Quantifying Primate Range and Activity in a Disturbed Primary Forest

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INTRODUCTION

The study of primate behavior has a storied history across psychology, ecology, conservation, and many other fields of social and biological research. Primate behavioral ecology can have cascading effects on the well-being and resilience of the ecosystems they inhabit. Research has shown that 75% of trees in neotropical forests have fruits that are adapted for vertebrate consumption (Andersen 1999), and therefore are dependent upon such consumers for the dispersal of their seeds (Terborgh et al. 2008). Primates are integral to the dispersal of seeds from arboreal nuts and fruits, and their niche within this role can range widely due to variation in diet composition, body size, home range, and foraging behavior (Andersen 1999, Meade & Rooper 2021).

Primates are threatened with extinction all across the globe, as an estimated 65% of all primate species are currently categorized as vulnerable, endangered, or critically-endangered by the IUCN (Fernandez et al. 2022). The majority of these species are distributed throughout forested neotropical systems (Mittermeier et al. 1989), where habitat destruction, the primary threat to primate populations throughout the world, is occuring at the fastest rates. These integral habitats are most often converted into agricultural plots, but cattle ranching, commercial logging, and illegal mining operations also contribute heavily to such destruction (Mitermeier et al. 1989). In order to sustain primate populations and their role as seed dispersers, and by proxy maintain the health and stability of neotropical forests, it is integral to further develop our understanding of primate behavioral ecology.

The aim of the present study is to compile activity budgets and characterize home ranges for each of the primate species that inhabit the Finca Las Piedras (FLP) Research Station in Madre de Dios, Peru. This 54 ha plot of primary terra firme forest has experienced notable disturbance from selective logging, forest fire, and land conversion. The diversity and ecology of mammals that inhabit a disturbed forest can be indicative of the system's relative health, as well as its resilience. Moreover, studying the behavioral ecology of endemic primates in disturbed systems can illuminate the adaptability of these species during regenerative periods (Meade and Rooper 2021). An array of primate species have been documented expanding their range of behavior in response to anthropogenic environmental change, including Macaca spp., Cebus sp., Sapajus sp., and others (Back et al. 2019). These accounts include the development of tool use, increases in diet breadth, and variation in activity budget compared to historical accounts. Peru is home to one of the most diverse primate fauna in the world (Mittermeier et al. 1989). The primates historically known to inhabit this reserve include the brown titi monkey (Plecturocebus brunneus), white-fronted capuchin (Cebus albifrons), Large-headed

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capuchin (Sapajus apella macrocephalus), Black-capped squirrel monkey (Saimiri boliviensis), brown-mantled tamarin (Leontocebus fuscicollis), black-headed night monkey (Aotus nigriceps), and red howler monkey (Alouatta seniculus). Apart from an inventory of the species present, studies on the primates of FLP are lacking and to date there have been no extensive studies that focus on primate behavior at this site.

Activity budgets of wild primates are widely utilized as a measure of captive primate welfare and present valuable information to captive wildlife management efforts (Melfi & Feistner 2002). Primates with low quality diets (i.e. those that subsist mainly on bark, leaves) tend to have smaller ranges and generally limit their time spent moving (Leonard & Roberston 1997). Leonard & Robertson 1997 reported the activity budgets of white-fronted capuchins (C. albifrons), large -headed capuchins (S. apella macrocephalus), and brown-mantled tamarins (L. fuscicollis), all of which ranked within the top 20% of the 16 species whose dietary quality was calculated. The activity budgets of the two capuchin species were largely similar, but demonstrated a marked difference from that of the brown-mantled tamarin. Capuchin feeding budgets were significantly larger than tamarins, and their resting budgets were especially truncated in comparison to L. fuscicollis. Activity budget and diet quality data were also presented for the dusky titi monkey (Plecterocebus moloch), which exhibited a notably poor diet, prolonged periods of rest, and a feeding budget comparable to L. fusciollis. These findings indicate that a measurable degree of plasticity exists in the activity patterns of primates species with overlapping ranges. Similarly, it is predicted that the results of this study will demonstrate significant variation between species in regards to their activity budgets. The frequency of itching behavior was also calculated in this study in order to assess if a discrepancy exists between species in the rate at which nervous behavior is exhibited in the presence of an observer (Whitehouse et al. 2017). It is predicted that species that more frequently inhabit the lower canopy (and are therefore closer to the observer) will exhibit stressful behavior more often. Camera traps were also utilized to collect activity data on primates, and it was predicted that itch frequency would be exhibited less often in the absence of an observer.

A study on a group of proboscis monkeys (Nasalis larvatus) found no significant difference between the proportions of time spent resting, feeding, or moving among cohabiting conspecifics, but did identify variation in the frequency and duration of rare behaviors such as grooming and copulation (Matsuda et al. 2009). Notable variation between wild populations of Sulawesi crested black macaques (Macaca nigra) has been observed, but this was largely attributed to the heterogeneity of their habitats in regard to geography and food abundance (Melfi & Feistner 2002).

In this study, the species-specific home ranges within FLP were calculated using minimum convex hulls, and visualized using kernel density estimates (Souza-Alves et al. 2021, Scary 2013). Studies of brown-mantled tamarins (L. fuscicollis) in western Pando, Bolivia indicate that home range varies between 25.9-40.1 ha (Yoneda 1981), though more recent studies in Southeastern Peru estimate smaller home range sizes of tamarin subgroups, some as low as 2.6 ha (Nymark 2023). The home range of tufted capuchins (S. apella) in Columbian lowland humid forest has been estimated to span 320 ha, and demonstrates little variation with season (C. Gómez-Posada et al. 2019). Squirrel monkeys (Saimiri spp.) troops can have home ranges that exceed 500 ha

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(Emmons & Feer, 1997), but more commonly these ranges vary between 75-240 ha (Pinheiro et al. 2013, Carretero-Pinzón et al. 2016) The home range of two sympatric groups of coppery titi monkeys (Plecterocebus cupreus) were founds to be 6.7 ha and 11.4 ha, respectively (Kulp & Heymann 2015). Among 5 neighboring red titi groups within a 650 ha reserve the mean home range size was found to be 4.0 ± 1.4 ha with a maximum of 7% overlap between groups (Van Belle et al. 2021). It is predicted that variation in home range size will be observed between primate species within FLP. It is also predicted that the magnitude of the area each species will inhabit and the hierarchy of home range size will follow similar trends as those indicated by past research and listed above.

