

## UNIVERSIDADE ESTADUAL PAULISTA "JÚLIO DE MESQUITA FILHO" INSTITUTO DE BIOCIÊNCIAS – RIO CLARO



## PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

# PADRÕES DE MOVIMENTAÇÃO DE MICOS-LEÕES PRETOS (*Leontopithecus chrysopygus*) EM UM FRAGMENTO DE MATA ATLÂNTICA NO INTERIOR DO ESTADO DE SÃO PAULO, BRASIL

FELIPE SOARES BUFALO

Dissertação apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Mestre em Ciências Biológicas (Zoologia).

Orientadora: Prof<sup>a</sup>. Dr<sup>a</sup>. Laurence Marianne Vincianne Culot

Rio Claro - SP 2020 FELIPE SOARES BUFALO

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## CERTIFICADO DE APROVAÇÃO

TÍTULO DA DISSERTAÇÃO: PADRÕES DE MOVIMENTAÇÃO DE MICOS-LEÕES PRETOS (Leontopithecus chrysopygus) EM UM FRAGMENTO DE MATA ATLÂNTICA NO INTERIOR DO ESTADO DE SÃO PAULO, BRASIL

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#### RESUMO

Primatas executam diariamente uma série de decisões acerca de quando, para onde e por que se mover. No entanto, pouco sabemos sobre quais são os fatores mais influentes no processo de decisão em primatas e, portanto, responsáveis por moldar rotas diárias, principalmente em pequenos fragmentos. Neste estudo buscamos entender quais aspectos sociais e ambientais influenciaram o processo de planejamento de rotas do frugívoro-insetívoro mico-leão-preto (BLT) em um remanescente de Mata Atlântica de 100 ha. Previmos que os locais de frugivoria seriam o principal fator para o direcionamento de rotas. Ainda, esperávamos que os limites físicos da área fossem fatores importantes para a condução de rotas diárias. Seguimos um grupo de BLT por 42 dias completos entre março e agosto de 2019, totalizando 379,9 horas de observação. Registramos a localização e os comportamentos do grupo através de amostragens de varredura a cada cinco minutos, bem como todos os eventos de alimentação, long calls e encontros entre grupos. Determinamos a distribuição espacial das espécies de frutos e dos locais de frugivoria usados mensalmente através de índices de agregação R, além das distâncias médias entre os indivíduos de cada espécie. Também determinamos, para cada mês, as distâncias médias entre locais aleatórios dentro da área utilizada e locais de frugivoria (empty space distances). Dividimos a área utilizada entre fronteira do território, área central e borda do fragmento e comparamos o uso entre elas. Aplicando o change point test em rotas diárias, identificamos os locais de mudanças significativa de direção, ou change points (CPs), e avaliamos o comportamento grupal associado a cada CP. O grupo utilizou uma área de 46,8 hectares e se deslocou, em média, 1773 m (± 461 m) por dia. Frugivoria e locomoção foram os comportamentos mais frequentes (29,9% e 29,8% das varreduras, respectivamente), seguidos de forrageio com 25,3%. Os encontros entre grupos ocorreram em um a cada 4 dias. Espécies de frutos apresentaram distribuições agrupadas, embora a distância média entre locais de frugivoria seja de 33,4 m (± 22,8 m). Os frutos consumidos com maior frequência corresponderam a plantas densamente distribuídas na área e disponíveis durante a maior parte do estudo, acessíveis, portanto, a curtas distâncias, independentemente do mês e do local. Encontramos um total de 55 CPs. Locomoção foi o comportamento mais frequente associado a CPs (34,54%), seguido de forrageio (25,45%) e frugivoria (12,7%). Embora a variação entre medianas não tenha sido significativa (p = 0,756), encontramos uma maior proporção diária de CPs na fronteira do território (0,021 ± DP 0,05 CPs / pontos de localização), seguida pela borda do fragmento (0,018 ± DP 0,03) e área central (0,008  $\pm$  DP 0,01). Nossos resultados indicam que, embora os frutos representem um item importante na dieta de BLTs, locais de frugivoria não parecem direcionar as rotas no fragmento estudado. Por outro lado, estar em um fragmento impõe limites estruturais e possível maior competição intraespecífica, responsáveis por obrigar mudanças de direção e consequentemente explicar maior densidade de CPs próximos às bordas (borda do fragmento e fronteira do território). Em conclusão, enquanto estudos anteriores em áreas maiores apontam locais de alimentação como o principal fator direcionando as trajetórias de primatas, nosso estudo sugere que o processo de planejamento de rotas pode depender do contexto.

#### Palavras chave: Leontopithecus chrysopygus, ecologia do movimento, change point test

#### ABSTRACT

In a daily basis, primates execute a wide variety of decisions concerning what, when and where to move. However, our knowledge about what are the most important factors influencing primates' decision processes and, therefore, shaping daily routes, is still insufficient, particularly in small forest fragments. Here we intended to understand what social and environmental aspects influenced the frugivorousinsectivorous black lion tamarins' (BLT) daily route planning process in a 100-ha Atlantic Forest remnant. We predicted that fruit feeding sites would be the principal factor driving daily routes. Also, we expected physical limits of the area to be important factors for route directing. We followed a group of BLT for 42 full days between March and August 2019, totaling 379.9 observation hours. We recorded the GPS location and group behaviors through scan sampling every five minutes, as well as all observed feeding events, long calls, and intergroup encounters. We determined the spatial distribution of fruit species and fruit feeding sites used monthly using the aggregation indexes R, and estimated the mean distances between fruit species' individuals. We also determined the mean distances that BLT should travel from random locations within the home range (i.e., the empty space distances) to reach a fruit feeding site each month. We divided the home range into territory border, central area and fragment edge and tested whether BLT preferred one of these zones. On each daily route, we identified the locations of significant direction changes, called change points (CPs), using the Change Point Test and assessed the group behavior associated to each CP. The group used an area of 46.8 hectares and traveled, on average, 1773 m (± 461 m) daily. Frugivory and locomotion were the most frequent behaviors (29.9% and 29.8% of the scans, respectively), followed by foraging with 25.3% of the scans. Intergroup encounters occurred one every 4 days. Fruit species presented clumped distributions (R < 0), although fruit spots were located, on average, every 33.4 m ( $\pm$  SD 22.8 m). Most frequently consumed fruit resources were plants densely distributed in the area and available during most of the study period, therefore accessible within relatively short distances whatever the moment of the year and the place. We found a total of 55 CPs. Locomotion was the most frequent behavior associated to CPs (34.54%), followed by foraging (25.45%), and frugivory (12.7%). Although the variance of the median was not significant (p = 0.756), we found a higher mean daily proportion of CPs at the territory border (0.021 ± SD 0.05 CPs/location points), followed by fragment edge (0.018 ± SD 0.03) and central area (0.008 ± SD 0.01). Our results indicate that, although fruits represent an important item in BLT's diet, fruit feeding sites did not seem to drive BLT's trajectories in the studied fragment. In contrast, being in a fragment imposes structural limits and a possibly higher intra-specific competition. When arriving to these limits, there are no other options than to change directions, which can explain the higher density of CPs close to borders (fragment edge and frontier with other group's home range). In conclusion, while previous studies in larger areas usually point fixed feeding sites as the main factor shaping primates' trajectories, our study suggests that the route planning process might be context-dependent.

