



Preliminary assessment of habitat uses and time budget by an urban group of white-footed tamarins (*Oedipomidas leucopus*, Callitrichidae)

Evaluación preliminar del uso del hábitat y del tiempo en un grupo urbano de tití gris (*Oedipomidas leucopus*, Callitrichidae)

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Abstract

High levels of species diversity and endemism in developing countries contrast with a dramatic expansion of human populations and urban development. This poses a challenge for wildlife and their ability to adapt to transformed and fragmented habitats. In the Neotropics, tamarins and marmosets (Primates: Callitrichidae) have established populations in urbanized areas, including the White-footed tamarin in north-western Colombia, where it is prone to metabolic syndrome presumably due to nutritional issues and reduced physical activity. We conducted an exploratory analysis of habitat use and activity budget of a group of the White-footed tamarin established in an isolated forest patch in Medellín, Colombia over a 12-month period. We applied multiple linear regressions to assess 1) the seasonal variation of diet and 2) the role of landscape features on the use of the available habitat. Resting was the most dominant behavior. The diet comprised a range of animal and plant items as well as a smaller proportion of anthropogenic food. The diet diversity showed an inverse relationship with the within-month humidity variation, indicating an adaptation to seasonal changes. The use of available area was associated with tree density and abundance of key plant species that are either consumed or used as part of corridors. Our results suggest that seasonal plasticity and generalist diet habits may be favored in species adapted to urbanized areas, but food oversupply may lead to sedentarism and compromise the health of urban fauna. Strategic planting of key tree species that provide food sources and facilitate dispersal is recommended.

Keywords: conservation, diet, plasticity, *Saguinus*, urban ecology, urban primate

Resumen

Los altos niveles de diversidad de especies y endemismo en países en desarrollo contrastan con una expansión dramática de poblaciones humanas y desarrollo urbano. Esto plantea un desafío para la vida silvestre y su capacidad adaptativa a hábitats transformados y fragmentados. En el Neotrópico, los titíes (Primates: Callitrichidae) presentan poblaciones en áreas urbanizadas, incluido el tití gris en el noroeste de Colombia, donde es propenso al síndrome metabólico, presu-

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Received: June 6, 2024; accepted: October 17, 2024; published: February 1, 2025.

miblemente debido a problemas nutricionales y actividad física reducida. Realizamos un análisis exploratorio del uso del hábitat y actividades de un grupo de titíes en un parche forestal aislado en Medellín, Colombia, durante un período de 12 meses. Aplicamos regresiones lineales múltiples para evaluar 1) la variación estacional de la dieta y 2) el papel de las características del paisaje sobre el uso del hábitat. El reposo fue el comportamiento dominante. La dieta comprendió diversos productos animales y vegetales y alimentos antropogénicos en menor medida. La diversidad de la dieta mostró una relación inversa con la variación intramensual de la humedad, sugiriendo una adaptación a cambios estacionales. El uso del área se asoció con la densidad de árboles y la abundancia de especies de plantas consumidas o utilizadas como corredores. Nuestros resultados sugieren que los hábitos alimentarios con plasticidad estacional y generalistas pueden favorecerse en especies adaptadas a ambientes urbanos, pero el exceso de oferta alimenticia puede conducir a sedentarismo y comprometer la salud. Se recomienda la plantación estratégica de especies arbóreas clave que proporcionen fuentes de alimento y faciliten la dispersión.

Palabras clave: conservación, dieta, ecología urbana, plasticidad, primate urbano, *Saguinus*

INTRODUCTION

Habitat transformation frequently leads to changes in phenotypes, biotic interactions, and composition of populations in urban wildlife communities (Alberti et al., 2017; Faeth et al., 2011). Among vertebrates, phenotypic changes in physiological, anatomical, and behavioral traits have been recognized. These include the evolution of body shape, behavioral response to noise pollution, life history traits such as birth season, litter size and juvenile growth rate, and physiological response to anthropogenic food sources (Ancillotto et al., 2015; Atwell et al., 2012; Irwin et al., 2010; Luther et al., 2016; Møller et al., 2015). Even though multiple species successfully exploit opportunities and resources and thrive in urbanized areas (Bateman & Fleming, 2012; Yirga et al., 2015), health shortfalls or lethal effects may be caused by infections, nutritional imbalance, pollution, predation, electrocution, and road accidents (Bateman & Fleming, 2012; Ditchkoff et al., 2006; Gregoire et al., 2002; Ilham et al., 2017; Werner & Nunn, 2020).

