Individual moving from one location to another
Vigilance	Behaviours that appear to signal awareness and/or alarm due to the presence of the observers
Food Item	Description
Arthropods	All invertebrates under the phylum Arthropoda
Fruits	Fruits, including seeds and exocarps
Leaves	Leaves from trees, vines or other plants

Analysis of Saki Behavioural Patterns

All photographs of sakis taken during the surveys were collated and organised by encounter and, where possible, individual. The species (burnished or monk saki) of photographed individuals was confirmed using descriptions from Chism et al. (in review). Individuals were categorised by age (adult, juvenile or infant; where juveniles and infants were distinguished as being approximately half and approximately a third of the size of adults respectively) and sex (male or female; distinguished by facial fur colouration) using the photographs as visual aids. No attempt was made to identify groups that may have been encountered more than once.

The times spent on each recorded behaviour and the time spent at each forest height in continuous focal samples were summed for each individual, and expressed as proportions of the total amount of time that the individual was sampled for. Frequencies for each behaviour were also calculated, as a measure of how often individuals switched between behaviours, by summing the total number of times each behaviour was recorded for each individual. Relative frequencies of each behaviour per ten minutes of sampling time were calculated by dividing the frequencies for each individual by the total sampling time of the individual, and multiplying by 10. The time spent on each recorded food item was also summed per individual, and expressed as proportions of the total time spent feeding and/or foraging by the individual.

All statistical analysis was conducted using the R statistical software (R Core Team 2015). All figures were created using the R packages 'ggplot2' (Wickham 2009), 'reshape' (Wickham 2007), and 'cowplot' (Wilke 2016). Saki behaviour was analysed through four different measures: the proportions of time spent on each behaviour, the frequencies at which behaviours were recorded per ten minutes, the proportions of time spent at each forest height, and the proportions of time spent per food item. Orthogonal contrasts were specified in R for all following factor analyses. Differences in the proportions of time spent on each behavior, forest height and food item, and in frequencies of each behavior, were analysed using linear mixed model Analyses of Variance (ANOVAs), with individual as a random effects factor, using the R package 'nlme' (Pinheiro et al. 2016). If significant differences were found, pairwise comparisons of differences between each behaviour, forest height and/or food item were made through Tukey's tests, using the R package 'multcomp' (Hothorn et al. 2008). To analyse the effects of age and sex on saki behavior, Analyses of Covariance (ANCOVAs) using type III sums of squares were performed on linear models fitted to each of the abovementioned response variables, with age, sex, and their interaction, as well as time of day as a covariate, as predictor variables. Each model was tested against a corresponding model without the interaction term using a Chi-squared test, to determine whether the interaction term significantly improved the fit of the model. In cases where this test yielded insignificant results, the interaction term was dropped. All models were weighted by the total sampling times per individual (or for proportions of time spent per food item, by the total time spent feeding and/or foraging) to account for the different sampling times. Any significant outcomes of the analyses were tested using a permutation test with 10,000 iterations to eliminate biases resulting from violations of the model assumptions.

The effect of forest height on the proportions of time spent per behaviour was also evaluated, using a separate dataset where the times spent per behaviour by each individual were partitioned by the forest height (high, mid-level, or low) that the behaviours were recorded in. The proportions of time spent per behaviour were then recalculated over the total time the individual spent at the forest height in question. The effect of forest height on these proportions were evaluated using two-way Analyses of Variance (ANOVAs) with type III sums of squares, on three different models, where (1) forest height, sex and their interaction, (2) forest height, age and their interaction, and (3) forest height, time of day and their interaction constituted the predictor variables. Chi-squared tests were used to determine whether the interactions significantly improved the fit of each model, as described above. The models were weighted by the total time that each individual had been recorded at respective forest heights. Significant outcomes were validated using a permutation test with 10,000 iterations.

Primate Inventory

Whenever a primate or group of primates was encountered during surveys, the time, forest type, species, number of individuals, and vertical distribution of individuals at first encounter was recorded in the same

way as for saki groups. Two or more species encountered simultaneously and within 25 m of each other were recorded as separate encounters in association with each other. For all encounters (including sakis) in flooded forests, the distance of the group to the river at first encounter was estimated as one of four categories: 0 m (on the river edge), 1 – 50 m, 50 – 100 m, and 100+ m from the river edge. Primate calls heard during the survey period were not counted as encounters unless the calling individuals were seen. Average group size for each encountered species was also calculated, excluding any encounters during which a reliable individual count was not obtained.

No attempts were made to identify groups that had been encountered more than once. Because of this and the non-standardised survey methods, abundances of primates in the surveyed forest types were not calculated. As the survey effort was concentrated in flooded forest types, encounter frequencies in non-flooded forests were standardised by multiplying the frequencies for each species by a factor, derived by dividing the flooded forest survey time by the non-flooded forest survey time.

Analysis of Primate Vertical Distributions

The vertical distribution of primate groups was expressed as the proportions of individuals (of the total number of individuals in the group) recorded high, mid-level, and low in the forest. An average height in the forest was calculated for each encountered primate group using arbitrary units, such that:

$$\text{Average forest height} = (\text{proportion of individuals high} \times 2) + (\text{proportion of individuals mid-level} \times 1) + (\text{proportion of individuals low} \times 0).$$

To account for variation in the proportions of individuals at each forest level, the effects of forest type and species on primate vertical distributions were analysed on each proportion rather than on average heights in the forest. These effects were analysed through separate two-way ANOVAs with type III sums of squares, using two different models: (1) with forest type, time of day, and their interaction as predictor variables, and (2) with species as a predictor variable. The effect of distance to the river on each proportion was evaluated on the flooded forest data only, using two-way ANOVAs with type III sums of squares and distance to the river, time of day and their interaction as predictor variables. Chi-squared tests were used to determine whether the interactions significantly improved the fit of each model, as described above. Any significant results were validated using permutation tests with 10,000 iterations.

Results

The total survey time in the ACRCCT was 122 hours and 9 minutes, divided into 98 hours and 30 minutes (80.64 % of total) spent in flooded forests, and 23 hours and 39 minutes (19.36 % of total) spent in non-flooded forests.

Sakis were encountered 28 times, with 23 hours and 28 minutes of the total survey time spent observing the encountered saki groups. All of the encounters occurred in flooded forests. For five of these encounters, photographs could not be obtained to confirm the species identity; these encounters were removed from the dataset. The groups in the remaining 23 encounters were confirmed to be monk sakis – herein referred to simply as sakis.

As many individuals were quick to hide or move away in the presence of observers, the group composition could only be confirmed in five encounters. These groups consisted of two adult males, 1 – 2 adult females, one juvenile, and one infant each. The presence of two or more adult males was also confirmed during another four encounters, and two or more females in another two encounters. Infants were present in a total of 11 encounters (one infant in ten encounters, two infants in one encounter).

Saki Behavioural Patterns

Continuous focal sampling was conducted on 25 individuals from 12 encounters, totaling 4 hours, 45 minutes and 10 seconds of sampling time. These individuals are treated as distinct, although the true sample size may be lower if the same groups were encountered and sampled on more than one occasion. Sampling between sex and age classes was unequal, with males and adults accounting for higher proportions of sampling time than females or juveniles and infants (Table 2). The sex of three of the 25 sampled individuals could not be determined from the photographs.

Table 2: The sex and age distribution of saki continuous focal samples.

Sex	Number of Individuals Sampled	Total Time Sampled*	Proportion of Total Sex
Male	14	2:49:40	59.50 %
Female	8	1:25:30	29.98 %
Undetermined	3	0:30:00	10.52 %
Age	Number of Individuals Sampled	Total Time Sampled*	Proportion of Total Age
Adult	18	3:28:40	73.17 %
Juvenile	6	1:06:30	23.32 %
Infant	1	0:10:00	3.51 %

*Measured as hours:minutes:seconds

Overall, the sampled sakis spent 30 % of observed time foraging or feeding, 28.87 % resting, 24.89 % travelling, 11.10 % showing vigilance towards the observers, 3.26 % self-grooming, 1.72 % in social interactions, and 0.17 % showing aggression (Table 3). As aggression was only recorded for one individual, this behaviour was excluded from statistical analysis. Significant differences were found in the proportions of time spent per behaviour ($F = 13.71$, $p = <0.0001$) and frequencies of behaviours displayed per ten minutes

($F = 17.91$, $p < 0.0001$). More specifically, sakis spent significantly higher proportions of time feeding, travelling and resting than self-grooming, being vigilant, or being social ($p < 0.035$ for each pairwise comparison). Sakis were also recorded travelling significantly more frequently than feeding, self-grooming, vigilance, or social behaviours; being social significantly less frequently than feeding, travelling, resting, and vigilance behaviours; and self-grooming significantly less frequently than feeding, travelling and resting behaviours ($p < 0.005$ for each pairwise comparison).