METHODS

Study Site

This study was conducted at the Finca Las Piedras (FLP) Research Station in the Tambopata region of Madre de Dios, Peru (Lat.: -12.22789; Long.: -69.11119). The site spans roughly 54 hectares in a near-rectangular shape and is located 3 km east of the Interoceanic highway, roughly 40 km North of the region's capital Puerto Maldonado. This site is composed of regenerating native plant forest, secondary planted forest, Mauritia palm swamp, and primary terra firme forest which experiences a prominent dry season that spans from August-October (Meade and Rooper 2021). Portions of Finca Las Piedras have been selectively-logged and historically used for agriculture, resulting in a landscape characterized by fragmented primary and regenerating secondary rainforest. The recent burning of a neighboring plot of primary forest in July 2023 has confiscated roughly 28.7 ha of habitat from endemic wildlife and created an additional 372 m of edge habitat directly bordering FLP. Plans exist to continue this burning along the entire Northern border of FLP, which will continue to decrease habitat availability and create more edge habitat around this site.

Data Collection

Data on primates was collected along preexisting trails on the Finca Las Piedras property. A system of 9 trails exists within the terra firme primary forest, and from these trails two paths North and South) were constructed that walked 2.52 and 2.33 km, respectively, and minimized overlap with respect to each other. The two paths were walked in both directions, which yielded 4 distinct routes on which data was collected. Reconnaissance walks were conducted at 5:30, 8:30, and 14:30. The two routes and the direction in which they were followed were alternated for each observation session. Data was collected between October 2nd and November 2nd, 2023. The start time, end time, and route walked were noted for each observation period. The observer aimed to walk routes at 1.25 km/h along trails, stopping at 100 m intervals to more closely observe the canopy and listen for auditory signals of primate presence such as branch damage and vocalizations (Peres 1999).

Upon observing a group of primates, data was collected on the species observed, number of individuals, time of day, mode of detection (sight or sound), and position relative to the ground (terrestrial, low canopy (<15m), or high canopy (>15m). After counting all visible members, the individual closest to the observer was chosen as the focal animal of an instantaneous behavior sample (Altmann 1974). This technique makes note of the duration of select behavior states as they are being performed by the focal animal during the particular observation period (Lehner 1991). Behavioral sampling for a focal individual persisted until the individual

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went out of sight for one cumulative minute (i.e. the point at which the collective number of seconds it has been out of sight sums to one minute) (Altmann 1974). At that point, the next closest member of the group was sampled in the same manner. This was repeated until all members of the group had been sampled or until the entire group had fled from sight. If at any point the focal individual left the observer's line of sight, the duration window of the behavior being exhibited at that time was terminated. Start and end times were noted to calculate the duration of each observation period (Harrison et al. 2009). The intervals between consecutive focal observation windows was minimized by determining the next-nearest individual while the current focal animal was out of sight. In this way, all consecutive instantaneous samplings over the duration of the observation period could be treated as a cohesive scan sample of the entire group (Altmann 1974).

The behavior states noted in this study include socializing, moving, resting, consumptive behavior, and miscellaneous. Behaviors were defined in a parallel manner to Melfi & Feistner 2002 and are described in Table 1. Contrary to their method, however, feeding and foraging were grouped together under the umbrella term "consumptive behavior" due to the brevity of feeding windows and difficulty distinguishing between these behaviors from long distances. From these data, species-level activity budgets were calculated by averaging the proportions of time spent exhibiting these behaviors by each group of a given species.

The frequency of itching behavior was also noted during observation periods. Though this is a form of autogrooming and therefore documented as a form of rest, scratching is an indicator of stress in primates (Whitehouse, 2017), and documenting this behavior separately can inform the observer of the subject's psychological state. The number of scratch-seconds (i.e. the number of seconds a focal individual spent scratching) were summed for all individuals during an observation period and divided by the duration of the observation period in decimal minutes to yield the parameter scratch-seconds min-1, which could be used to compared the frequency of stressful behavior between species. Single scratches

BEHAVIOR	DESCRIPTION
Socializing	Copulation, non-copulatory mounting, allogrooming, chasing, and physical altercation (biting, hair-pulling, attack)
Moving	Locomotion that involves displacement (running, jumping, walking, climbing). Windows of movement were considered over once an individual was stationary for 3 consecutive seconds
Resting	An absence of movement while abstaining from social behavior, especially when lying along branches. Autogrooming included
Consumptive Behavior	Includes foraging and feeding. **Foraging** is defined as intensive scanning or manipulation of substrate material with the eyes and hands, and generally involves slow movement toward potential food sources. **Feeding** is defined as the acquisition (reaching for, picking, and/or manipulating) and active consumption (placing into mouth, chewing, manipulating cheek contents) of foraged food source
Miscellaneous	Any behavior not specifically noted above

Table 1. Description of Noted Behaviors. Analogous to behavioral descriptions in Melfi & Feistner 2002, with the exception of the grouping of foraging and feeding behaviors into "consumptive behavior".

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were assigned the value of 1 scratch-second, even if the duration of scratching lasted less than 1 second. Additionally, the number of transitions between behaviors was recorded over the course of the observation period so the rate of transition between states could be compared between and within species.

Camera traps (Browning BTC-5HDPX) were also utilized to supplement data collected on reconnaissance walks and to gain insight on how primate behavior may differ in the absence of a human observer (Candland et al. 1972). Utilizing camera traps for data collection improves the likelihood of capturing the presence of more secretive primates, species with particularly small populations, groups whose ranges overlap only slightly with FLP, and nocturnal primates such as A. nigriceps which has been observed on site. Four camera traps were placed off trail around FLP between September 27th and October 2nd 2023. Cameras were oriented along the axis of diagonally-felled trees and nexuses of woody vines no more than 3 m from the ground. These represented an interface between terrestrial and arboreal spaces and were hypothesized to have higher primate traffic while also being easily accessible. Given the brevity of the study period, maximizing the data collected was a priority. Therefore, the systematic placement of cameras in a grid to avoid bias, as is often preferred in occupancy studies (Bowler et al. 2016), was of lesser concern.

Videos captured on motion-activated camera traps were manually analyzed and the identity and behaviors of any primates were recorded in a similar fashion as if they had been witnessed on a reconnaissance walk, with one exception. For activity data collected on videos, if an individual left the camera frame its focal window was closed and data collection began on the next-nearest individual immediately where applicable. Activity data from consecutive videos of the same species taken within 10 minutes of each other by the same camera were considered to occur within the same observation period. Foliage was trimmed within 1.5 m of camera traps to avoid non-target stimulation (i.e. movement of branches), which can greatly increase the load of footage to be sorted (Gregory et al. 2014).

Data Analyses

The coordinates of each primate encounter was noted using GPS Tracks 4.1.9. From this data, the home range of each species within FLP was constructed with kernel density estimates using the Density Analysis plug-in with QGIS 3.32.1. Kernel density estimates employ space-use data to construct a heatmap that visualizes the probability that given areas will be utilized by the species, group, or individual in question (Worton 1989). Kernel densities using 85 m probability bandwidth were constructed for each of the primate species encountered over the course of this study. Minimum convex hulls were also constructed for each species encountered based on encounter coordinates (Souza-Alves et al. 2021, Scary 2013). This method of home range estimation has been criticized recently, as some studies suggest that it overestimates the area used by species. This bias is most pronounced when using convex hull estimates for intraspecific comparison of home range, and when especially large datasets were used (Nilsen et al. 2008). Because home range is only compared between species and the pool of data is relatively sparse, this was considered to be an acceptable source of error in the present study.