#### Keywords: Leontopithecus chrysopygus, movement ecology, change point test

# SUMMARY

1	INTRODUCTION	9
2	METHODS	11
2.1	Study area	11
2.2	Data collection	12
2.3	Data analysis	13
3	RESULTS	14
4	DISCUSSION	
5	CONCLUSION	
	REFERENCES	

#### 1 INTRODUCTION

Primates, when compared to other groups of mammals, stand out for having significantly larger brains, being consequently known for their great cognitive abilities and capacity to solve various types of problems (CLUTTON-BROCK e HARVEY, 1980; TOMASELLO e CALL, 1997; DUNBAR, 2000; SHETTLEWORTH, 2010). In a daily basis, besides performing complex social interactions within and among groups, primates execute a wide variety of decisions concerning territory defense, predator avoidance and where, when and what to feed on. Such decisions are known to influence primates' daily trajectories around their home ranges (TRAPANESE *et al.*, 2018). However, our knowledge about what are the most important factors influencing primates' decision processes and, therefore, shaping daily routes, is still scarce (HOLYOAK *et al.*, 2008; NATHAN *et al.*, 2008; TRAPANESE *et al.*, 2018), particularly in altered areas, such as small forest fragments, whose own limits or structural changes at forest edges can represent important factors for route directing (NOSER e BYRNE, 2014).

Primates' ranging patterns have been investigated on several species dwelling in different kinds of environments, from savannas to tropical forests (JOHNSON et al., 2015; REYNA-HURTADO et al., 2017; TRAPANESE et al., 2018). Among the most important factors discussed in the literature, the availability and distribution of feeding resources have been identified as key drivers of movement for several primate species (SHETTLEWORTH et al., 1988; GARBER, 1989; BOYER et al., 2006; JANSON, 2016; REYNA-HURTADO et al., 2017), also influencing grouping patterns between individuals, size of home ranges and distances traveled daily (BOYER et al., 2006; RAMOS-FERNÁNDEZ et al., 2006; ALBERT et al., 2013; JOHNSON et al., 2015). Nonetheless, questions such as 'what characteristics make a food spot important to the point of directing a route' or 'what criteria do primates use to choose between available fruit species' are still little explored. Moreover, in wild complex environments, where the location of feeding resources may be relatively unpredictable, navigating between available out of sight resources while avoiding predators and patrolling the area for the presence of competitors can be cognitively demanding (GARBER et al., 2009; MERKLE et al., 2014). Therefore, as a strategy to reduce cognitive costs of foraging (BERTOLANI, 2013), previous studies have suggested that some specific terrain features, or landmarks (i.e. river bodies, hills, structural changes in the vegetation, important feeding sites or territory borders), whose locations are memorized and consequently repeatedly used, are also important factors for primates' route orientation (NOSER e BYRNE, 2007; DOLINS, 2009; ASENSIO et al., 2011; GARBER e PORTER, 2014).

The interpretation of travel routes and the identification of animal preferences pose significant challenges for researchers. In order to reduce subjective results, the Change Point Test (CPT) (BYRNE *et al.*, 2009) enables statistical assessments of where and when travel decisions are made along an animal's trajectory. The CPT relies on the identification, to a predetermined margin of confidence, of points of significant direction change (CPs) on daily routes. These CPs can be interpreted as the locations at which primates direct their trajectories and when, along the day, these events occur (BYRNE *et al.*, 2009). CPs can be 1) reference points for primates (i.e. important landmarks for spatial orientation, such as hills or river bodies); 2) traveling goals (i.e. reaching a specific feeding site, fighting a conspecific group or monitoring determined regions of the home range); or 3) physical barriers

imposed by the configuration of the area, which can, in turn, also become reference points (i.e. fragment edges, river bodies, roads) (BYRNE *et al.*, 2009; NOSER e BYRNE, 2014). By identifying the factors associated to route planning in wild primates, we can better understand interspecific variations in spatial cognition; assess how environmental features influence movement; verify the existence of resources of greater importance and, consequently, understand what nutritional and morphological characteristics are being primarily selected to supply their physiological needs (CUNNINGHAM e JANSON, 2007; BAN *et al.*, 2016).

In the Neotropics, primate movement has been previously investigated mostly in continuous forests (TRAPANESE et al., 2018). The Brazilian Atlantic Forest, on the other hand, is known for presenting a high degree of fragmentation due to lasting human activities. In fact, only 12% of its original extension is still preserved, mostly in the form of fragments smaller than 50 ha (RIBEIRO et al., 2009; JORGE et al., 2013). Small forest fragments are known for presenting higher abundances of successional tree species and a reduction not only of canopy size, but also of both large fruiting tree density and diversity (ARROYO-RODRÍGUEZ e MANDUJANO, 2006; LAURANCE et al., 2006). Changes in plant species composition due to fragmentation processes are known to induce primate species to rely less on native fruit species consumption and, consequently, compensate the acquisition of daily calories with the ingestion of other food items (TUTIN, 1999; IRWIN, 2007; CHAVES et al., 2012; DE LUNA et al., 2017; BICCA-MARQUES et al., 2020; DONATI et al., 2020). Moreover, diversity and distribution of feeding resources are directly linked to primates' movement. There is a strong tendency for primates to travel long distances daily and visit a higher number of species in areas with high resource diversity sparsely distributed (RAMOS-FERNÁNDEZ et al., 2004; REYNA-HURTADO et al., 2017), while low resource diversity and dense homogeneous distribution across the area may induce primates to move short distances between conspecific feeding sites daily (BOYER et al., 2006; REYNA-HURTADO et al., 2017).

It is known that more than 80% of the primate species in the Neotropics (140 out of the 171 species) are threatened somehow by human activities, most of them leading to habitat loss and fragmentation (ESTRADA *et al.*, 2017). In the Atlantic Forest, there are 26 primate species, of which 19 are endemic and most are restricted to small forest fragments (CULOT *et al.*, 2018). Among the primate species threatened by habitat fragmentation, the black lion tamarin (BLT) (*Leontopithecus chrysopygus*), endemic to the state of Sao Paulo, draws attention. Besides its largest wild population at Morro do Diabo State Park, and the recent described occurrence at the Carlos Botelho State Park (RODRIGUES *et al.*, 2016), the species is mostly distributed in small fragments and riparian forests along the interfluve of the Tiete and Paranapanema rivers (CULOT *et al.*, 2015). Considered threatened according to the IUCN Red List of Threatened Species (REZENDE *et al.*, 2020), the BLT is a small sized primate (ranging from 550 to 575 grams), highly territorial (PERES, 1989), mostly frugivorous (ROSENBERGER e COIMBRA-FILHO, 1984), and known to travel around 2000 meters daily (VALLADARES-PADUA, 1993; KEUROGHLIAN e PASSOS, 2001).