Table 3: A summary of the statistical parameters of behaviours recorded during continuous focal samples.

Behaviour	Average Proportion of Time Spent (\pm St. Dev.)	Average Frequency per 10 minutes (\pm St. Dev.)	Average Duration (\pm St. Dev.)*	Number of Individuals Observed
Feeding	30.00 % (29.19)	3.93 (3.32)	0:57 (1:07)	22
Resting	28.87 % (16.70)	5.59 (3.77)	0:36 (0:34)	22
Travelling	24.89 % (22.74)	7.14 (4.30)	0:24 (0:24)	24
Vigilance	11.10 % (4.47)	4.22 (4.01)	0:16 (0:15)	20
Self-grooming	3.26 % (13.14)	1.49 (1.70)	0:12 (0:05)	15
Social	1.72 % (3.55)	0.67 (1.69)	0:20 (0:18)	7
Aggression	0.17 % (0.83)	0.08 (0.40)	0:12 (NA)	1

*Shown as minutes:seconds

Only one infant was sampled for behaviour; as such, this sample was excluded from all statistical analyses. The infant was in the company of a juvenile male for the duration of the sample, and spent 5 % of its time feeding (on arthropods only), 90.17 % resting, 4 % showing vigilance, and 0.83 % in social interactions.

In the analyses of sex, age, and time of day effects on behavioural proportions and frequencies, the interaction between sex and age was not found to significantly improve the fit of any of the models and was dropped in each case. A significant effect of age was found on the proportion of time spent travelling by sakis ($F = 4.61$, $p = 0.049$), whereby juveniles appear to spend more time travelling than adults (Figure 1). Sex and time of day were not found to significantly affect the proportions of time spent by sakis on any of the behaviours.

A significant effect of sex was found on the frequencies displayed of vigilance ($F = 6.17$, $p = 0.033$), and social behaviours ($F = 4.46$, $p = 0.042$). Specifically, male sakis displayed vigilance significantly more frequently than females did, whereas females displayed social behaviours significantly more frequently than males did (Figure 2). Moreover, the total frequencies of all displayed behaviours per ten minutes differed significantly by sex ($F = 6.92$, $p = 0.031$), whereby males displayed higher frequencies of behaviours than females did. No significant differences in frequencies of behaviours were found by age or time of day.

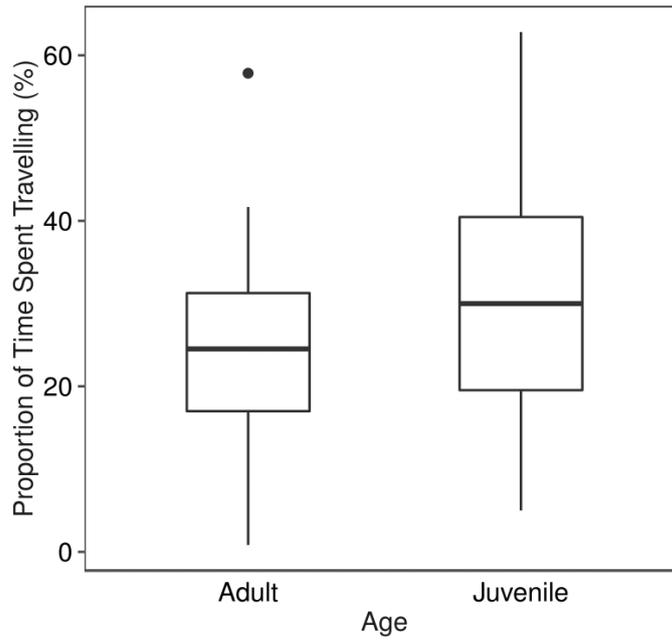


Figure 1: The proportions of time spent travelling by sakis, per the age of the individual.

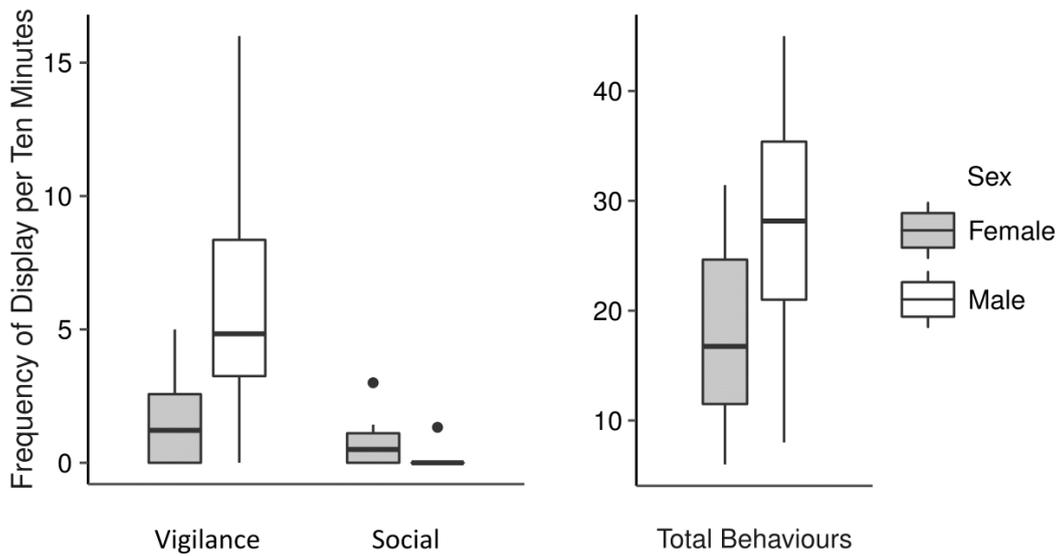


Figure 2: The frequencies at which vigilance and social behaviours, as well as all behaviours in total, were displayed per 10 minutes by male and female sakis.

The vertical position of focal individuals was recorded for 19 of the 25 sampled individuals, totaling 3 hours, 42 minutes and 40 seconds of data. Only four of the 19 sampled individuals were observed at the low level in the forest during sampling; therefore, to reduce bias from unequal sampling, behaviours recorded in the low forest level were excluded from the following analysis.

In the analysis of forest height effects on the proportions of time spent per behaviour, the interaction terms of forest height with age, and forest height with time of day were not found to significantly improve the models, and were dropped in each case. The interaction term of forest height with sex was also dropped from all models, except those fitted to the proportions of time spent feeding and resting (Chi-squared test $p < 0.015$ in both cases). The interaction between forest height and sex was found to significantly affect both feeding ($F = 9.36$, $p = 0.013$) and resting ($F = 6.00$, $p = 0.043$) proportions. No other significant effects were found on the proportions of time spent per behaviour.

To further investigate the significant interaction effect, the effects of forest height on the times spent per behaviour were analysed for each sex separately. Males were found to spend a significantly higher proportion of time feeding high than mid-level in the forest ($F = 16.91$, $p = 0.0021$), while no such difference was found for females. No significant differences were found for the proportion of time spent resting by forest height for males or females, although there again appears to be a larger difference in proportions between forest heights for males than for females (Figure 3).