Activity budgets compiled from activity data collected on reconnaissance walks were subjected to one-way ANOVA tests to assess if the mean proportions of time spent exhibiting selected behaviors varied between species. Regression analysis was also used to investigate the potential correlation between the amount of time spent exhibiting these behaviors and environmental variables, in this case daily average temperature and time of day. Further, activity budgets were compiled from activity data gathered from camera trap videos. These budgets were compared against activity budgets assembled from data recorded during direct observation periods via one-way ANOVA. Itch frequency outcomes for each species was also subjected to the same analysis as activity data. All ANOVA and Regression Analysis was carried out using R 4.3.1. P-values less than or equal 0.05 were considered significant.

RESULTS

The goal of the present study was to compile activity budgets of the primate species that inhabit the Finca Las Piedras Research Station, and to characterize their home range and densities therein. Data was collected via reconnaissance walking surveys along preexisting trails that traverse the site's primary terra firme forest. Surveys were conducted between October 2nd and November 2nd, 2023, resulting in 59.25 cumulative survey hours. Henceforth, the term "observation" refers only to instances in which activity data was collected on a primate group, and "encounter" refers to any instance (including observation periods) in which a reliable estimate of location could be made by either auditory or visual perception of a primate group.

44 primate encounters of four species were recorded over the course of this study. Across 23 observation periods, a total of 254.38 contact minutes (4.24 contact hours) of activity data were documented between the four primate species: brown titi monkey (Plecturocebus brunneus), Large-headed capuchin (Sapajus apella macrocephalus), Black-capped squirrel monkey (Saimiri boliviensis), and brown-mantled tamarin (Leontocebus fuscicollis).

Home Range Analysis

Brown titi monkey (Plecturocebus brunneus).

The brown titi monkey (referred to as PLBR) was encountered 16 times over the

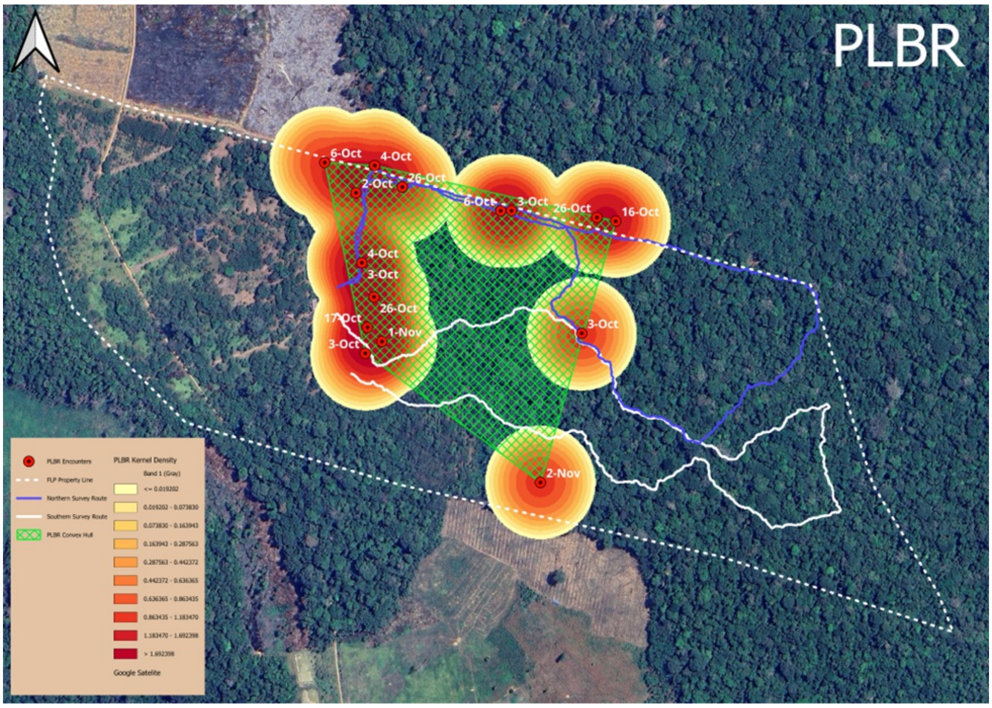

Figure 1. Map of PLBR Homerange: Heatmap and Convex Hull. Kernel density heatmap calculated using 85 m probability radius from encounter points. Heatmap locations with darkest colors indicate the highest probability of use by PLBR. The minimum convex hull calculated from 16 encounter coordinates had an area of 12.339 ha.

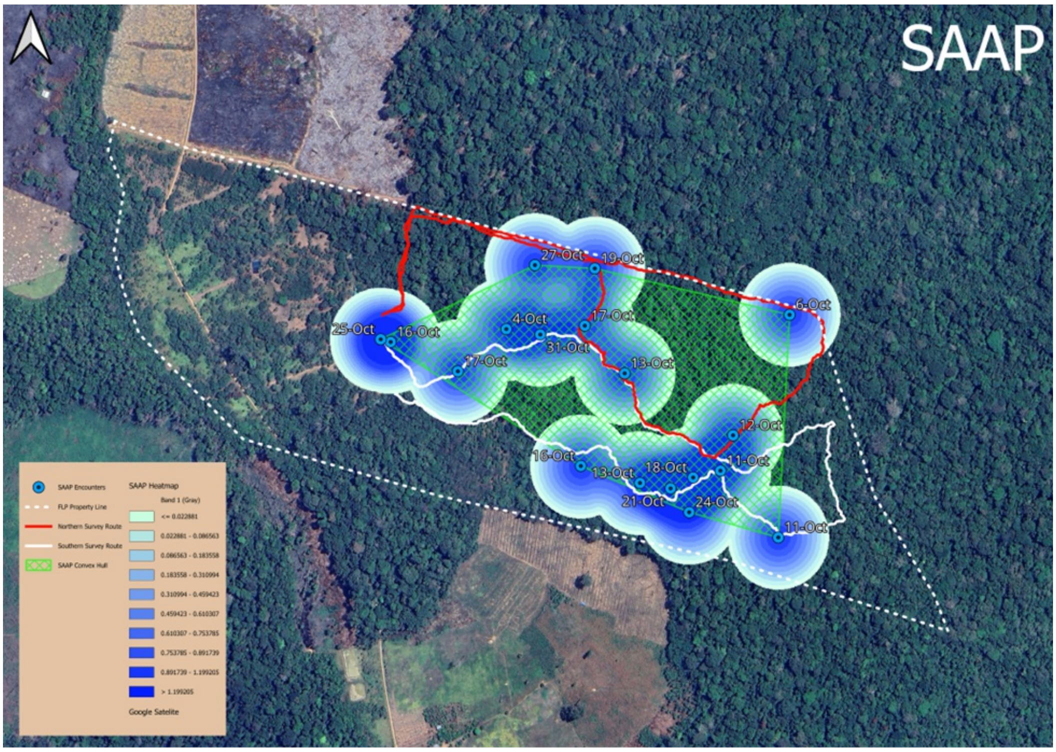

Figure 2. Map of SAAP Homerange: Heatmap and Minimum Convex Hull. Kernel density heatmap calculated using 85 m probability radius from encounter points. Heatmap locations with darkest colors indicate the highest probability of use by SAAP. The minimum convex hull calculated from 19 encounter coordinates had an area of 17.468 ha.