Urban macaques, for instance, exhibit plasticity in a broad spectrum of behaviors, including variability in ranging patterns, altered paths and daily activity, selection of sleeping sites, and adaptation to human food and feeding time (Ilham et al., 2017; Jaman & Huffman, 2013; Klegarth et al., 2017; McLennan et al., 2017). Plasticity has also been identified in other Old-World primates such as sifakas, vervet monkeys and baboons, whose feeding behaviors seem to have changed to optimize access to food resources

and avoid predation or conflicts with humans in anthropogenic environments (Irwin et al., 2010; Patterson et al., 2017; Warren, 2009).

In Neotropical primates, tamarins, and marmosets (Callitrichidae) are particularly resilient to habitat disturbance and several species are frequently found in urban and peri-urban patch forests (Gordo et al., 2013; Teixeira et al., 2015). While their diet is adaptable to the availability of local resources including human-supplied food, nutritional imbalance, and increased death due to car accidents and electrocution by exposed power lines threaten their survival in urban areas (Gordo et al., 2013; Leite et al., 2011; Rodrigues & Martinez, 2014; Soto-Calderón et al., 2016). Further threats emerge from the fact that habitable forest patches are commonly small and isolated, where limited access to food resources, small population sizes, erosion of genetic diversity and inbreeding may contribute to local extinctions (Farias et al., 2015; Grativol et al., 2001). Identifying challenges and habitat requirements for primates in urbanized environments is, therefore, necessary to manage and conserve primates and other vertebrates in cities.

Despite controversy regarding the pertinence and viability of urban biological conservation, there is growing evidence and perception of cities as biodiversity hotspots (Heilig, 2011; Ives et al., 2016; La Sorte et al., 2014). Also, the exponential growth of human populations and their concentration in urban areas implies that rural environments are gradually transformed into developed areas with degraded and fragmented

habitats. This transformation creates a conflict between wildlife and an expanding human population that is particularly acute in urban areas of less developed countries, where biodiversity is concentrated, and human populations reach the highest growth rates (Estrada et al., 2017; Heilig, 2011; Lamoreux et al., 2006; Orme et al., 2005). Over the next two decades, the most significant urban expansion in biodiversity hotspots will take place in Central and South America, with the greatest impact in key sites for the conservation of Endangered and Critically Endangered species with limited geographic distributions (Seto et al., 2012). A prerequisite to tackling this conflict is understanding human-primate interactions and the requirements for wild species to persist in cities.

Among neotropical primates, a suitable model for understanding the behavioral response and habitat use in urban areas is the White-footed tamarin (*Oedipomidas leucopus*, Günther, 1876), formerly known as *Saguinus leucopus*. This is a Vulnerable (VU) species endemic to north-western Colombia (IUCN, 2021) that currently persists in a few isolated forest patches within the urban matrix and peri-urban forests of the city of Medellín, Colombia (Cuartas-Calle, 2001). Compared to rural tamarins, these tamarins are known to have

higher cholesterol levels and overweight likely related to high consumption of carbohydrates and reduced physical activity (Soto-Calderón et al., 2016). One of these urban groups is habituated in the central campus of the University of Antioquia (UA), which bestows an excellent opportunity to study the adaptation of wild species to urban environments and their interactions with humans. Ours is a preliminary study aimed to examine the habitat use, time budget, social interactions, and seasonal variation of these behaviors in a group of White-footed tamarins established in the main campus of UA (Figure 1). This study provides us with the baseline to develop a tool to integrate biological conservation and education in urban areas.

MATERIALS AND METHODS

Study subjects

A single group of *O. leucopus* has occurred in the main campus of UA for at least 15 years. In 2013, this group was conformed of two adult males and two adult females. They were baited daily with bananas and captured the same day in October 2013 using a collective trap with ten individual cells (Savage et al., 1993). They were weighed on a spring scale (Pesola®, Baar, Switzerland), sedated



Figure 1. Map of the University of Antioquia campus, divided into 24 1-hectare quadrats, where a group of white-footed tamarins (*O. leucopus*) was studied. Trees are represented by green circles and paved roads appear in white. “Creative Commons UdeA-Ciudad Universitaria-Medellin” by Alejandro Rojas (SajoR) is licensed under CC-BY-SA-2.5.

by medical staff with 12 mg/kg intramuscular Ketamid® (ketamine-midazolam), and body condition was assessed by palpation of bony prominences.