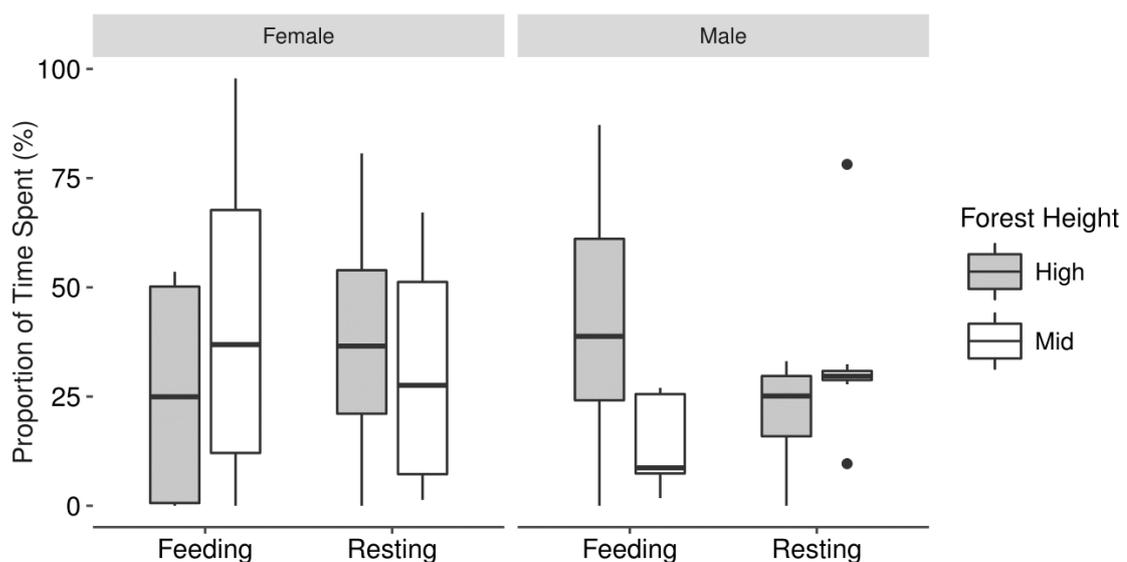


Figure 3: The proportions of time sakis spent feeding and resting at high and mid-levels in the forest, shown for male and female sakis.

To summarise the results on saki behavioural patterns, sakis appear to spend significantly higher proportions of time feeding, travelling and resting than self-grooming, being vigilant or being social. Briefly put, sakis also displayed travelling, feeding, resting and vigilance behaviours more frequently than self-grooming and social behaviours. Age differences were only found for the proportions of time spent travelling, while sex differences were found in the frequencies at which vigilance and social behaviours, as well as the total array

of behaviours, were displayed per ten minutes. Finally, differences between forest heights in the proportions of time spent feeding and resting were found when the sex of the individual was taken into account.

Saki Use of Forest Strata

Overall, sakis spent 43.88 % (\pm 40.61 %) of the sampled time high in the forest, 54.54 % (\pm 39.25 %) of time at mid-level, and 1.57 % (\pm 3.91 %) of time low in the forest. Sakis were found to spend significantly more time both high and mid-level than low in the forest ($p < 0.001$ for both comparisons). Only one sampled individual utilised all three forest heights during samples, whereas eleven individuals utilised two heights, and seven individuals utilised one forest height during samples.

The interaction between sex and age did not significantly improve the fit of the analysed models, and was dropped from the analysis of age, sex and time of day effects on time spent in each forest height. A significant effect of age was found on the proportion of time spent by sakis high ($F = 5.47$, $p = 0.034$) and mid-level ($F = 5.84$, $p = 0.032$) in the forest. No significant effects sex or time of day were found on the time spent at any of the forest heights. Therefore, the results shows that the use of forest strata differs between saki age classes: more specifically, it appears that juveniles spend a higher proportion of time high in the forest than adults do, and vice versa for the proportion of time spent mid-level in the forest (Figure 4).

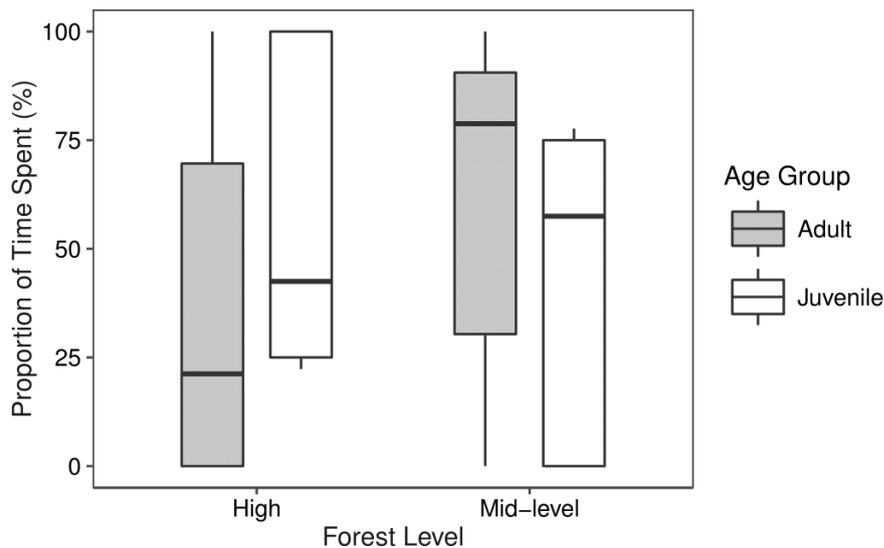


Figure 4: The proportions of time spent by adult and juvenile sakis at high and mid-levels in the forest.

Saki Feeding Habits

Of the total time sakis spent feeding and/or foraging, sakis spent 49.26 % of their time on fruits, 45.20% of their time on arthropods, and 5.54% of their time on young leaves (Table 4). Sakis spent significantly higher proportions of time feeding on fruits than on arthropods, and significantly lower proportions of time on leaves than on arthropods ($p < 0.0001$ for both comparison). The interaction term of sex with age did not significantly improve the fit of the analysed models, and was dropped in each case. No significant effects of

age, sex, or time of day were found on the proportions of time spent on fruits or arthropods. The effects of these variables were not analysed on the proportion of time spent on leaves, as only four individuals were observed feeding and/or foraging for this food item. Therefore, the data does not show differences in the feeding habits of sakis by sex, age or time of day.

Table 4: The statistical parameters of feeding and foraging observations in saki continuous focal samples.

Food item	Average Proportion of Feeding/Foraging Time Spent (\pm St. Dev.)	Average Duration (\pm St. Dev.)*	Number of Individuals Observed
Arthropods	45.20 % (44.62)	0:31 (0:24)	14
Fruits	49.26 % (45.26)	1:13 (1:22)	13
Leaves	5.54 % (19.77)	0:19 (0:11)	4

*Shown as minutes:seconds

Ad Libitum Observations of Saki Behaviour

Of the 11 saki encounters for which continuous focal samples were not obtained, five groups hid in the subcanopy and did not reappear during the encounter, two groups moved away and could not be followed, and four groups were highly inactive (of which two were encountered during heavy rain). Three other encountered groups were also quick to hide in our presence; however, these sakis resumed activity within an hour of hiding, and samples could be obtained. Sakis were also observed to hide during two encounters for approximately 30 seconds each, both times in apparent response to the proximity of a bird of prey.

Signs of vigilance to our presence were recorded in all encountered groups except for one. In this case, the group was observed foraging from a tall tree on the river edge, and was clearly visible from the far side of the river. The observed vigilance behaviours included emitting an apparent alarm call, consisting of a series of chirps and growls; descending lower into the forest and watching us; and shaking and jumping on branches. The latter behaviour often resulted in branches breaking and falling our vicinity. Male adults were often the individuals observed to descend and watch us, during which other individuals would hide. During one encounter, a male adult was observed to move away from its group while emitting the aforementioned alarm call, stopping occasionally to watch us, in an apparent attempt to lure us away from the group.

In addition to observations of feeding in continuous focal samples, sakis were observed feeding as a group in seven encounters; of which groups were observed to feed on fruits from fruiting trees in six encounters, and on insects from a bee nest in one encounter. Social behaviours that were observed consisted of grooming and playing. The only observations of aggression occurred when two saki groups had been encountered within the same forest patch. Although the two groups were not observed simultaneously, the groups were distinguished by (a) different group compositions, and (b) because Anthony Turgeon and Dik Rengifo were still following the former group when the latter was encountered by Manuel Huayllahua-Silva and myself. During the latter encounter, sakis emitted vigorous calls that differed from the previously heard alarm calls. On one occasion, these calls were emitted directly after calls from another saki group (potentially the former group) were heard in the vicinity.