course of this study. The majority of observations of this species were made via sound, as this species' characteristic vocalizations were easily followed by the observer in order to estimate the group's location. The average size of PLBR groups encountered was 2.60 individuals. The minimum convex hull constructed from encounter points spanned 12.339 ha. PLBR were densely concentrated in the corner nearest to the recently-cleared tract of what used to be primary forest, and appeared to avoid the property's Eastern sect, especially the Southeastern portion. PLBR groups were encountered in high canopy positions in 40% of observations, and low canopy positions in 60% of observations. Figure 1 visualizes the minimum convex hull and kernel density heatmap for PLBR based on GPS coordinate entries.

Large-headed capuchin (Sapajus apella macrocephalus).

The large-headed capuchin (referred to as SAAP) was encountered 19 times over the course of this study. Both sight and sound were useful in observing this species, as their large size made them relatively easier to spot high in the canopy and caused branches to break frequently when SAAP moved along them. The average size of SAAP groups encountered was 5.30 individuals. The minimum convex hull constructed using encounter points was found to be 17.468 ha, the largest of the four species whose home ranges were compared. SAAP were found to inhabit nearly the entire tract of primary forest on which FLP sits, but with preference shown for the forest's center, Southeastern corner, and Western edge that borders FLP's base camp, according to kernel densities. SAAP groups were encountered in high canopy positions in 50% of observations, low canopy positions in 41.7% of observations, and terrestrially in 8.3% of observations. Figure 2 visualizes the minimum convex hull and kernel density heatmap for PLBR based on GPS coordinate entries.

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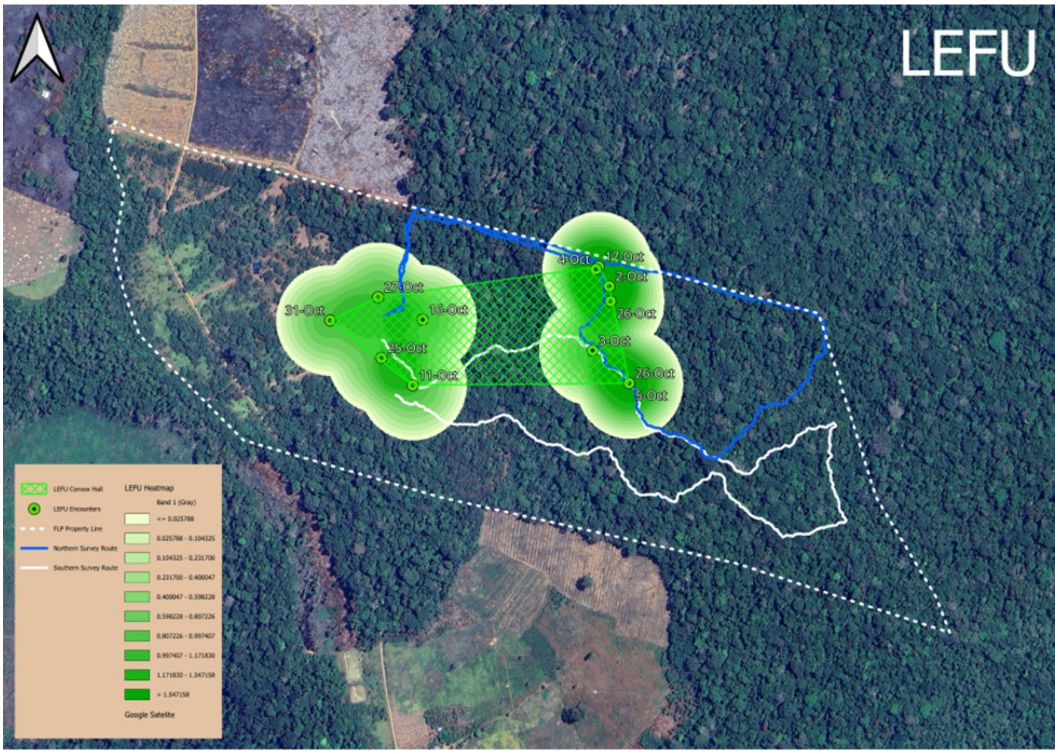

Figure 3. Map of LEFU Homerange: Heatmap and Minimum Convex Hull. Kernel density heatmap calculated using 85 m probability radius from encounter points. Heatmap locations with darkest colors indicate the highest probability of use by LEFU. The minimum convex hull calculated from 12 encounter coordinates had an area of 6.814 ha.

Brown-mantled tamarin (Leontocebus fuscicollis).

The brown-mantled tamarin (referred to as LEFU) was encountered 12 times over the course of this study. As the smallest primate observed onsite, its tendency to inhabit low canopy positions was useful locating this species. The minimum convex hull constructed from encounter points was found to be 6.814 ha. The average size of LEFU groups encountered was 4.71 The heatmap returned for LEFU appears to show two highly disjoint distributions; one that spans the North-central portion of FLP's primary forest and another that is characterized by secondary forest to the West of the primary forest's edge. LEFU groups were encountered in high canopy positions in 12.5% of observations, low canopy positions in 62.5% of observations, and terrestrially in 25% of observations. Figure 3 visualizes the minimum convex hull and kernel density heatmap for PLBR based on GPS coordinate entries.

Black-capped squirrel monkey (Saimiri boliviensis).