The largest male (610 g) exhibited good body condition and was fitted with an LB-35 VHF transmitter of ~18 g (Telonics, Mesa, AZ, USA), representing less than 3% of the animal's body weight. The transmitter was programmed with a duty cycle of 12 hours from 6 AM to 6 PM. The transmitter signal was detected with a RA-2AK antenna and a TR-4 receiver (Telonics). The radio-transmitter was active for 18 months when the tagged tamarin was captured, and the device removed. No sign of injury or scars caused by the device was detected.

Between 1.5 and 2.0 ml ($\leq 1\%$ body mass) of blood was extracted directly through venipuncture of the femoral artery for hematological, parasitological, and genetic analyses. A subcutaneous volume of saline solution equal to the amount of collected blood was administered to each tamarin to replenish the amount of liquid taken, and their eyes were hydrated with artificial tear drops. After manipulation, tamarins were cushioned with a blanket, returned to their original trap cell, and released at the same site of capture while it was still daytime.

Study area

The main campus of UA, founded in 1969, is located on the East bank of the Medellín River in the city of Medellín (north-western Colombia), at 1,479 m a.s.l. ($6^{\circ} 16' 03''$ N; $75^{\circ} 34' 06''$ W). The climate is Equatorial with temperature variations between 17 and 28 °C and two annual rainy seasons (Reynolds et al., 2017). This campus consists of a heterogeneous landscape immersed within the urban matrix and is protected through Agreement No. 23, 2009 of the Medellín City Council. The campus has an approximate area of 24 ha, 53% of which corresponds to vegetated areas with lawns, gardens, and forest corridors, with 186 tree species of at least 10 cm diameter at breast height (Cárdenas, 2011). A total of 68 bird species in 26 families have been recorded in UA, along with other native species of vertebrates encompassing reptiles (iguanas and lizards) and mammals (opossums, bats, squirrels, foxes, and

tamarins) (Ávila et al., 2021; Londoño Zapata et al., 2006).

Data collection

Resting, traveling, feeding, grooming, conspecific aggression and interaction with other vertebrate species and humans were recorded for 12 months following a focal sampling approach. Since the tamarin group of interest was small (only four members) and cohesive, it was possible to record the time invested in a predominant activity of the entire group during the observation period (Altmann, 1974). Food items were classified as fruit pulp, leaves, seeds, bark, flowers and hunted animals. Human food offered individually or through wildlife feeders was also recorded as fruit, processed sugar, and flour-based items. No meat was observed in the anthropogenic food.

Data were collected during an annual cycle from November 2013 to October 2014, i.e., leaving one month after the animal trapping to allow the target group to return to its natural routine. Data collection in January 2014 was not possible and data were collected the following year in January 2015. Observations were made in three-hour sessions in consecutive intervals of 6–9 AM, 9 AM–12 M, 12 M–3 PM and 3–6 PM during different days of the week, including weekends, for a total of 196 observation hours during the entire year (6.33 days of observation per month).

We identified seasonal variation in the diet by estimating the time invested in the consumption of food items and the Simpson diversity of diet (SiD) every month. The latter considers the number of different food items the tamarins feed on and the relative proportion in which these items were consumed each month. Daily measurements of relative humidity, average temperature, and precipitation were retrieved from the weather station database of the Enrique Olaya Herrera airport, located 5.6Km from UA at an altitude of 1,490 m a.s.l. (TuTiempo, 2017).

The university campus was partitioned into 24 1-ha quadrats (100x100m) (Figure 1). The individual identification of georeferenced tree species was made using a guide provided by the environmental management department of the university. The abundance of tree species, the tree density (TD),

and the Simpson diversity of species (SiS) were estimated for each quadrat. In this case, the SiS considers the number of tree species present and the relative abundance of each species.

Statistical analyses

Time Model

To assess the influence of climatic variables and feeding time on the SiD (the response variable), we applied a multiple linear regression using MASS v7.3-51.1 (Venables & Ripley, 2002) and Leaps v3.1 (CRAN, 2020) implemented in the R statistical environment v3.5.3 (RCoreTeam, 2022). The explanatory variables were the fraction of time devoted to feeding, the monthly average of temperature, relative humidity, and precipitation, as well as the within-month standard deviations of these climatic variables. A selection of variables to choose the best model was made through a Stepwise Regression Analysis using the Bayesian Information Criterion (BIC). Then, a Box-Cox transformation was performed to improve the linear relationship between the chosen variables. A range between -2 and +2 of the lambda parameter was used to find the optimal value associated with the Box-Cox transformation. The models were validated with Shapiro-Wilk normality tests applied to the regression errors.