Primate Inventory

The total survey time designated to the primate inventory was 98 hours and 41 minutes – of which 75 hours and 2 minutes of time (76.03 %) was spent surveying flooded forests, and 23 hours and 39 minutes (23.97 %) was spent surveying non-flooded forests. A total of 109 primate encounters of nine species, including the sakis, were recorded during the inventory (Table 5). Group size varied from 1 – 63 individuals, with the largest and smallest average group sizes observed in squirrel monkey and coppery titi monkey groups respectively. Saddleback tamarin was the only species not recorded in flooded forests, whereas pygmy marmosets, red howler monkeys, sakis and white-fronted capuchins were not encountered in non-flooded forests. The average body mass of all species encountered in the flooded and non-flooded forest types are 2.12 kg and 1.16 kg, respectively.

Table 5: Characteristics and presence/absence data for each primate species encountered in the ACRCTT.

Species	Body weight (kg)*	Average group size (number of groups**)	Group size range	Presence per forest type	
				Flooded	Non-Flooded
Brown capuchin (<i>Cebus apella</i>)	2.9	5.26 (19)	1 - 13	x	x
Coppery titi monkey (<i>Callicebus cupreus</i>)	1.05	3.53 (17)	2 - 5	x	x
Moustached tamarin (<i>Saguinus mystax</i>)	0.51	4.50 (6)	1 - 7	x	x
Pygmy marmoset (<i>Cebuella pygmaea</i>)	0.15	8 (1)	8	x	
Red howler monkey (<i>Alouatta seniculus</i>)	6.5	4.00 (1)	4	x	
Saddleback tamarin (<i>Saguinus fuscicollis</i>)	0.39	4.60 (5)	3 - 6		x
Saki (<i>Pithecia monachus</i>)	2.2	5.37 (19)	3 - 8	x	
Squirrel monkey (<i>Saimiri boliviensis</i>)	0.94	26.50 (14)	7 - 63	x	x
White-fronted capuchin (<i>Cebus albifrons</i>)	2.7	17.00 (1)	17	x	
Total species number				8	5

*Average body weights per species obtained from Bennett et al. 2001.

**The number of groups for which a reliable individual count was obtained, and from which average group sizes were calculated.

Interspecific Associations between Primates

22 of 109 encounters occurred as associations between two or more primate species. Squirrel monkey and brown capuchin groups were most often associated with each other, with five observations of association between these species. Moustached tamarins and saddleback tamarins were observed to associate on two occasions. Sakis were observed to associate with only squirrel monkeys on one occasion, and with two species on each of two occasions: once with a brown capuchin and squirrel monkeys, and once with coppery titi monkeys and a pygmy marmoset. Only one brown capuchin and pygmy marmoset were recorded in each case, although for the pygmy marmoset a reliable count of individuals was not obtained. No direct interactions were observed between the associated species, except in the association between sakis and the brown capuchin: the brown capuchin leaped and landed onto a tree branch that the sakis were resting on. In response, the sakis promptly moved from the branch to another location.

Primate Encounter Frequencies

The species with the highest absolute encounter frequencies over the survey period were squirrel monkey (26 encounters), brown capuchin (24 encounters) and the sakis (23 encounters), while red howler monkey and pygmy marmoset were the least encountered species, encountered once and twice respectively. When encounter rates were standardised by survey effort in each forest type, the species with the highest relative encounter rates were squirrel monkey (21.5 % of encounters), saddleback tamarin (20 % of encounters) and moustached tamarin (17.5 % of encounters)(Table 6). The standardised encounter frequency in non-flooded forests was almost double that of flooded forests. Furthermore, all species encountered in both forest types had higher standardised encounter frequencies in non-flooded than flooded forests.

Table 6: The total (standardised) encounter frequency per primate species and per forest type.

Species	Total Encounter Frequency	Encounter Frequency per Forest Type	
		Flooded	Non-flooded
Brown capuchin	46	22	24
Coppery titi monkey	37	16	21
Moustached tamarin	48	1	47
Pygmy marmoset	2	2	0
Red howler monkey	1	1	0
Saddleback tamarin	55	0	55
Saki	23	23	0
Squirrel monkey	59	23	36
White-fronted capuchin	4	4	0
Total encounter number	275	92	183

Of the eight species encountered in flooded forests, all eight were recorded within 1 – 50 m of the river edge. Brown capuchins, sakis and squirrel monkeys were encountered in all four distance categories. Coppery titi monkeys were encountered in all categories except 50 – 100 m from the edge; assuming the environmental conditions in this distance category do not significantly differ from the others, their presence 50 – 100 m from the river may also be inferred. All other recorded species were only recorded within 1 – 50 m of the river edge (Figure 5).

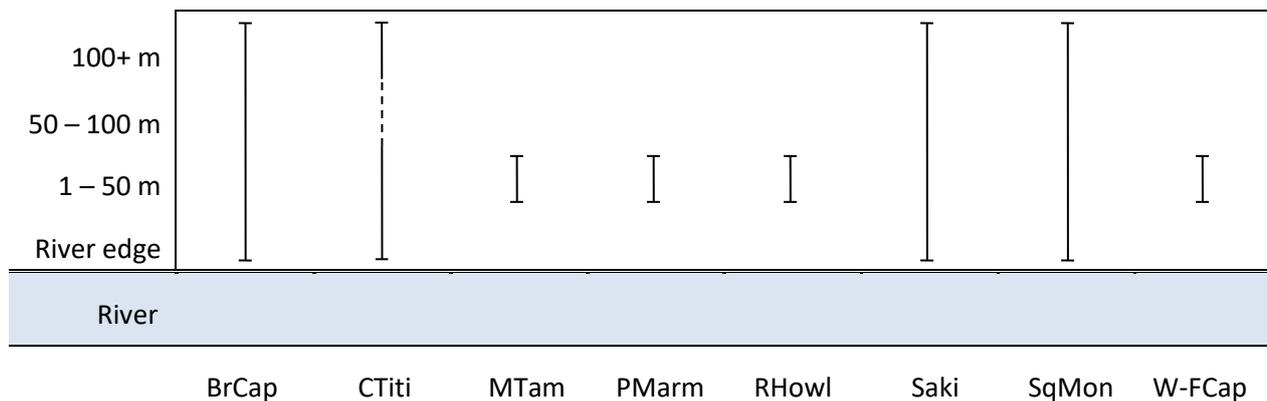


Figure 5: The range, relative to the river edge, at which species encountered in flooded forests were found. Species names are abbreviated as follows: brown capuchin = BrCap, coppery titi monkey = CTiti, moustached tamarin = MTam, pygmy marmoset = PMarm, red howler monkey = RHowl, squirrel monkey = SqMon, white-fronted capuchin = W-FCap.

Primate Vertical Distributions

The vertical distribution of individuals at first encounter was collected for 82 of the 110 encounters. 72 of these encounters occurred in flooded forests, and were also analysed for the effect of distance to the river on primate vertical distributions. The largest proportions of individuals were found high in the forest in brown capuchin, red howler monkey and saki groups; mid-level in coppery titi monkey, moustached tamarin, saddleback tamarin, squirrel monkey, and white-fronted capuchin groups; and low in the forest in pygmy marmoset groups (Figure 6).

The interaction terms of forest type with time of day and of distance to the river with time of day did not significantly improve either of the analysed models, and were dropped in each case. No significant effects of forest type or distance to the river were found on the proportion of individuals at any of the forest heights. Time of day was found to significantly affect the proportion of individuals found mid-level in the forest ($F = 4.56$, $p = 0.034$), although the correlation is weak ($R^2 = 0.06$). This effect was insignificant in the model analysed for the effect of distance to the river (where only flooded forest data was included), and when forest type was removed as a predictor in the model. Therefore, while the results show no effect of habitat type on the vertical distribution of primate groups, the proportion of individuals per group found mid-level in the forest significantly increased with time of day, when accounting for forest type (Figure 7).