The black-capped squirrel monkey (referred to as SABO) was observed only 5 times over the course of this study. The minimum convex hull constructed from encounter points was found to be 2.128 ha. The average size of SABO groups encountered was 5.0 individuals, though the misleading nature of this value is explained in this study's discussion. The convex hull and heatmap produced from encounter data on this species demonstrate an apparent preference for the Southeastern quadrant of the site's primary forest. Though, the scarcity of data that could be collected on this species is likely to impart bias on this result. Figure 4 visualizes the minimum convex hull and kernel density heatmap for SABO based on GPS coordinate entries. SABO groups were only observed in low

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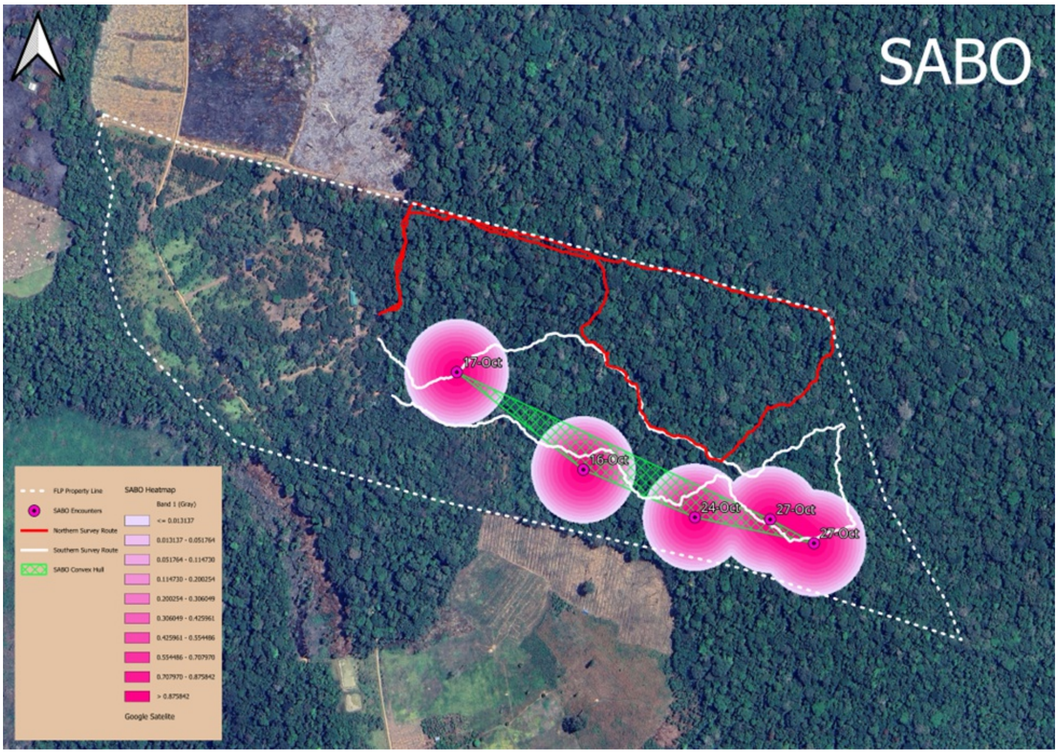

Figure 4. Map of SABO Homerange: Heatmap and Minimum Convex Hull. Kernel density heatmap calculated using 85 m probability radius from encounter points. Heatmap locations with darkest colors indicate the highest probability of use by SABO. The minimum convex hull calculated from 5 encounter coordinates had an area of 2.128

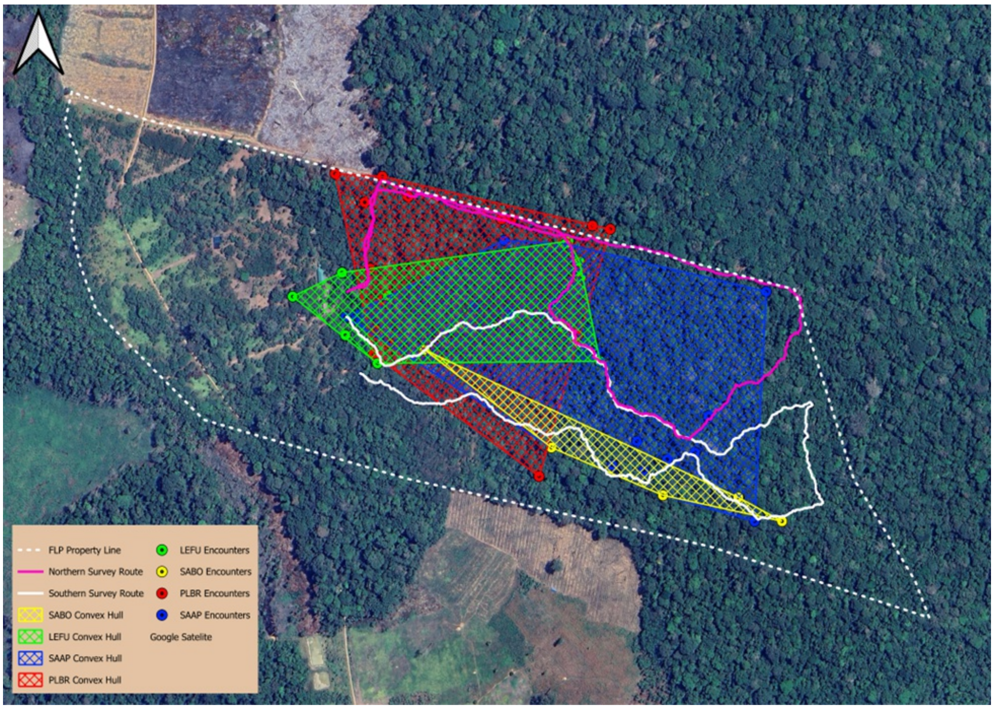

Figure 5. Interspecific Overlap of Home Ranges Based on Minimum Convex Hulls. Map of all primate home ranges within FLP according to minimum convex hull calculations. This map demonstrates the overlap in range between these species, indicating high primate density and interspecific overlap near basecamp within a few hundred meters of the primary forest's Western edge.

canopy positions. Figure 5 demonstrates the overlap of home ranges between primate species according to minimum convex hull estimates.

Activity Budgets

Behavioral data was gathered over 23 total observation periods that occurred during reconnaissance surveys. A total of 254.38 contact minutes (4.24 contact hours) of behavioral data were recorded on the four primate species (LEFU: N=7, 91.6 min. SAAP: N=10, 124.35 min. PLBR: N=5, 34.783 min. SABO: N=1, 3.65 min). This data was utilized to compile activity budgets for each of these species individually to assess if the proportions of time spent on select behaviors varied significantly between groups. Summaries of the activity budgets compiled for each species can be found in Table 2 and Figure 6. The proportions of time spent on the selected behaviors were not found to vary significantly between groups (One-way ANOVA: Socializing; F=0.577, p-value=0.673, Moving; F= 0.806, p-value=0.506, Resting; F= 2.696, p-value=0.113, Consumptive Behavior; F=1.189, p-value=0.341, Miscellaneous; F=0.806, p-value=0.506). Data was also collected on the frequency of itching behavior, reported as the parameter scratch-seconds min-1 (ss m-1), to investigate the relative levels of stress exhibited by focal individuals during observation periods. The mean frequency of itching (µss m-1) was not found to vary significantly between species (LEFU; µss m-1=2.986, SAAP; µss m-1=1.525, PLBR; µss m-1=0.2880, SABO; µss m-1= 1.909. One-way ANOVA: F=0.876, p-value=0.357).