Once we understand how different factors such as resource distribution and availability, territory defense or environmental features influence the decision-making process related to movement, it becomes possible to better predict how changes in the environment, including anthropogenic changes,

could affect the movement and, as a consequence, important ecological roles such as seed dispersal (CHAPMAN e RUSSO, 2006; RUSSO *et al.*, 2006; CÔRTES e URIARTE, 2013; HEYMANN *et al.*, 2019). In this study, we aimed to understand what aspects of the environment and the social life of BLTs are responsible for directing their daily routes in an Atlantic Forest fragment. Considering the high importance of frugivory on BLT's diet, we predicted that fruiting trees would be the principal factor shaping their trajectories. As a consequence, we predicted that the majority of the CPs would be associated to fruit feeding sites. However, considering the space limitation expected for a small (~ 100 ha) forest fragment and the high degrees of territoriality in lion tamarins, we also predicted that a large proportion of CPs would be associated to territory defense and fragment edges.

#### 2 METHODS

#### 2.1 Study area

We conducted the study in a 100-hectares private Atlantic Forest fragment in the municipality of Guareí, São Paulo. With a mean elevation of 635m, the region presents a humid subtropical climate, with hot summers and dry winters. Mean annual temperature is 20.9°C, ranging from 15°C to 29.5°C during the rainy season (October to March); and from 10.1°C to 27.1°C in the dry season (from April to September) (CEPAGRI, 2018). Rainfall in the region is characterized by an annual mean of 1233 mm, with the lowest precipitation values in July (27 mm) and the highest in January (203 mm) (CEPAGRI, 2018).

The municipality of Guareí is characterized by urban and large rural areas, among which stand out livestock activities (cattle, horse and poultry rearing), agriculture (watermelon, corn, sugarcane, soy and wheat plantations) and forestry areas. As a result, it is estimated that only 23.6% of the total area of the municipality is occupied by narrow Atlantic Forest remnants (PINTO, 2017).

Belonging to Fazenda Santo Antônio, the study site (23°25'07"S, 48°14'27"W) comprises an area of 100 ha of secondary Semi-deciduous Atlantic Forest, around which the matrix alternates between sugarcane crops, eucalyptus plantations and pasture (Figure 1). The study site is 11.2 km distant from the Angatuba Ecological Station, which houses the closest BLT population. In the study site, BLTs are the only primate species and, according to our observations, there are at least 15 individuals from 3 different groups of 5 individuals each. Also, other mammals such as collared peccarys (*Pecari tajacu*), giant anteaters (*Myrmecophaga tridactyla*), southern tamanduas (*Tamandua tetradactyla*), maned wolves (*Chrysocyon brachyurus*), tayras (*Eira barbara*), cougars (*Puma concolor*) and ocelots (*Leopardus pardalis*) have been found in the area (personal observations).



Figure 1: Land use map and location of the study site in the municipality of Guarei, Sao Paulo state. Orange lines represent trail system implemented in the area.

#### 2.2 Data collection

We followed a group of five habituated BLTs from sleeping site to sleeping site from 2 to 9 days per month between March and August 2019. We registered the daily routes by recording the group's location every five minutes with a GPS device (Garmin 64S) with a mean accuracy of 10m (± SD 1.3m) (N=720 coordinates). We characterized each spatial point according to the main activity performed by the individuals of the group. The idea was not to establish an activity budget of BLTs, but to identify how BLTs use specific areas of their home range. Therefore, using scan sampling method (ALTMANN, 1974), we recorded the main activity for the group every 5 minutes. Group activity consisted in the activity evidenced by the largest number of individuals at sight during the scan. BLTs form cohesive groups, with individuals presenting coordinated activities, rarely distancing themselves from each other (SUSSMAN e KINZEY, 1984; VALLADARES-PADUA, 1993). We categorized the activities as follow: 1) Resting or social activities = BLTs lie down with eyes closed or display associated social interactions, such as grooming or play; 2) Frugivory = group feeds on fruits; 3) Foraging = active search, handling and ingestion of animal prey; 4) Gummivory = group feeds on gum; 5) Locomotion = group travels through the home range; 6) Marking = group rapidly rubs pelvic and thoracic glands against environmental structures; 7) Fur rubbing = group rubs the body against tree trunks in order to collect balsam; 8) Encounter = BLTs display agonistic vocalizations and/or aggressions to individuals from other groups; 9) Long calls = group vocalizes characteristically, often aiming territory demarcation; 10) Idle = individuals are stationary, with eyes open, and may present vocalizations or vigilant behavior, and 11) Unknown = group behavior could not be assessed due to lack of visibility.

We recorded all long call events and the occurrence and duration of all feeding events with the 'all occurrence sampling' method (ALTMANN, 1974) during the whole BLTs' activity period. All feeding plants were marked with individual tags in the field, identified to the species level and had the position recorded with a GPS device. We measured all fruit feeding trees' diameter at breast height (DBH), which is regarded as an accurate method for estimating fruit abundance for tropical tree species (CHAPMAN *et al.*, 1992). Considering that lianas and other scandent plant species may benefit from larger host trees which consequently grant access to higher canopies and higher light incidence (CAI *et al.*, 2007; SMITH *et al.*, 2017), we took the host tree's DBH for the lianas, epiphytes and scandent shrub species recorded.

#### 2.3 Data analysis

Considering the fact that location points recorded every five minutes present high autocorrelation, we assessed home range using the Autocorrelated-Gaussian reference function KDE (AKDE) using the package 'ctmm' (FLEMING e CALABRESE, 2019) because this method, differently from classical methods, does not assume independent and identically distributed data to run estimations (NOONAN *et al.*, 2019). We also estimated home range size through more classical methods, Minimum Convex Polygon (MCP) and Kernel Density Estimation (KDE), to allow comparison with other studies (Package adehabitatLT) (CALENGE, 2006) (Table S1). We estimated daily path lengths (DPL) from the sum of the distances travelled between successive location points recorded during each day. We performed all data analysis considering only full-day follows (from sleeping site to sleeping site). Also, we excluded from the analysis all following days in which we could not know BLTs' location for more than 60 consecutive minutes. Therefore, we considered 42 full days and a mean of seven following days per month (± SD 2.6 days) (Table S2).