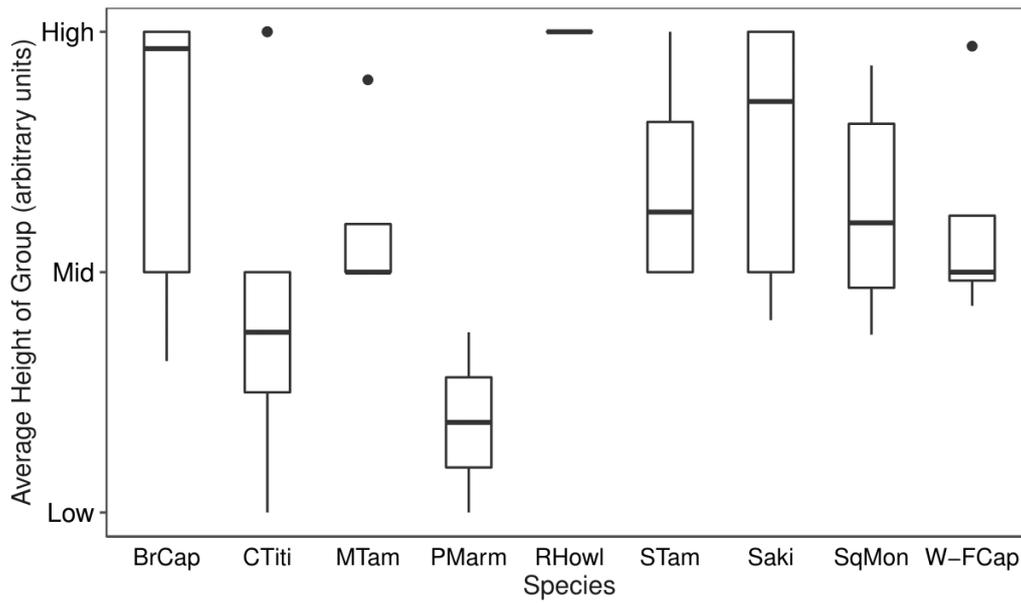


Figure 6: The average forest heights calculated for each primate species. Species names are abbreviated as described in Figure 5.

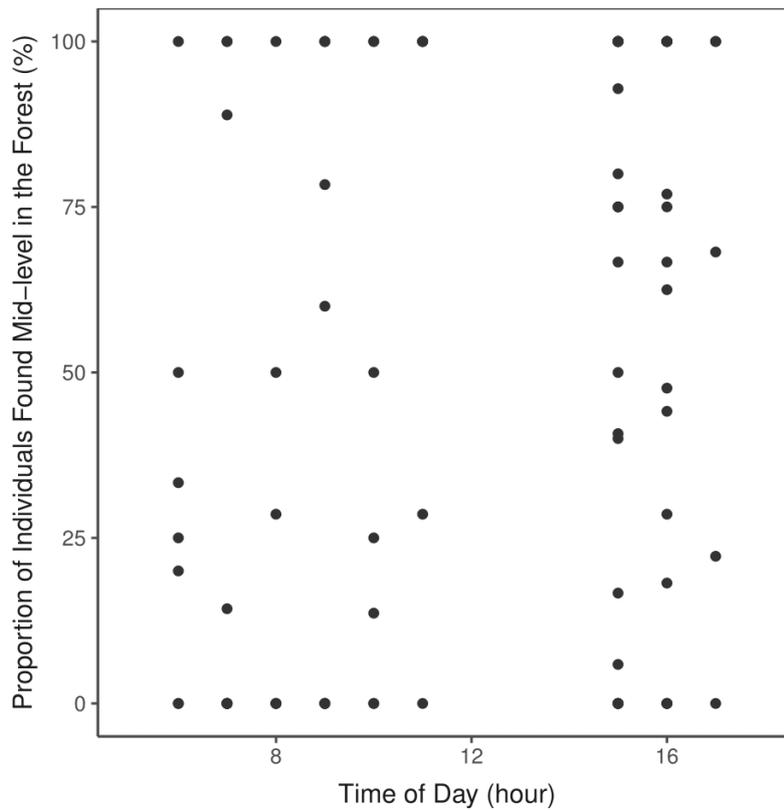


Figure 7: The relationship between time of day and the proportion of individuals per primate group recorded at mid-level in the forest.

Statistical differences in vertical distributions by species were evaluated only for brown capuchins, coppery titi monkeys, sakis, and squirrel monkeys (a total of 64 encounters), since vertical distribution data was collected for fewer than four groups each of the other encountered species. Species was found to significantly affect the proportion of individuals per group recorded low in the forest ($F = 9.25$, $p = 1.0E-04$). A Tukey's test shows that this effect lies in a significant difference between coppery titi monkey groups and all three other species groups ($p < 0.022$ for each pairwise comparison). Based on these results and Figure 8, a significantly higher proportion of individuals in coppery titi monkey groups are found low in the forest than in brown capuchin, squirrel monkey or saki groups.

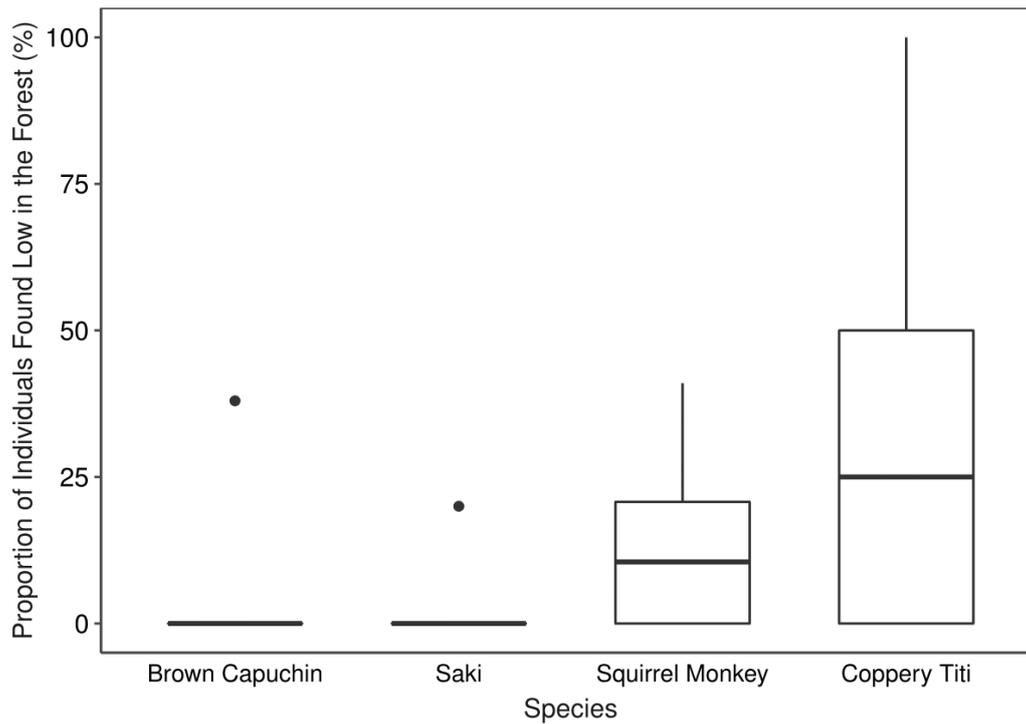


Figure 8: The proportions of individuals in brown capuchin, coppery titi monkey, saki and squirrel monkey groups found low in the forest.

Discussion

This study was conducted with the purpose of gaining insight into the behaviour of a potentially undescribed morph of saki monkey occurring at the ACRCTT reserve, and into the primate community it occurs within. A number of differences in saki behavioural patterns and use of forest strata have been identified here, depending on the sex and age of the individual, and the forest height that the individual was present at. The primate inventory confirmed the presence of nine primate species in the ACRCTT, with the highest diversity recorded in flooded forests, but the highest standardised encounter frequencies recorded in non-flooded forests. The vertical distributions of primates within groups were not found to differ by habitat type; however, species identity and time of day both affected vertical distributions. These patterns shed light on the coexistence of primates in the ACRCTT, and how the sakis fit into this community.