Behavior	LEFU	PLBR	SAAP	SABO
Consumptive Behavior	0.1435	0.1901	0.3098	0.0812
Miscellaneous	0	0	0.0034	0
Moving	0.2739	0.2463	0.3594	0.45
Resting	0.5601	0.5636	0.3090	0.4688
Socializing	0.0224	0	0.0181	0

Table 2. Activity Budget Decimal Values for Each Species. Table of all values that compose the activity budget of each species of primate for which behavioral data was collected. Reported values represent the proportion of time the species spent on each of the corresponding behaviors on average across individual observation periods.

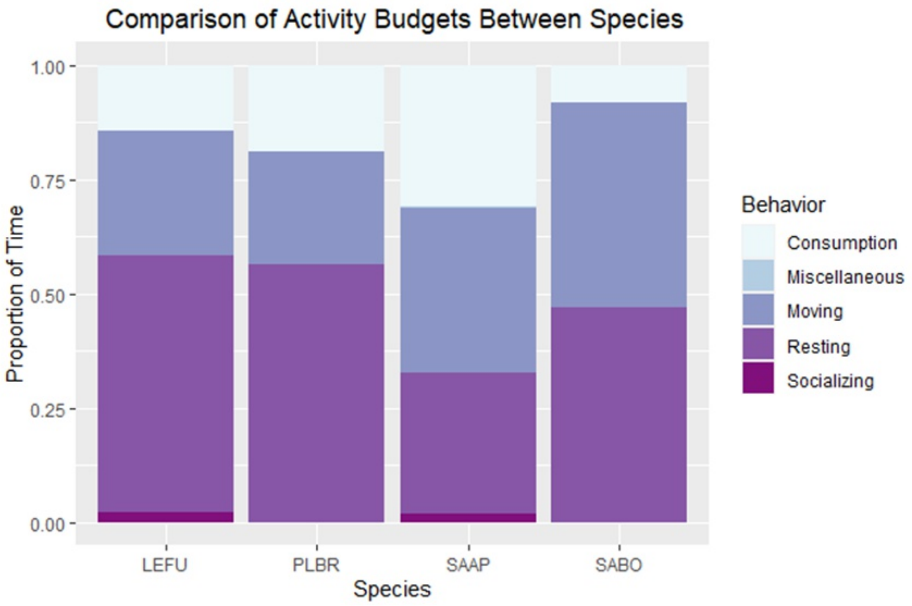

Figure 6. Comparison of Activity Budgets Between Species. Visualizes the average proportions of time each species spent exhibiting select behaviors over the course of observation periods. Activity budgets were not found to be significantly different between species (One-way ANOVA: Socializing; F=0.577, p-value=0.673, Moving; F= 0.806, p-value=0.506, Resting; F= 2.696, p-value=0.113, Consumptive Behavior; F=1.189, p-value=0.341, Miscellaneous; F=0.806, p-value=0.506).

Regression analysis was also carried out on activity data (including itch frequency) pooled between species to investigate whether a significant correlation exists between the proportions of time spent on these activities and environmental variables; in this case, average temperature and time of day. Analysis of activity data and its relationship with the average temperature did not indicate any significant correlation between these two parameters (Regression: Socializing; R2= 0.0064, T=0.135 , p-value=0.717, Resting; R2=2.01e-5, T=4.22e-4, p-value=0.984, Moving; R2=0.0074, T=0.157, p-value=0.696, Consumptive Behavior; R2=0.0079, T=0.1683, p-value=0.686, Miscellaneous; R2=0.0019, T=0.004, p-value=0.842, Itch Freq.; R2=0.0085, T=0.181, p-value=0.675). The regression analysis of activity data against the time of day at which data was recorded returned largely the same insignificant values (Regression: Socializing; R2= 0.0066, T=0.140 , p-value=0.712, Resting; R2=0.1106, T=2.61, p-value=0.121, Moving; R2=, T=0.0277, p-value=0.870, Miscellaneous; R2=0.0572, T=1.275, p-value=0.272, Itch Freq; R2=0.1209, T=2.888, p-value=0.104), but did demonstrate a significant relationship between the time of day and the proportion of time spent feeding and/or foraging (Regression: Consumptive Behavior; R2=0.1902, T=4.931, p-value=0.0375).

Camera Traps

Four camera traps were placed off trail within the primary forest, particularly along diagonally-felled trees or liana nexuses that could act as go-betweens between arboreal and terrestrial environments. The primary purpose of utilizing camera traps was to supplement activity data gathered directly on reconnaissance walks with activity data that could be recorded without an observer present. Camera traps captured seven primate encounters totalling 12.05 indirect contact minutes. During the transfer of files from traps, at least four videos containing primate footage were corrupted and could not be used when compiling activity budgets. Three primate species were captured on video, including the white-fronted capuchin (Cebus albifrons) which prior to trap collection had not been confidently observed in this study. Figure 7 shows still images of camera trap footage on each of the three species captured on video.

Activity data from video observations of LEFU (N=4, 9.483 min) and SAAP (N=2, 1.85 min) was used to create activity

Figure 7. Still Images of Camera Trap Footage. From left to right; brown-mantled tamarin (Leontocebus fuscicollis, LEFU) exhibiting social behavior (allogrooming), white-fronted capuchin (Cebus albifrons) consuming an insect held in its right hand, and large-headed capuchin (Sapajus apella macrocephalus, SAAP) resting as it scans the canopy above.

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Behavior	LEFU (Camera)	LEFU (Sight)	SAAP (Camera)	SAAP (Sight)
Consumptive Behavior	0.2828	0.1435	0.25	0.3098
Miscellaneous	0	0	0	0.0034
Moving	0.0856	0.2739	0.1074	0.3594
Resting	0.5646	0.5601	0.6425	0.3090
Socializing	0.0670	0.0224	0	0.0181

Table 3. Activity Budget Decimal Values for Comparison Between Modes of Observation. Values correspond to the average proportions of time spent by LEFU and SAAP on select activities during observation periods in which data was gathered by direct or indirect means. Species and mode of observation are denoted along the top row.