To determine the spatial distribution of fruit resources visited by the BLTs, we estimated the aggregation index *R* according to the Clark-Evans criterion (function 'clarkevans.test', package spatstat) (CLARK e EVANS, 1954; DONNELLY, 1978; BADDELEY *et al.*, 2015) for each study month (all fruit species) and for each fruit species (all study months). R values corresponded to the ratios of the observed mean nearest neighbor distances between feeding sites to that expected for a Poisson point process. Taking into account that the test considers, as null hypothesis, that feeding sites are randomly distributed (R = 1), R values below 1 indicate a clustered distribution while R values above 1 indicate that feeding sites are evenly distributed across the area. Finally, accounting for the fact that nearest neighbor distances between feeding sites can be underestimations of the real distances between feeding sites (i.e. the true nearest neighbor may lay outside of the home range), and intending to avoid bias, we used the Cumulative Distribution Function correction method in our R estimations (CLARK e EVANS, 1954; DONNELLY, 1978). Test significance could not be obtained when less than 13 individuals were sampled and the minimum number of individuals needed for the test to estimate R was 3. Also, we estimated mean nearest neighbor distances for fruit species using the spatstats' function 'nndist' (Table S3).

We created distance maps and estimated mean empty space distances (i.e. mean distances from random locations in the area to data points sampled) for the individuals of the fruit feeding sites

visited each month (functions 'distmap' and 'distfun', package 'spatstat'). We tested whether the spatial distribution parameters of feeding sites (aggregation indexes R and mean nearest neighbor distances) affected both number of visits and mean feeding bout duration per species with, respectively, a generalized linear model with negative binomial distribution and linear model (functions 'glm.nb' and 'lm'). Finally, we also applied a linear model to verify if mean visit time was affected by fruiting tree's DBH.

We tested route directionality for the 42 daily routes using the change-point test (CPT), which allows, in an objective way, the detection of statistically significant turning points along BLTs' daily routes (BYRNE *et al.*, 2009). Each route started at a sleeping site and ended at the end of the day again at a sleeping site. We applied the test backwards on daily routes, analyzing sequentially segments of each route, from the last sleeping site until a change-point (CP) was detected. This CP then became the starting point for the test to run again and so on until detecting the first CP of the route. We tested the number of vectors (*q* value, from 1 to 10) to be considered on each segment before the detection of each CP to choose the best q value. The best q value is the one allowing the identification of the greatest number of CPs; in our study, with a test sensitivity of p < 0.01, it was equal to 6 (55 change points identified) (Figure S1) (BYRNE *et al.*, 2009).

In order to assess the influence of territory defense and fragment edge on BLTs' movement, we divided the area used by the study group into three zones: 1) fragment edge, a 100m-width zone characterized by the fragment limits with surrounding matrices; 2) territory border, a 100m-width zone consisting in the boundary between the study group's territory and neighboring conspecific groups; and 3) central area, corresponding to the rest of the home range. The width of the zone created along forest edge takes into account the distance to which edge effects can have the greatest impact in terms of forest structure, likely to affect BLTs' behavior, such as the reduction of canopy height and change in the height of greatest foliage density (LAURANCE et al., 2002). We also chose a width of 100m for the territory border because previous studies show that BLTs' long calls spread until around this distance in the forest (PINTO, 2017) and this type of vocalization is commonly used in territory defense (PERES, 1989). We created the 100m-width zones by building buffers in QGIS 3.4 (QGIS Development Team, 2016) from the respective borders and then cut the intersection areas to avoid resampling. We considered the border of the home range created by the 90% Kernel Density Estimation (KDE, package 'adehabitatHR') (CALENGE, 2006) to exclude rare excursion events (WORTON, 1989; NOONAN et al., 2019), otherwise included if we used the 95% AKDE home range estimation. We then used a Kruskal-Wallis rank sum test and pairwise Wilcoxon rank sum post hoc test (functions 'kruskal.test' and 'pairwise.wilcox.test', respectively) to compare the medians of daily density of use; median of daily proportions of CPs relative to location points; and medians of daily density of long calls, between the three zones. Also, we applied a Chi-square test (function 'chisq.test') to compare the density of fruit feeding sites among the zones. We performed all data analysis in R 3.6.1 (R Core Team, 2019).

#### 3 RESULTS

We observed the group for 379.9 hours and registered a total of 4402 location points. The home range estimated by our AKDE was 60.8 ha, with confidence intervals ranging from (46.8 ha to 76.62 ha). Considering that we never recorded matrix use and intergroup competition was high in territory borders during the study period, the narrow confidence intervals (46.8 ha) corresponded to the black lion tamarins' used area during the study period (Figure S1). The group presented mean step lengths of 20 m ( $\pm$  SD 21.5 m), corresponding to a mean velocity of 4 meters/minute ( $\pm$  SD 0.75 m/min). BLTs traveled daily 1773 m ( $\pm$  SD 461m); the shortest distance was recorded in August (930m) and the highest (2962m) in May (Table S2). The most frequent group behaviors associated to GPS locations were frugivory (1298 records corresponding to 29.9% of the total number of scans), locomotion (1265, 29.8%) and foraging (1095, 25.3%) (Table 1). We found that resting or social activities corresponded to only 2.0% of the scans (n = 86). Together, encounters and long calls corresponded to 77 locations (1.7% of the scans), although disputes with other groups were registered on 11 out of the 42 days of observation. With all occurrence sampling, we registered 438 locations associated to long calls, corresponding to a mean of 13.5 ( $\pm$  SD 7.3) long calls per day.

We recorded 459 frugivory events on 275 individuals belonging to 12 plant species. The number of visits per species varied between 1 and 174, being *Pereskia aculeata* the most visited species. On the other hand, the mean time BLTs spent feeding on the recorded plant species ranged from 1.9 minutes ( $\pm$  SE 0.54) in *Annona emarginata* to 44.96 minutes ( $\pm$  SE 33.8) in *Ficus sp.* (Figure 2). Lianas represented 40% of the total number of BLTs' visits to fruit feeding sites, while palm trees represented 26% of the visits, scandent shrubs 23%, trees 10% and epiphytes only 0.002% (Table S3).

Behaviera	Group s	scans	Change points (CPs)		
Benaviors	n	%	n	%	
Frugivory	1298	29.94	7	12.72	
Locomotion	1265	29.76	19	34.54	
Foraging	1095	25.28	14	25.45	
Idle	265	6.24	2	3.36	
Resting or social activities	86	2.04	3	5.45	
Encounter	57	1.29	2	3.7	
Fur rubbing	24	0.54	0	0	
Long call	20	0.45	1	1.81	
Gummivory	19	0.43	1	1.81	
Marking	0	0	0	0	
Unknown	273	6.22	6	10.9	
Total	440	2	55		

Table 1: Behaviors recorded by group scans and behaviors identified as change points (CPs). Data presented as numbers (n) and percentages (%) out of the total group scans and CPs.



Figure 2: Mean feeding bout duration in the 12 fruit species consumed by BLTs in the study site. Error bars represent standard error (SE). Number of fruit feeding bouts recorded in each fruit species displayed above each bar.