Saki Behavioural Patterns

The presence of more than one adult male and/or female was confirmed in approximately half of the saki encounters, including the five encounters in which the full group compositions were confirmed. *Pithecia* species are traditionally thought to form monogamous groups with one adult pair (Izawa 1976, Neville et al. 1976, Buchanan-Smith et al. 2000, Norconk 2007, Aquino et al. 2009b); however, observations of multi-adult groups are becoming increasingly common (Norconk 2007, Aquino et al. 2009b, Norconk and Thompson 2011, Porter et al. 2015, van Belle et al. 2016). Previous research suggests that multi-adult saki groups may occur as a result of potential cooperative benefits from the presence of multiple adults, such as increased territorial defense and foraging capacity (Thompson et al. 2012, Porter et al. 2015), or slow dispersal rates for young adults born into the group (di Fiore et al. 2007, van Belle et al. 2016). Such cases may occur, for instance, in areas where group density is high relative to habitat availability (Norconk 2006, 2007). As we did not attempt to identify groups and their home ranges during this study, the total number of saki groups at the ACRCTT remains unknown. Further research should also aim to verify the observations of multi-adult saki groups at the ACRCTT, as the age of individuals, particularly sub-adult offspring that resemble adults in size and fur colouration, could have been mistaken in the field.

That sakis were found to spend significantly higher proportions of time feeding, travelling and resting than other behaviours makes sense, as these constitute the basic behaviours required for survival. That juveniles were found to spend higher proportions of time travelling than adults is also understandable, and likely relates to their explorative natures in comparison to older individuals (Doran 1997). Aggression was observed during one encounter, and corresponded to the only case during which two separate saki groups were recorded in each other's vicinity. Such between-group displays of aggression have previously been documented in sakis (Izawa 1976, Norconk 2007, Thompson et al. 2012, Porter et al. 2015). In contrast, the proportion of observed time spent on social behaviours, as well as the number of individuals found to display them, was lower than might be expected in relation to previous studies of saki groups (di Fiore et al. 2007, Thompson and Norconk 2011, Palminteri and Peres 2012). This may be a bias resulting from stress due to the presence of the observers (Blanchard et al. 2001), considering that vigilance towards the observers was recorded during approximately one-tenth of the sampling time.

The frequency of behaviours displayed was analysed as a measure of energy use, assuming that frequent switching between behaviours consumes a high amount of energy; therefore, as males were found to display higher total frequencies of behaviours than females, the results suggest that the saki males exhibit more high-energy behavioural patterns than females do. This pattern could imply a differential investment

between sexes in different activities: for instance, many studies indicate that in pair-bonded primates where females primarily care for offspring, males may indirectly increase rearing success by providing energy-demanding services such as territorial defence to the female (Trivers 1972, Wittenberger and Tilson 1980, Kleinman and Malcolm 1981, Lancaster 1985, Fuentes et al. 2002). This has also been hypothesised for sakis, of which males are shown to invest little energy into direct care of offspring (de Luna et al. 2010, Fernandez-Duque et al. 2013). This hypothesis is also supported for the ACRCCTT saki population in that males were found to display vigilance significantly more frequently than females. As this difference did not extend to the proportions of time spent displaying vigilance by each sex, it would seem that both sexes engage in vigilance, although males integrate it more into their behaviour. This was also apparent during sampling, as males tended to descend lower into the forest upon the arrival of observers, whereas females and juveniles often retreated to the upper forest strata. This pattern explains both the lower sample sizes obtained for females and juveniles relative to males and adults, and the significant difference in use of forest strata between adults and juveniles.

The apparent preference for upper forest strata shown by the sampled sakis coincides with observations of forest use for other sakis in the western Amazon (Mittermeier and van Roosmalen 1981, Happel 1982, Peres 1993a, Palminteri et al. 2012b). Interestingly, primate studies indicate that while small-bodied species tend to be found in lower forest strata, potentially to reduce their vulnerability to aerial predators (Terborgh 1983, Boinski et al. 2003), sakis are often the exception to this pattern (Peres 1993b, Buchanan-Smith et al. 2000, Heymann et al. 2002, Sheth et al. 2009). Inhabiting upper forest strata may be favorable for sakis, for instance, to gain access to canopy resources such as a higher abundance of fruits (Schaefer and Schmidt 2002). Certain adaptations, such as the sakis' ability to remain remarkably inconspicuous for extended periods of time, may also facilitate this by increasing the ability for sakis to conceal themselves from predators (as observed on two occasions during this study). Furthermore, sakis are known to preferentially inhabit mature or old-growth forests with dense canopies (Buchanan-Smith et al. 2000, Norconk and Grafton 2003, Palminteri et al. 2012b), which are likely to provide better shelter from aerial predators than disturbed or secondary forests. While these patterns are well supported, there is currently no evidence for vertical stratification in behavioural patterns according to sex in sakis as the results of this study suggest. As for all the behavioural analyses conducted in this study, between-group variation may inflate some of the differences found between sakis of different ages and sexes; as such, the validity of this pattern could be better tested by analysing long-term behavioural data from single groups at a time.

Pithecia are often identified as granivorous (Norconk 1996, Peres 1993a, Norconk 2007), and are thus thought to be less affected by seasonal variations in fruit abundance than other frugivorous primates (Norconk 1996, Palminteri et al. 2012a). However, other studies have recorded fruit pulp as the primary food source for sakis (Mittermeier and van Roosmalen 1981, Happel 1982, Peres 1993a, Charpentier et al. 2015). The proportions of seeds and fruit pulp ingested by the sakis in this study are not known, as fruit parts were not differentiated in the samples. Meanwhile, the fact that sakis were seen foraging for fruits and arthropods for equal proportions of time implies a high dietary diversity, as has also been shown in other studies of sakis (Happel 1982, Norconk 1996, Norconk and Conklin-Brittain 2004, Norconk 2007), although this measure of feeding habits does not convey the proportion of energy the sakis gained from each food type. The longer recorded durations of fruit feeding than arthropod feeding, and the more frequent observations of fruit feeding as a group than arthropod feeding, suggest that fruits (and/or seeds) may constitute a primary food source for the sakis, whereas arthropods may be fed on opportunistically. This is supported by the fact that sakis that were recorded eating arthropods were rarely observed to move far from their original position to

forage, and that the only observation of group feeding on arthropods occurred at a bee nest, where bees were likely to be abundant and easily accessible.

Traditionally, different saki species have been regarded as eco-species, inhabiting similar ecological niches in geographically separate habitats (Peres and Janson 1999). As such, little is known about the mechanisms of niche differentiation in sympatric saki species. Unfortunately, burnished sakis were not encountered during this study, limiting the inferences that can be made about the niche differentiation between the two saki populations in the ACRCTT. Jackson (2016) found that the monk sakis were significantly more abundant in the ACRCTT than the burnished sakis during the late wet/early dry season, although both species were recorded in flooded forests. In contrast, the fact that only monk sakis were encountered in flooded forests in this study, despite the high survey effort, suggests that some seasonal habitat differentiation may occur between the species. Such differentiations typically occur as a result of seasonal variations in the availability of a limited resource, and are often observed in Neotropical primate communities in relation to seasonal fruit abundance (Terborgh 1983, Bourlière 1985, Peres 1994, Schreier et al. 2009); however, this is an unlikely cause of the potential habitat differentiation between these populations, as this study coincided with a period of high fruit abundance. Rather, since many western Amazonian saki species prefer upper forest strata (Happel 1982, Peres 1993a), habitat differentiation between the two populations in the ACRCTT could be driven by competition for other resources in the upper forest. To validate this, further studies are required that confirm the differential use of forest types by the saki populations in the ACRCTT, and that investigate the behavioural patterns in both populations over multiple seasons.