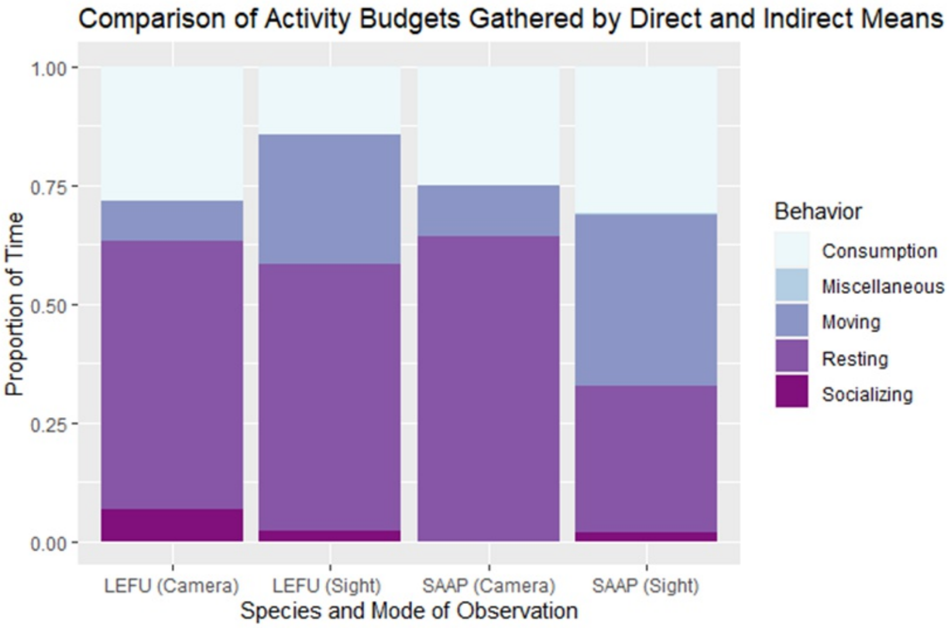

Figure 8. Comparison of Activity Budgets Gather by Direct and Indirect Means. Stacked bar chart comparing the average proportions of time spent by LEFU and SAAP on select activities during observation periods in which data was gathered by direct or indirect means.

budgets for indirectly observed primates, and were compared against activity budgets gathered via direct observation. Data for this analysis was pooled across species. Variation in activity between primates observed directly and indirectly was largely insignificant (One-way ANOVA: Socializing; F=0.999, p-value=0.673, Resting; F=0.263, p-value=0.612, Moving; F=10.92, p-value=0.0026, Consumptive Behavior; F=1.687, p-value=0.205, Miscellaneous; F=0.621, p-value=0.437), but ANOVA analysis indicated that a significant difference in the proportion of time spent moving between these two groups (One-way ANOVA: Moving; F=10.92, p-value=0.0026). The mean frequency of itching behavior was not found to vary between modes of observation (LEFU (Sight); μss m-1=2.986, SAAP (Sight); μss m-1=1.525, LEFU (Camera); μss m-1=0.7154, SAAP (Camera); μss m-1= 1.741. One-way ANOVA: Itch Freq; F=0.876, p-value=0.357). Table 3 and Figure 8 summarize the comparison between activity budgets compiled on

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LEFU and SAAP using data gathered via direct (sight) and indirect (camera) methods.

DISCUSSION

Over the course of this study, five species of primate were observed via direct or indirect methods; brown titi monkey (Plecturocebus brunneus), Large-headed capuchin (Sapajus apella macrocephalus), Black-capped squirrel monkey (Saimiri boliviensis), brown-mantled tamarin (Leontocebus fuscicollis), and white-fronted capuchin (Cebus apella). Neither reconnaissance walks nor review of trap footage provided evidence of the black-headed night monkey (Aotus nigriceps) or red howler monkey (Alouatta seniculus), both of which have been documented as inhabitants of this site. Despite this, multiple eye-witness accounts from site residents suggest these species are present on site, placing them in both the primary forest (black-headed night monkeys) and palm swamp (black-headed night monkeys and red howler monkeys). The fact that only the primary forest was surveyed to investigate the richness and home range of primates at FLP is a likely explanation for these species being missing from the record of species gathered during this study. Increasing the survey area to include habitat outside of the primary forest presents an avenue for expanding the present study to increase its breadth and improve its ability to collect a comprehensive primate faunal record of FLP.

The minimum convex hulls of SAAP, LEFU, and PLBR demonstrated a high degree of overlap between the Western edge and the center of the site's primary forest. Sharing such a large portion of home range (LEFU: ≈100%, PLBR: >40%) would suggest a significant degree of resource and niche partitioning occurs between these three species. Past studies have shown that resource partitioning among cohabiting primates is accomplished by utilizing distinct plant food sources, foraging in exclusive canopy positions, and sourcing arthropod prey from distinct substrates (Singh et al. 2011). This study did record noticeable variation in the canopy positions these three species utilized, though no reliable claims can be made in regards to the significance of these differences. Both SAAP and Cebus albifrons were encountered individually in mixed troops formed with SABO, indicating a notable degree of overlap between the ranges of these species as well. This association, specifically between capuchins and squirrel monkeys, is a well-documented phenomenon. The formation of interspecific associations such as this is hypothesized to improve foraging efficiency of its constituent members while also decreasing their predation risk (Daoudi-Simison 2020).

Results from home range analysis did demonstrate that notable variation exists within the home range sizes of distinct species, but did not support the prediction that home ranges would vary according to similar trends established by prior studies. Home range calculations of SAAP and SABO compiled in this study vary greatly from literature values (C. Gómez-Posada et al. 2019, Emmons & Feer, 1997, Pinheiro et al. 2013, Carretero-Pinzón et al. 2016). It is almost certain that the ranges of these species extend outside of FLP, likely to its Northeast and Southeast where the extremes of these ranges lie and where the most contiguous tracts of primary forest persist beyond the property's borders. The great variability in LEFU home range estimates among past studies make it difficult to draw conclusions about the accuracy of this study's home range estimate for LEFU (Yoneda 1981, Nymark 2023). If the convex hull does in fact encompass the entirety of this species's range within FLP,

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it is likely that the LEFU present at FLP represent only a smaller subgroup of a larger population whose range expands to the site's North. It should be noted that this habitat is under direct threat from neighboring landowners who wish to clear this forested area for agricultural use. PLBR minimum convex hull within FLP most closely approaches literature values for this species' home range compared to other species discussed in this study (Van Belle et al. 2021, Kulp & Heymann 2015). The counter-calling behavior that was often exhibited by PLBR during reconnaissance walks indicates that multiple PLBR groups inhabit this site (Van Belle et al. 2021). Thus, it is likely that the home range calculated for PLBR represents the summed home ranges of at least two distinct groups of this species.