The fruit feeding sites visited by the BLTs presented clustered distribution patterns in all months (R < 1, p < 0.002). The average empty space distance for fruit species visited for the entire study period was 33.4 m ( $\pm$  SD 22.8 m) (Figure 3). Eight of the 12 fruit species presented R values lower than 1 (Table S3). Of these, *Annona emarginata* was the only species for which we did not obtain statistical significance (p = 0.216). Mean nearest neighbor distances varied from 24.6 m ( $\pm$  SD 17.3 m) in *Pereskia aculeata* to 190.3 m ( $\pm$  SD 140.4 m) in *Rhamnidium elaeocarpum* (Table S3). We found that BLTs visited significantly more the fruit species with short mean nearest neighbor distances (Estimate = -0.018, p = 0.003) (Figure 4A) and spent more time feeding on fruit species with both lower R values ( $R^2$  = 0.6, p = 0.02) (Figure 4B and C, respectively). However, we found no significance on the correlation between R and DBH ( $R^2$  = 0.3, p = 0.09).



Figure 3: Spatial representation of feeding plant species visited by BLTs on each month during the study period. The area displayed corresponds to the group's 95% KDE home range estimation. Darker pixel colors indicate higher feeding sites concentration. *R* values correspond to aggregation index values obtained for each month. *R* values smaller than 0 indicate clustered sites distribution, while R values higher than 0 indicate sparse distributions. For all months sampled, p values were 0.002, indicating feeding sites presented significant clustered distributions. "D" values represent mean empty space distances and respective standard deviations, in meters (mean distances between feeding sites and random locations).



Figure 4: Regression models for frugivory according to plant species' spatial distribution and size (DBH). Panel "A" is a Generalized Linear Model with negative binomial distribution between number of visits and mean nearest neighbor distances, in meters, between individuals of the plant species recorded from frugivory events. "Estimate" is the size of the effect of mean nearest neighbor distance on the number of visits. Panel "B" is a linear regression model between mean visit duration, in minutes, per plant species and the Aggregation Indexes *R* obtained according to Clark-Evans criterion. Panel "C" is a linear regression model between mean visit duration, in minutes, and plant species' mean diameter at breast height (DBH), in centimeters. "R2" is the percent of the deviance observed in mean visit duration explained by the independent variables *R* and DBH.

Thirty-two out of the 42 days analyzed contained at least one CP. We found a total of 55 CPs distributed all over the area used by the group of BLTs and a mean of 1.3 CPs (± SD 1.2) per day. The most frequent behaviours associated with CPs were locomotion (n = 19, 34.5%), foraging (n = 14, 25.4%) and frugivory (n = 7, 12.7%). Resting or social activities were associated with 3 CPs (5.4%) and encounters with other groups corresponded to only 2 (3.7%) (Table 1, Figure 5). The medians of daily densities of location points were significantly different between the zones of the area used (Kruskal-Wallis  $X^2 = 29.7$ , p < 0.001), being the central area significantly more used than the fragment edge (p < 0.01), and the territory border (p = 0.007) (Table 2). The fruit feeding sites visited by the group presented a higher density in the central area, followed by territory border and fragment edge, although we obtained no test significance ( $\chi^2$  = 4.343, p < 0.114). We found that the medians of daily densities of long calls were significantly different between the three zones (Kruskal-Wallis  $X^2 = 12.99$ , p = 0.001), with higher densities in the central area, followed by the territory border and fragment edge, and we found a significant difference between central area and the fragment edge (p < 0.001). The medians of daily density of encounters did not differ between the three zones (Kruskal-Wallis  $X^2 = 0.862$ , p = 0.650), although we observed higher maximum values in the territory border. When comparing the median of daily proportions of CPs in relation to location points in the different zones, we found no significance (Kruskal-Wallis X<sup>2</sup> = 0.558, p = 0.756) (Table 2, Figure 5A). Nevertheless, we observed higher mean daily density values for the territory border (0.02 CPs/location points ± SD 0.05), followed by the

# fragment edge (0.018 CPs/location points $\pm$ SD 0.03) and the central area (0.008 CPs/location points $\pm$ SD 0.01).

Table 2: Space use comparison between the three zones of the area used (territory border, central area and fragment edge). Daily values correspond to median, with range (minumun and maximum) values, for each of the zones from all 42 study days. Density values represent the number of observations in each zone corrected by each zone's area, in hectares. The proportions of CPs were obtained by dividing the number of CPs by the number of location points in each zone, for each of the 42 days. "X<sup>2</sup>" corresponds to Chi-square (<sup>1</sup>) and Kruskal-Wallis Rank Sum (<sup>2</sup>) tests' results for comparisons between the three zones, with respective significance (p) values. Significance p values also reported for the comparisons between the three zones with pairwise Wilcoxon Rank Sum post hoc tests.

	Fragment edge	Territory border	Central area	Χ2	р	Central area vs fragmen t edge	Central area vs territory border	Territory border vs fragment edge
Area (ha)	17.53	8.42	20.22	-	-	-	-	-
Density of fruit feeding sites	2.511	8.309	9.844	4.343 <sup>1</sup>	0.114	-	-	-
Daily density of location points	1.4 (0 – 3.8)	1.5 (0 – 7.8)	3.1 (0.7 – 4.5)	29.702 <sup>2</sup>	< 0.001	< 0.001	0.007	0.114
Daily proportion of CPs	0.0 (0 – 0.2)	0.0 (0 – 0.3)	0.0 (0 – 0.1)	0.558 <sup>2</sup>	0.756	-	-	-
Daily density of long calls	0.0 (0 – 0.5)	0.0 (0 – 2.4)	0.2 (0 – 0.7)	12.994 <sup>2</sup>	0.001	< 0.001	0.088	0.281
Daily density of encounters	0.0 (0 - 0.1)	0.0 (0 - 0.7)	0.0 (0 – 0.5)	0.862 <sup>2</sup>	0.650	-	-	-



Figure 5: Distribution of change-points (CPs) and daily routes throughout the study area. 100 meters buffers were created on the territory border and fragment edge to estimate the rate of use and proportion of CPs in each zone. The behaviors associated with CPs are represented by different colored shapes. "RES" represents 'Resting or social activities'. Percentages represent the proportion of CPs associated with each behavior in relation to the total number of CPs. Panel A indicates the distribution of daily proportions of CPs (ratio between CPs and GPS location points for each of the 42 study days) in each of the three zones considered. There was no significant difference in the median of proportion of CPs between the three zones (Kruskal-Wallis Rank Sum test).