Although over 120 hours were spent in the field, less than five hours of continuous focal samples were obtained. This problem is consistently reported in existing research (Izawa 1976, Pinto et al. 2013), and stems from multiple factors, including the tendency of sakis towards cryptic behaviours and long periods of inactivity, the difficulty of habituating them, and the dense vegetation of forests that they typically inhabit (Izawa 1976, Pinto et al. 2013). In only one case, where a group was encountered feeding in a tree on the river edge, could focal samples be obtained in this study without noticeable biases resulting from our presence. This limitation, coupled with the high variability of the observed saki behavioural patterns as evidenced by the extraordinarily high standard deviations for each measure (Tables 3 – 4), implies that real patterns in the behaviour of this potentially undescribed saki morph will be exceedingly difficult to discern. The use of sampling methods such as scan sampling, where behaviours are recorded at set time intervals over longer periods of time (Altmann 1974), could allow for more consistent patterns of saki behaviour to be recorded in future studies. Pseudo-replication by the sampling of the same individuals in different encounters may also have occurred in this study, and should be accounted for in future research.

Primate Inventory

Of the 14 primate species previously recorded in the ACRCTT, no encounters were made with groups of black spider monkey (*Ateles paniscus*), burnished saki (*Pithecia inusta*, sensu Marsh 2014), Peruvian red-necked owl monkey (*Aotus nancymae*), Poepig's woolly monkey (*Lagothrix poeppigii*), or red bald-headed uakari monkey (*Cacajao calvus rubicundus*). Of these species, black spider monkeys, Poepig's woolly monkeys and red bald-headed uakari monkeys are uncommon and rarely recorded in the vicinity of the ARC (Huayllahua-Silva, pers comm.), whereas Peruvian red-necked owl monkeys are nocturnal and, hence, rarely encountered during daytime surveys. The lack of encounters with burnished sakis does not reflect their relative abundance in the reserve (Huayllahua-Silva, pers comm.); however, comparisons with previous primate inventories cannot be made as these inventories do not distinguish between the saki species present at the reserve.

The average group sizes per species reported in this study correspond well with other averages reported in the northern Peruvian Amazon (Izawa 1976, Neville et al. 1976, Freese et al. 1982, Bennett et al. 2001, Heymann et al. 2002, Aquino et al. 2005, Haugaasen and Peres 2009, Aquino et al. 2014, Aquino et al. 2015). Likewise, the interspecific associations observed in this study agree with previous findings, with associations between squirrel monkeys and capuchins, and between tamarin species, constituting the most commonly reported associations (Neville et al. 1976, Terborgh 1983, Buchanan-Smith et al. 2000, Heymann et al. 2002, Haugaasen and Peres 2009, Aquino et al. 2014). Many studies also report high proportions of interspecific association between sakis and other primates (Neville et al. 1976, Buchanan-Smith et al. 2000, Aquino et al. 2009b, Haugaasen and Peres 2009). Such associations appear to occur most often as a result of randomly coinciding travelling routes and feeding sites (Haugaasen and Peres 2009). As associated groups were almost never seen to interact, this may also apply to the associations observed in this study; however, longer observation periods for the associated groups would be required to validate this.

The relative encounter frequencies of primates in this study agree with those of previous ACRCTT mammal surveys, conducted annually between 2012 – 2015 in the dry season (Dosantos Santillán 2013, 2014, 2015, Dosantos Santillán and Tegnér 2015), with the exception of the high encounter frequencies reported for squirrel monkeys. As squirrel monkeys are recorded at high frequencies in other areas within the region (Freese et al. 1982, Bennet et al. 2001, Heymann et al. 2002), this difference may be attributed to other factors, such as seasonal variations in primate abundances. Overall, patterns of primate abundances and a strong hunting pressure indicate that larger-bodied primates, particularly brown capuchins, red howler monkeys, and woolly monkeys, have reduced in number in the region (Puertas and Bodmer 1993, Aquino et al. 2009a). Primate hunting was strictly banned in the ACRCTT in 2008 in an effort to protect the extant primate community, and the high encounter frequencies of brown capuchins recorded in this study and by Dosantos Santillán and Tegnér (2015) suggest that at least this species benefits from the protected area.

Although a higher species richness was recorded in flooded forests than non-flooded forests, the standardised encounter frequency in non-flooded forests was almost double that of flooded forests. This is in complete contrast with previous research (Freese et al. 1982, Peres 1997, Peres and Haugaasen 2009, Palminteri et al. 2011, Aquino et al. 2014), and with the expectation that primates would be concentrated in riverside forests where more trees would be fruiting. The large variation in survey effort is likely to have biased these results, as both the longer time spent and the larger area covered increases the likelihood of encountering more species in the flooded forest surveys (MacArthur and Wilson 1967). This is supported by the fact that the two least commonly encountered species (pygmy marmoset and red howler monkey) were only encountered in flooded forests, although these species have previously been recorded in non-flooded forests in the ACRCTT (Dosantos Santillán 2015, Dosantos Santillán and Tegnér 2015). As the survey method was chosen to maximise the chance of encountering sakis, the encounter frequencies for any species that associate with the same habitats as the sakis are also likely to be inflated.

The non-flooded forest area in this study consisted of a mosaic of various seasonally inundated forest types that were not yet flooded during the survey period. As such, many forests surveyed as flooded and non-flooded forests could have corresponded to the same forest types, implying that the different primate assemblages encountered in each survey area are better explained by flooding level than by forest type. That said, the almost complete lack of encounters with tamarins in flooded forests, despite the disproportionately high survey effort, suggests that these species associate with non-flooded areas. This pattern may have arisen because their small body sizes render them vulnerable to drowning or predation by aquatic animals, or because many understory food sources, which tamarins are known to feed on (Peres 1997), are submerged

in flooded forests. Furthermore, the average body mass of the primates encountered in the flooded forests was higher than that in non-flooded forests, suggesting that larger-bodied species associate with flooded forests. This has also been found elsewhere (Freese et al. 1982, Peres 1997), and may be related to the higher concentration of fruits found in flooded forests during the wet season (Peres 1997, Haugaasen and Peres 2009).

Interestingly, all of the species encountered in flooded forests were encountered within 1 – 50 m of the river, where the majority of human activity in the ACRCTT is concentrated. This suggests that the primate groups that inhabit the surveyed area are accustomed to the presence of humans. On the other hand, all of the species encountered in flooded forests except for brown capuchins, coppery titi monkeys, sakis, and squirrel monkeys were encountered only within 1 – 50 m of the river edge. While survey effort was also concentrated along the river, such restrictions in habitat type could arise from differences in vegetation structure and disturbance dynamics occurring near the river edge (Laurance et al. 1998). Many primates, including pygmy marmosets, are associated with the structurally heterogeneous habitats created by such disturbances (Peres 1993b, Peres 1997, Buchanan-Smith et al. 2000).

Although statistical differences in species' vertical distributions could only be evaluated between four species due to a lack of data, the significantly different distributions between the titi monkeys and the other species agree with the results of previous studies that show smaller-bodied species utilising lower forest strata than larger-bodied species (Terborgh 1983, Peres 1993b, Buchanan-Smith et al. 2000, Heymann et al. 2002, Sheth et al. 2009). As explained above, sakis are often the exception to this pattern, consistently occurring in higher forest strata than other small-bodied species. While this result is evidence of niche differentiation in the ACRCTT primate community, further study would be required to determine what mechanisms drive differentiation between species that co-occur in the same habitats and forest strata. Time of day may represent one dimension by which such species could differentiate, as indicated by the correlation with time of day and the proportion of individuals recorded at mid-level in the forest in this study. However, the low R^2 value for this correlation, and the fact that primates are known to exhibit a large variation in behaviour across different environmental and social contexts (Bronikowski and Altmann 1996, Schreier et al. 2009, Schaffner et al. 2012), suggests that many other factors also contribute to this differentiation.

Overall, the validity of the reported primate diversities and encounter frequencies in each surveyed forest type was probably affected by the non-standardised survey method used in this study. As such, this inventory represents a more general snapshot of the ACRCTT primate community that provides preliminary insights into how sakis coexist with other primates at the reserve. As the potentially undescribed monk saki morph was only encountered in flooded forests, despite previous studies indicating that other *Pithecia* species preferentially inhabit non-flooded forests (Mittermeier and van Roosmalen 1981, Terborgh 1983, Buchanan-Smith et al. 2000, Sheth et al. 2009, Palminteri and Peres 2012), habitat use may drive differentiation between these sakis and some species, such as tamarins and the burnished sakis, in the wet season, whereas differentiation by diet, forest strata and other dimensions may occur between the sakis and other syntopic species. To investigate these factors further, long-term studies are required where the real abundances of primates are calculated relative to the proportion of different habitats available, the dietary preferences of each primate species are recorded, and seasonal differences can be evaluated.