The prediction that primate activity budgets would vary significantly between species was not supported by one-way ANOVA analysis of activity data (One-way ANOVA: Socializing; F=0.577, p-value=0.673, Moving; F= 0.806, p-value=0.506, Resting; F= 2.696, p-value=0.113, Consumptive Behavior; F=1.189, p-value=0.341, Miscellaneous; F=0.806, p-value=0.506). At first glance of the summaries of activity data from direct observation, a few obvious problems are apparent. Firstly, neither PLBR nor SABO were observed exhibiting social behavior. Both of these species are highly social, as PLBR are socially monogamous and pair-bond for life with their partner (Adret et al. 2018), and SABO form troops composed of more than 200 individuals (Izawa 1976). These massive assemblies were encountered on reconnaissance walks, but the only time a reliable count could be made was during the observation period of a five-individual group, hence the misleading nature of this species' mena group size reported earlier. The absence of direct social interaction with conspecifics in these species activity records is likely the result of a sampling error, as these groups were the two least observed species (PLBR: N=5, 34.783 min. SABO: N=1, 3.65 min). Observer presence is likely a larger stressor to these groups relative to SAAP and LEFU, and thus discourage more "comfortable" behaviors such as allogrooming or sexual displays that could increase their exposure to predation (i.e. by the threat posed by the unfamiliar observer) (Wasserman et al. 2018, Cords 1995). This could be a larger explanation for the limited degree of socializing across all species documented in this study.

In general, the brevity of this study introduced a notable degree of bias in the results and limited the potential for significance. This is especially true in regards to the activity budgets compiled for each primate species. Brief observation periods frequently lacked (or recorded uncharacteristically brief windows of) one or more common behaviors (most often consumptive behavior and/or resting). The resultant data, distributed more widely than may be the case in long-term studies, was inherently accompanied by larger standard error values that diminished the possibility of returning significant differences between groups. Harrison 2009, in a comparison of methods for collecting activity budgets from orangutans, suggests focal animals studies should define a minimum follow duration, and should only utilize data gathered on surveys that satisfy this criteria for analyses. The results of this report lend support to this design recommendation. As mentioned in the methods of this study, maximizing data collection was a priority given the truncated collection window, and for this reason all activity data was subjected to analysis.

Another limit to this study was that the primates being surveyed were unhabituated.

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Habituated groups are highly preferred to those less familiar with human presence in studies that focus on characterizing home range or compile activity budgets of primates (Matsuda et al. 2009, Back et al. 2009, Van Doorn et al. 2010, Kulp & Heymann 2015, Souza-Alves et al. 2021, Van Belle et al. 2020). Attempting to collect data on unhabituated groups proved difficult; promising observation periods frequently turned into fleeting encounters as the groups fled quickly from sight upon perception of the observer's presence. This scenario was especially common with PLBR, evident in its 16 encounters accompanied by only 5 observation periods. Again, the duration of this study imposed more limitations here, as habituation of these groups was not feasible within the project's time frame. Developing a reciprocal familiarity between human observers and this site's primate populations, as well as their constituent subgroups, would have been of great use in this study. Not only would habituation have improved both the quality and volume of activity data collected (Williamson & Feistner 2010), but knowledge of group dynamics within species would have better informed the interpretation of home range estimates. This would be especially useful in the case of LEFU, whose kernel density estimate returned two disjoint distributions, and PLBR, whose population is known to be divided into multiple groups.

The use of camera traps in this study was intended to supplement activity data gathered by direct observation and to expand the number of species documented within FLP. The quantity of camera traps at the disposal of researchers and inability to use traps in the high canopy due to equipment and training constraints limited this study's potential to conduct a more robust primate inventory. Past studies have been successful in their use of camera traps to expand the known range of primates (Fang et al. 2020) and increase estimates of primate diversity (Pebsworth & LaFleur 2014). Had the application of camera trapping been expanded in this study, a more precise picture of the ranges of these primates, as well as the breadth of species that this site supports, could have been painted. This represents another opportunity for the expansion of this work, especially considering the success of these traps within a relatively short frame of time and in suboptimal positions.

The comparison of activity budgets compiled with directly and indirectly-gathered data presented similar issues to the between-species comparison of directly-gathered data. SAAP was never observed to exhibit social behavior on camera trap footage despite this species' social propensity and large group size (MAXGroup Size=12, μGroup Size= 5.3) documented in this study. Considering less than 2 minutes of activity data could be gathered on SAAP using camera trap footage, this is again likely due to sampling error that would be reduced by a longer study period, the use of more camera traps, and refined camera placement in distinct canopy environments to increase capture frequency. Moreover, the nature of the comparisons being made between these methods of observation come with their own inherent flaws. Most notably, the comparison between time spent moving using a field of view that is statically fixed (in the form of a camera) and one possessing a dynamic pivot (observer's neck). The only significant output from ANOVA analysis between these groups was the proportion of time spent moving (One-way ANOVA: Moving; F=10.92, p-value=0.0026) . This outcome makes sense, as a moving individual could not be tracked for more than a few seconds after displacement began given the limits of

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camera trapping. It is evident that camera trapping is not an effective tool for a comparison of this nature, but its potential to document other, more sedentary behavior states remains.

The parameter scratch-seconds min-1 and analysis of itch frequency presents a particularly intriguing and, to date, novel application of camera traps in the study of wild primate populations. Studies on scratching behavior among primates have been conducted using video footage from captive enclosures (Whitehouse et al. 2016) or employ cameras opportunistically during follows in the wild (Fröhlich et al 2019, Pika & Mitani 2009). Using camera traps for this nature of study presents an opportunity to record such behaviors among wild primates in the absence of human presence, which neither aforementioned method can accomplish on its own. The influence of human presence on animal behavior is of great concern among behavioral and ecological studies (Souza-Alves et al. 2010) for the potential bias it imparts on data and the ethical concerns that arise with habituation (Goldsmith 2005). Assessing the frequency of itching (as a result of stress that human observers exert on wild primates, habituated or not) between directly and indirectly observed primate groups provides an ideal means of utilizing this technology in comparative behavioral studies. Differences in these values within this study were found to be insignificant (One-way ANOVA: Itch Freq; F=0.876, p-value=0.357), though robust studies on this subject may arrive at different conclusions with larger data pools and more refined methods. Evidence of reduced vigilance, likely resulting from the absence of a predatory threat, in the form of extensive allogrooming (Cords 1995) was observed in LEFU on camera footage. In a single indirect observation period, there were nearly as many bouts of allogrooming (N=5) as were recorded over the entirety of this study (N=6) via direct methods. This speaks to a possible disparity in primate behavior that is dependent on the mode of observation, despite contrary analysis outputs.

Though this study's shortcomings are evident, its results are nevertheless informative. Targeted camera trapping of arboreal mammals in near-terrestrial environments proved effective, and guidance on improving this methodology is provided. Means to expand behavioral studies on primate stress to include camera traps in novel manners is proposed. Though preliminary, home range estimates of cohabiting primate species were documented and direction for future efforts to further similar work in this area is suggested. A high degree of overlap between resident primate species suggests notable resource partitioning between species, which provides a basis for future studies at FLP on this topic. The present study provides a foundation for a number of projects that could continue its work via more focused, refined methodology in hopes of resolving the questions that arose in its composition and remain yet unanswered.

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