#### 4 DISCUSSION

In a 100-ha Atlantic Forest fragment, contrary to expected, we found that fruit feeding sites was not the most important factor shaping BLTs' trajectories, although fruits were an important item in the diet. We suggest that these findings may result from the characteristics of the resources present in the study area: many small trees or lianas not too far apart, leading to repeated short feeding bouts. Consequently, BLTs did not seem to have to plan travel routes for feeding sites, once short travels in any direction would lead to an available fruit spot. On the other hand, although not significantly different, we observed that the majority of CPs were located on both fragment edge and territory border. This spatial distribution of CPs, also frequently associated to locomotion, suggests that the turning points along BLTs' daily routes represent more physical (fragment edge) or social (territory boundary) barriers than true traveling goals. Although BLT is a species known for presenting home ranges larger than 300 hectares in areas of continuous forest (VALLADARES-PADUA, 1993), the area used by our group corresponded to only 46.8 ha. Our estimations corroborate with the observed home ranges for BLT groups in small forest fragments and riparian forest areas (MAMEDE-COSTA, 1997; MEDICI, 2001), as well as for golden lion tamarins in small forest patches (LUCAS *et al.*, 2019). These smaller home ranges can be a consequence of the space limitations and increased intergroup competition. In fact, intergroup aggressions were recorded on 26% of the following days in the study fragment while in Morro do Diabo State Park, an area of 37156 ha, encounters with conspecific groups were reported for only 15% of the following days (n = 4, total of 27 following days) (SILVA, Unpublished data). Our findings suggest that smaller fragments may present higher frequencies of encounters, suggesting higher intergroup competition. Moreover, despite the importance of matrix crossings for the management of primate populations confined to small forest fragments (MORAES *et al.*, 2018) and although matrix use has been previously reported for BLTs in the region (SANTOS, 2016; PINTO, 2017), the study group never used the matrix nor crossed to other connected forest remnants during the study period, suggesting no landscape supplementation (DUNNING *et al.*, 1992; ARROYO-RODRÍGUEZ e MANDUJANO, 2009).

More than 55% of BLTs' location points in the study area were associated to feeding and foraging. We found that frugivory corresponded to the most frequent group behavior, which corroborates previous studies which reported lion tamarins' diets to be composed by more than 70% of fruits (BUFALO et al., 2016). However, BLTs foraged on animal prey more and rested or performed social activities less than in larger areas where they have been previously studied. In Caetetus Ecological Station, a forest fragment of 2179 ha, BLTs were reported to devote from 12.8% to 19.8% of their time foraging (KEUROGHLIAN e PASSOS, 2001). In Morro do Diabo State Park, foraging corresponded to only 3% of BLTs' activity budget (VALLADARES-PADUA, 1993). Resting or social activities corresponded to only 2.04% of our total scans, while in Caetetus and Morro do Diabo, BLTs have been reported to spend, on average, 15.4% and 49.1% of the activity budgets, respectively (VALLADARES-PADUA, 1993; KEUROGHLIAN e PASSOS, 2001; SILVA, Unpublished data). Therefore, we understand that important consequences of fragmentation, such as the reduction in diversity and abundance of important fruit species (LAURANCE et al., 2000; ARROYO-RODRÍGUEZ e MANDUJANO, 2006; LAURANCE et al., 2006) may indeed influence BLTs' behavior, increasing their time searching for animal prey in smaller areas. The apparent reduced proportions of resting or social activities may indicate that the study group needed to dedicate more time to foraging and territory surveillance due to possible higher competition.

Among the most consumed fruit species, *Syagrus romanzoffiana* and *Celtis iguanaea* were available during all study months. Both species have been previously reported as important items on BLTs' diet in other areas (PASSOS, 1992; MAMEDE-COSTA e GODOI, 1998). Specifically, *Syagrus romanzoffiana* is considered a key plant species in BLTs' diet, since it is known to fructify for almost the whole year, representing a valuable resource even during the dry season, when fruits of other species can be scarce (KEUROGLIAN, 1990; PASSOS, 1992; MAMEDE-COSTA e GODOI, 1998). However, *Pereskia aculeata*, a liana available on 4 of the 6 study months, accounted alone for almost 40% of all visits to fruit feeding sites. This plant species also presented the shortest mean nearest neighbor

distances, with individuals less than 25 m distant to each other, on average (Table S3). As a consequence of environmental and climatic changes, increases on liana abundance and biomass have been evidenced for tropical forests (PHILLIPS *et al.*, 2002; WRIGHT *et al.*, 2004; PHILLIPS *et al.*, 2005; LAURANCE *et al.*, 2014; SMITH *et al.*, 2017), competing with other plant species for light, water and nutrients and affecting negatively the fitness of hosting trees (GARCÍA LEÓN *et al.*, 2018), especially in fragmented landscapes (CAMPBELL *et al.*, 2014). In fact, in Morro do Diabo State Park lianas corresponded to 23% of frugivory scans during an 8 month-sample (KAISIN, unpublished data). Therefore, our results may suggest that fruit consumption in the study area was not necessarily associated to species preference, but actually to a reduction on fruit diversity in a liana dominated fragment.

Despite a low fruit diversity, BLTs relied differently on the available fruit species based on their spatial distributions and DBH. The fruit species that the group visited more frequently were indeed closer to each other (i.e. shorter mean nearest neighbor distances). Nonetheless, the fruit species in which the group fed for longer periods of time presented higher mean DBH, a good proxy for fruit productivity (CHAPMAN et al., 1992), and were more isolated in clumps across the area. As observed for wild whitefaced sakis (*Pithecia pithecia*), choosing to feed on large and isolated fruit sites can minimize intragroup competition and reinforce intergroup dominance over important feeding sites, compensating the high energy costs to traveling greater distances (CUNNINGHAM e JANSON, 2007). Also, visiting rare resources such as high-caloric fruits or water holes can provide important nutrients necessary for individuals' daily management. In fact, routes to such resources have been demonstrated to be goal oriented (CUNNINGHAM e JANSON, 2007; JANMAAT et al., 2013), as in the case of female western chimpanzees (Pan troglodytes verus), which have been reported to orient travel routes to reach rare fatrich fruit resources (BAN et al., 2016). Therefore, although further investigations are still necessary to better confirm our findings, our results suggest that BLTs tend to maximize the consumption of rare fruit species, as well as on larger feeding sites, even though visits can be associated with higher energy costs due to longer distances between individuals.

Despite the importance of frugivory in BLTs diet, only 12.7% of CPs were associated to fruit feeding locations. Important feeding sites, such as out of sight fruit trees, have been reported to direct most of daily routes for both old-world (i.e. mouse lemurs (*Microcebus murinus*) (JOLY e ZIMMERMANN, 2011), northern pig-tailed macaques (*Macaca leonina*) (ALBERT *et al.*, 2013), white-handed gibbons (*Hylobates lar*) (ASENSIO *et al.*, 2011), chacma baboons (*Papio ursinus*) (NOSER e BYRNE, 2014) and western chimpanzees (*Pan troglodytes verus*) (BAN *et al.*, 2016)); and new world primates (i.e. white-faced saki monkeys (*Pithecia pithecia*) (CUNNINGHAM e JANSON, 2007), Geoffroy's spider monkeys (*Ateles geoffroyi*) (BOYER *et al.*, 2006; REYNA-HURTADO *et al.*, 2017), black-horned capuchin monkeys (*Sapajus nigritus*) (JANSON, 2016) and Weddell's saddleback tamarins (*Saguinus fuscicollis weddelli*) (PORTER e GARBER, 2013)). Moreover, a recent study on BLTs at Santa Maria, a 594 ha Atlantic Forest fragment, has reported that fruit feeding sites corresponded to the majority (28%) of the CPs identified (MESSAOUDI, 2015). When investigating the spatial distribution of fruit feeding sites in our study area, we found that they were densely distributed all over the area in all studied months. Consequently, wherever in the area, the mean distance BLTs had

to travel to visit a next available fruit feeding site was shorter than 30 m. In fact, considering the mean step lengths obtained, this distance could be traveled in less than 10 minutes. Therefore, finding and heading to the next fruit feeding site was not an expressive challenge for BLTs in our study site and was thus not probably the main issue in the decision process of route planning. Consequently, fruit feeding tree locations did not shape BLTs' trajectories in our study site.