Conclusion

The results of this study provide important insights into the behavioural ecology of *Pithecia*, validating many previous observations of saki behaviour in the western Amazon. In particular, the evidence of multi-adult saki groups in the ACRCTT and their preferential use of upper forest strata is widely supported by existing research. The study also documents a high dietary diversity in the studied sakis, although fruits and/or seeds appear to constitute their primary food source. Furthermore, support is provided for a differentiation in the roles of males and females in saki groups, as males were found to exhibit higher-energy behavioural patterns, and display vigilance significantly more frequently than females. However, many questions about saki behavioural patterns remain, particularly in relation to interspecific variations in behaviour and ecological niches. Although the primate survey conducted here suggests that habitat differentiation may occur between the sympatric burnished sakis and the potentially undescribed monk saki morph in the wet season, comparative studies are needed to validate this hypothesis and examine real differences in the behavioural ecology of these populations. The primate survey also provides evidence of vertical stratification at least between coppery titi monkeys and sakis, squirrel monkeys and brown capuchins, as well as of a potential association between tamarins and non-flooded forests. However, surveys with a standardised methodology are required to ascertain real abundances and further associations between species and the habitats in the ACRCTT. The large variations in saki behavioural patterns and primate vertical distributions also suggest that intra- and inter-species dynamics within the ACRCTT primate community are influenced by a number of abiotic and biotic factors that remain to be evaluated. Given the high diversity and frequency of primate groups encountered in this study, the ACRCTT and other such protected areas clearly provide essential opportunities for the *in situ* investigation of such factors, as well as for the overall conservation of primates in the Amazon.

Acknowledgements

This project was conducted in conjunction with ongoing research by Dr. Janice Chism of Winthrop University. I would like to thank Dr. Janice Chism and Richard Jackson for sharing their extensive knowledge of the saki monkeys at the ACRCTT and for their contributions to planning and discussing this research. I also thank Dr. Paul Beaver and the staff of Amazonia Expeditions for their contributions to the planning and practicalities of my stay at the ACRCTT, and for sharing their knowledge about the region and the primates at the ACRCTT. I would also like to thank Manuel Huayllahua-Silva, Anthony Turgeon and Dik Rengifo for their invaluable assistance in the field, as well as the staff at the Amazonia Research Center for making me feel welcome and comfortable for the whole of my stay. Further thanks go to my supervisor at Uppsala University, Dr. Mats Björklund, for his comments on the analysis and writing for this report, and to Dr. Göran Arnqvist for his advice on the statistical analysis for the project. Finally, this project would not have been possible without the Minor Field Studies scholarship, granted to me by the Committee for Tropical Ecology at Uppsala University, and funded by the Swedish International Development Authority (Sida).

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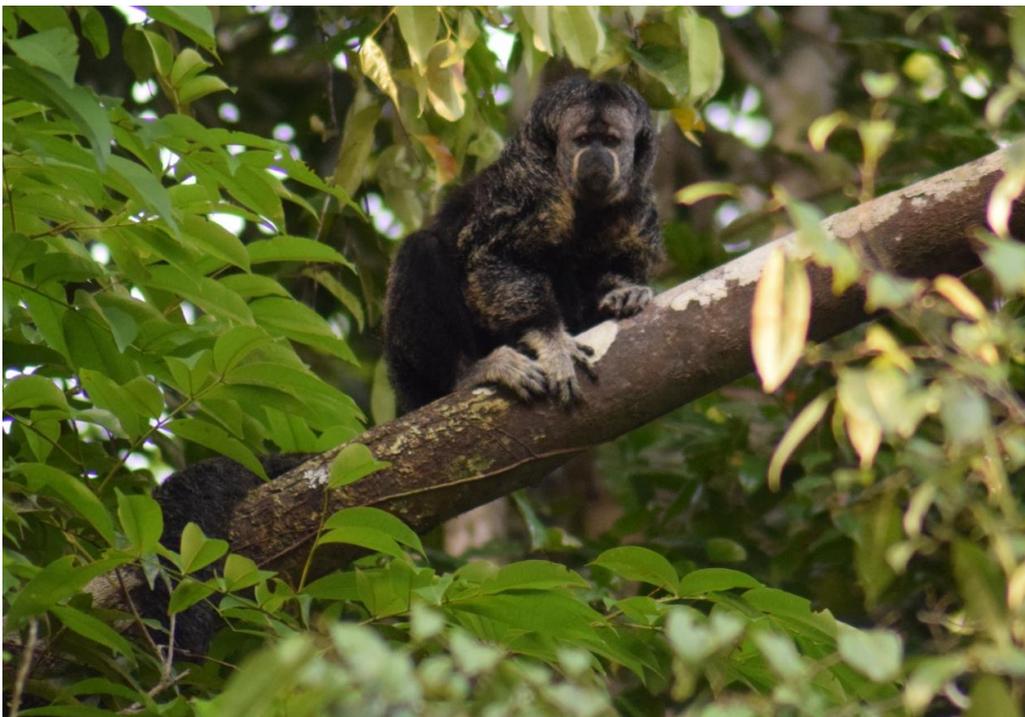
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Appendices

Appendix 1a: Photograph of a male from the potentially undescribed monk saki (*Pithecia monachus*, *sensu* Marsh 2014) population at the ACRCTT. Taken by Emily Lehtonen.



Appendix 1b: Photograph of a female from the potentially undescribed monk saki (*Pithecia monachus*, *sensu* Marsh 2014) population at the ACRCTT. Taken by Emily Lehtonen.



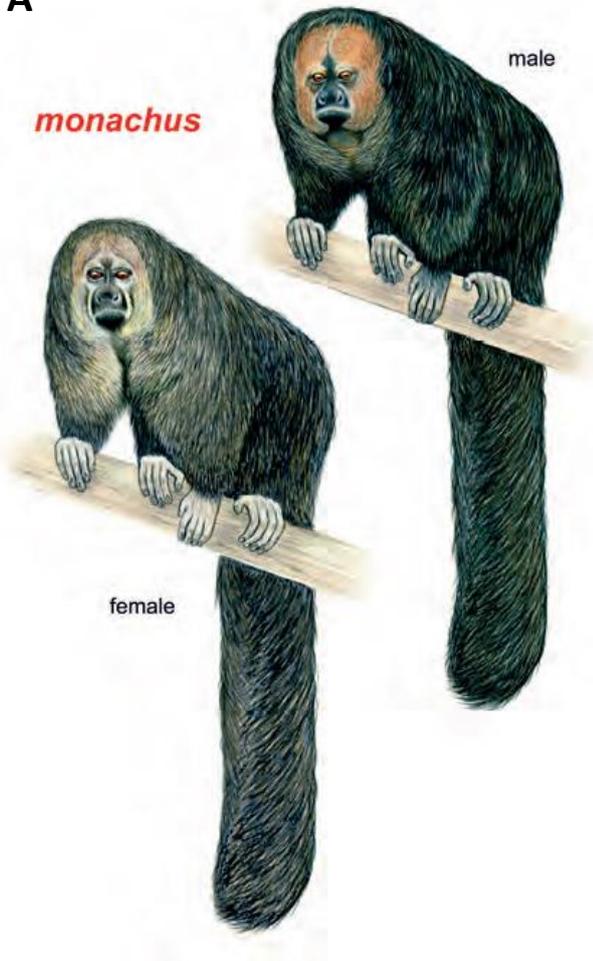
Appendix 2: Photograph of a male from the burnished saki (*Pithecia inusta*, *sensu* Marsh 2014) population at the ACRCTT. This species is not sexually dichromatic. Taken by and used with permission from Alfredo Dosantos Santillán.



Appendix 3: Illustration of the (A) monk saki, *Pithecia monachus*, and (B) burnished saki, *Pithecia inusta*, as described by Marsh (2014). Illustrated by and taken with permission from Stephen Nash.

A

monachus



B

inusta