BLTs spent significantly more time in the central area than in the territory border or in the fragment edge. This might be a consequence of the highest density of visited feeding trees in the central area. However, since we do not have data about the availability of resources, we cannot affirm this cause-effect relationship. Although reaching fruit resources in the study area did not necessarily demand moving long distances, the study group traveled long distances daily, agreeing with other observations for the species (VALLADARES-PADUA, 1993; KEUROGHLIAN e PASSOS, 2001). Moving around the home range can be associated with other important behavioral and ecological aspects of primates' daily activities, such as the search for animal prey (PORTER e GARBER, 2013; GARBER e PORTER, 2014), monitoring phenology and fruit availability of different plant species (CUNNINGHAM e JANSON, 2007; DI FIORE e SUAREZ, 2007) and patrolling territory borders for the presence of conspecific groups (NOSER e BYRNE, 2007). CPs were mostly associated with locomotion and foraging, suggesting that daily routes were mostly directed by other physical and social aspects of the environment, such as fragment edge and territory frontiers. As expected by the territorial behavior of lion tamarins (PERES, 1989), long calls were most frequent in the territory border, although we only obtained significance in the difference between central area and fragment edge. Moreover, the two encounter-related CPs identified were located inside the territory border buffer. On the other hand, we found that fragment edge presented the highest proportion of CPs among the zones considered and, therefore, consisted in an important barrier for BLTs' movement at the study site. Therefore, once movement and foraging are behaviors highly associated, we understand that monitoring the area for the presence of competitors while inspecting fruit sites' productivity and foraging for animal prey represented a great importance for BLTs' route planning process and structural limits of the area (i.e. territory frontiers with other groups' home range or vegetation limits imposed by fragment edges) were decisive for directing daily routes in a small forest fragment.

#### 5 CONCLUSION

Despite the high importance of fruit consumption in BLTs' daily activities and the already highlighted importance of such resources for the species' daily route planning process in other areas (MESSAOUDI, 2015), our findings suggest a tendency for BLTs to adjust travelling goals in relation to resource availability and distribution. Our findings reinforce, however, that even though reaching fruit feeding sites did not depend on traveling long distances, BLTs presented a tendency to maximize fruit consumption of large and rare fruit species. Moreover, we observed that, in a small forest fragment with high intergroup competition for space and resources, sites related to territory defense and physical barriers imposed by matrices present a high importance to route direction. However, we highlight the importance of further studies to better understand the extension of the influence of fragment size and both resource availability and distribution on BLTs' ranging patterns.

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#### **APPENDIX**

#### Supplementary material

Table S1: Home range estimations, in hectares, according to three different methods. 95% Minimum Convex Polygon (MCP); 95%, 90% and 50% Kernel Density Estimations (KDE); and 95% Autocorrelated-Gaussian reference function KDE (AKDE).

	Area (ha)
95% MCP	45.84
95% KDE	49.7
90% KDE	41.42
50% KDE	14 97
95% AKDE	60.81 (46.8 – 76.62)

Table S2: Proportions of group behaviors recorded with scan sampling every five minutes for 42 days. Daily path lengths (DPL), in meters, represent the sum of all steps recorded during each day. Behaviors shown as proportions of group behaviors recorded each day during scan sampling. "Unknown" represents the proportion of scans in which we could not assess group behavior due to low visibility. "N scans" represent the total number of scans recorded in each day.

Date	DPL (m)	Frugivory	Foraging	Gummivory	Locomotion	Resting	Idle	Encounter	Long calls	Marking	Fur rubbing	Unknown	N scans
15/03/19	1628.9	0.223	0.351	0.000	0.191	0.085	0.074	0.000	0.000	0.000	0.000	0.074	94
16/03/19	1328.63	0.264	0.181	0.000	0.375	0.111	0.069	0.000	0.000	0.000	0.000	0.000	72
11/04/19	2123.08	0.260	0.183	0.000	0.404	0.029	0.096	0.000	0.000	0.000	0.000	0.029	104
12/04/19	2296.71	0.142	0.264	0.000	0.472	0.009	0.047	0.000	0.000	0.000	0.000	0.066	106
13/04/19	1799.2	0.130	0.120	0.000	0.500	0.050	0.060	0.000	0.070	0.000	0.000	0.070	100
15/04/19	1200.18	0.340	0.149	0.000	0.447	0.000	0.053	0.000	0.000	0.000	0.000	0.011	94
16/04/19	1546.58	0.248	0.073	0.000	0.413	0.046	0.165	0.000	0.000	0.000	0.000	0.055	109
17/04/19	1608.15	0.245	0.300	0.000	0.273	0.027	0.118	0.018	0.000	0.000	0.000	0.018	110
18/04/19	2034.43	0.252	0.183	0.000	0.530	0.000	0.017	0.000	0.000	0.000	0.000	0.017	115
19/04/19	1374.13	0.261	0.261	0.000	0.359	0.033	0.022	0.000	0.000	0.000	0.000	0.065	92

20/04/19	2213.97	0.277	0.161	0.000	0.446	0.000	0.098	0.000	0.000	0.000	0.000	0.018	112
13/05/19	2962.43	0.170	0.255	0.000	0.330	0.000	0.104	0.009	0.066	0.000	0.000	0.066	106
14/05/19	2096.76	0.337	0.144	0.000	0.404	0.000	0.048	0.000	0.000	0.000	0.000	0.067	104
15/05/19	2883.76	0.219	0.200	0.000	0.314	0.000	0.114	0.000	0.038	0.000	0.000	0.114	105
16/05/19	1550.74	0.395	0.158	0.000	0.351	0.000	0.018	0.000	0.009	0.000	0.026	0.044	114
17/05/19	2335.1	0.204	0.194	0.009	0.398	0.000	0.102	0.028	0.000	0.000	0.000	0.065	108
18/05/19	1155.83	0.480	0.108	0.000	0.343	0.010	0.029	0.000	0.000	0.000	0.000	0.029	102
20/05/19	1717.92	0.400	0.191	0.000	0.322	0.000	0.026	0.000	0.000	0.000	0.009	0.052	115
10/06/19	2076.13	0.296	0.157	0.000	0.324	0.000	0.074	0.093	0.000	0.000	0.000	0.056	108
11/06/19	1201.13	0.344	0.250	0.000	0.302	0.000	0.042	0.000	0.000	0.000	0.000	0.063	96
12/06/19	2168.97	0.359	0.117	0.000	0.282	0.000	0.097	0.010	0.000	0.000	0.000	0.136	103
13/06/19	1593.91	0.330	0.275	0.000	0.312	0.000	0.018	0.000	0.000	0.000	0.000	0.064	109
14/06/19	2098.05	0.179	0.316	0.000	0.342	0.009	0.034	0.085	0.000	0.000	0.000	0.034	117
15/06/19	1712.07	0.282	0.359	0.000	0.256	0.034	0.026	0.000	0.000	0.000	0.000	0.043	117
17/06/19	2453.62	0.260	0.337	0.000	0.365	0.000	0.029	0.000	0.000	0.000	0.000	0.010	104
11/07/19	1545.96	0.418	0.110	0.000	0.275	0.000	0.033	0.000	0.011	0.000	0.000	0.154	91
12/07/19	1780.69	0.263	0.364	0.000	0.246	0.025	0.025	0.000	0.000	0.000	0.000	0.076	118
13/07/19	1223.95	0.471	0.255	0.000	0.235	0.000	0.020	0.000	0.000	0.000	0.000	0.020	102
15/07/19	1663.87	0.306	0.408	0.000	0.184	0.000	0.061	0.000	0.000	0.000	0.000	0.041	
16/07/19	1860.17	0.215	0.327	0.056	0.243	0.019	0.028	0.000	0.000	0.000	0.009	0.103	107
17/07/19	1841.14	0.306	0.296	0.000	0 194	0.061	0.020	0.041	0.000	0.000	0.000	0.082	98
18/07/19	1020.61	0.606	0.154	0.000	0.163	0.000	0.058	0.000	0.000	0.000	0.000	0.019	104
19/07/19	1670.02	0.368	0.264	0.028	0.274	0.009	0.038	0.000	0.000	0.000	0.009	0.009	106
20/07/19	1659.93	0.369	0.297	0.000	0.216	0.000	0.063	0.000	0.000	0.000	0.000	0.054	111
11/08/19	1490.11	0.301	0.292	0.000	0.159	0.027	0.150	0.000	0.000	0.000	0.044	0.027	113
12/08/19	2104.28	0.188	0.202	0.000	0.162	0.027	0.103	0.017	0.000	0.000	0.026	0.128	117
13/08/19	2280.49	0.219	0.404	0.044	0.158	0.000	0.061	0.044	0.000	0.000	0.000	0.070	114
14/08/19	1734.59	0.225	0 441	0.029	0.100	0.000	0.049	0.000	0.000	0.000	0.000	0.039	102
		0.220	V. (T)	0.020	0.110	0.000	0.040	0.000	0.000	0.000	0.000	0.000	102

15/08/19	1120.98	0.380	0.240	0.000	0.150	0.060	0.040	0.030	0.000	0.000	0.000	0.100	100
19/08/19	930.45	0.288	0.463	0.000	0.063	0.000	0.188	0.000	0.000	0.000	0.000	0.000	80
20/08/19	1612.76	0.266	0.367	0.000	0.101	0.000	0.009	0.147	0.000	0.000	0.000	0.110	109
21/08/19	1780.64	0.336	0.207	0.01	0.069	0.000	0.026	0.000	0.00	0.000	0.086	0.267	116

Table S3: List of fruit species consumed by the group of black lion tamarins. "Life form" listing plant species according to species' growth classification. "Number of individuals" corresponds to the total number of trees sampled from frugivory events, for the 12 species, from July 2018 to August 2019. "Number of visits" corresponds to the number of frugivory events on the species during the study period. Mean and standard deviation (SD) values for "DBH" (diameter at breast height) measures, in centimeters, for the plant species recorded. Aggregation index *R* and p values were obtained according to the 'clarkevans.test' function (package 'spatstat'). "*R*" corresponds to the ratios of the observed mean nearest neighbor distances between feeding sites to that expected for a Poisson point process. The test considers as null hypothesis that feeding sites are randomly distributed (*R* = 0). R values below 1 correspond to an even distribution and *R* lower than 1 suggests that trees are distributed in clusters across the area. We considered a significance level of p = 0.05 on the analysis. Mean and standard deviation (SD) of species' 'Nearest neighbor distances', in meters, obtained with the function 'nndis', package 'spatstat'.

Plant species	Life form	Number of individuals	Number of visits	DBH	(cm)	Aggre	Aggregation index		t neighbor nces (m)
				Mean	SD	R	р	Mean	SD
Pereskia aculeata	Liana	124	173	43.56 <sup>1</sup>	24.26 <sup>*</sup>	0.739	0.002	24.56	17.34
Syagrus romanzoffiana	Palm tree	70	114	20.7	3.07	0.741	0.002	35.71	33.14
Celtis iguanaea	Scandant shrub	47	99	41.50 <sup>*</sup>	31.80 <sup>*</sup>	0.321	0.002	25.55	52.7
Annona emarginata	Tree	22	20	28.08	9.2	0.769	0.216	60.35	37.8
Dyospiros inconstans	Tree	9	14	39.21	20.4	0.664	-	103.66	42.71
Ficus sp.	Tree	3	4	85.33	7.03	0.354	-	165.39	160.26
Rhamnidium elaeocarpum	Tree	4	4	29.95	10.5	0.627	-	190.26	140.42
Eugenia sp.	Tree	1	2	26.70 <sup>†</sup>	-	-	-	-	-
Cissus sucicaulis	Liana	2	2	25.76 <sup>*</sup>	20.13 <sup>*</sup>	-	-	-	-
Cordia ecalyculata	Tree	1	1	43.99 <sup>2</sup>	-	-	-	-	-
Unidentified sp.	Liana	1	1	19.01 <sup>*†</sup>	-	-	-	-	-
Rhipsalis cereuscula	Epiphyte	34	1	53.62 <sup>*</sup>	27.07*	0.331	0.002	33.93	47.55

<sup>&</sup>lt;sup>1</sup> For liana, epiphyte and scandant shrub species, DBH values were taken from host trees.

<sup>&</sup>lt;sup>2</sup> For plant species with only one individual sampled, DBH value represent the individual measure, not mean



Figure S1: Number of change points (CPs) identified for each (0-10) q value considered for each of the 42 following days. Darker black line indicates the total number of CPs identified for each q value for the 42 days. We considered q = 6 for the analysis, since it corresponds to the last q value of continuous increase in the number of CPs.



Figure S2: 95% Home range estimation obtained with the Autocorrelated-Gaussian reference function KDE (AKDE). Darker pink contour line delineates the estimated 95% home range area (60.81 ha), whereas two lighter pink lines indicate 95% confidence ranges (46.8 ha and 76.62 ha). Considering that matrix use was never recorded in the area during the study period and intergroup competition was high in territory borders, the narrow confidence intervals of the AKDE (46.8 ha) correspond to the black lion tamarins' used area during the study period.