Space Model

We also applied a Multiple Linear Regression to study the preferences and factors determining the use of the available habitat, where the Percentage of Time invested in each Quadrat (PTQ) was the response variable of the model. The covariates ($m = 29$) were SiS and TD per quadrat in the 15 quadrats occupied by the tamarins, and the abundance of the 27 arboreal species comprising at least 1% of the trees in the study area and present in at least eight of the 15 occupied quadrats (supplementary table 1). We implemented the Brute Force Algorithm in MASS v7.3-51.1 (Venables & Ripley, 2002) and Leaps v3.1 (CRAN, 2020) using the R statistical environment v3.5.3 (RCoreTeam, 2022), and the BIC criterion to choose the most suitable models.

RESULTS

The exploratory study was conducted in an isolated forest patch on the main campus of the University of Antioquia, in Medellín, Colombia during an entire annual cycle. The tamarins spent 25% of their time resting, followed by traveling through vegetation or buildings (17%), feeding (10%), grooming (7%), interaction with birds, agonistic reaction to dogs and other interactions with non-human vertebrates (0.6%), and interaction with

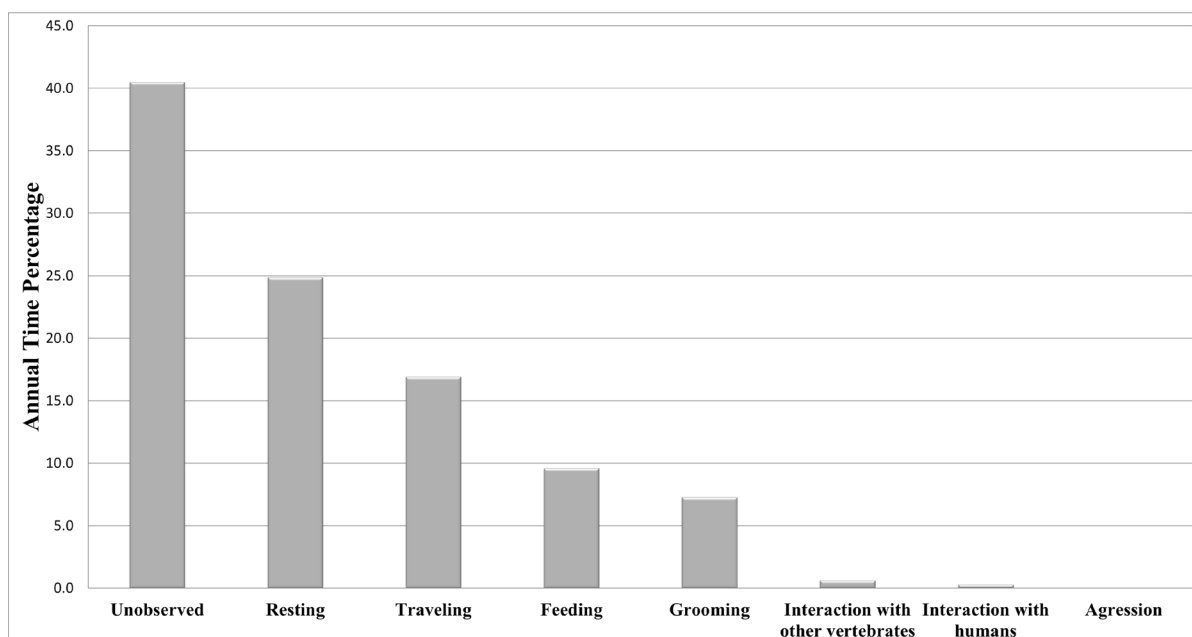


Figure 2. Annual activity budget of urban *Oedipomidas leucopus* expressed in time percentage (effective observation time of 195 hours and 48 minutes).

humans (0.3%) (Figure 2). Aggressive behaviors between group members were infrequent reaching only 0.02% of the total observation time. Time spent on building roofs was 41% and identification of specific behaviors in such areas was not possible. Regarding the time invested directly in feeding, two peaks of activity were evidenced in the morning

between 8 and 9 AM and then between 10 and 11 AM, followed by a third peak of even longer feeding time between 2 and 3 PM. After this, there was a rapid reduction in this behavior (Figure 3). These three time slots combined account for 38% of the daily time budget dedicated to feeding.

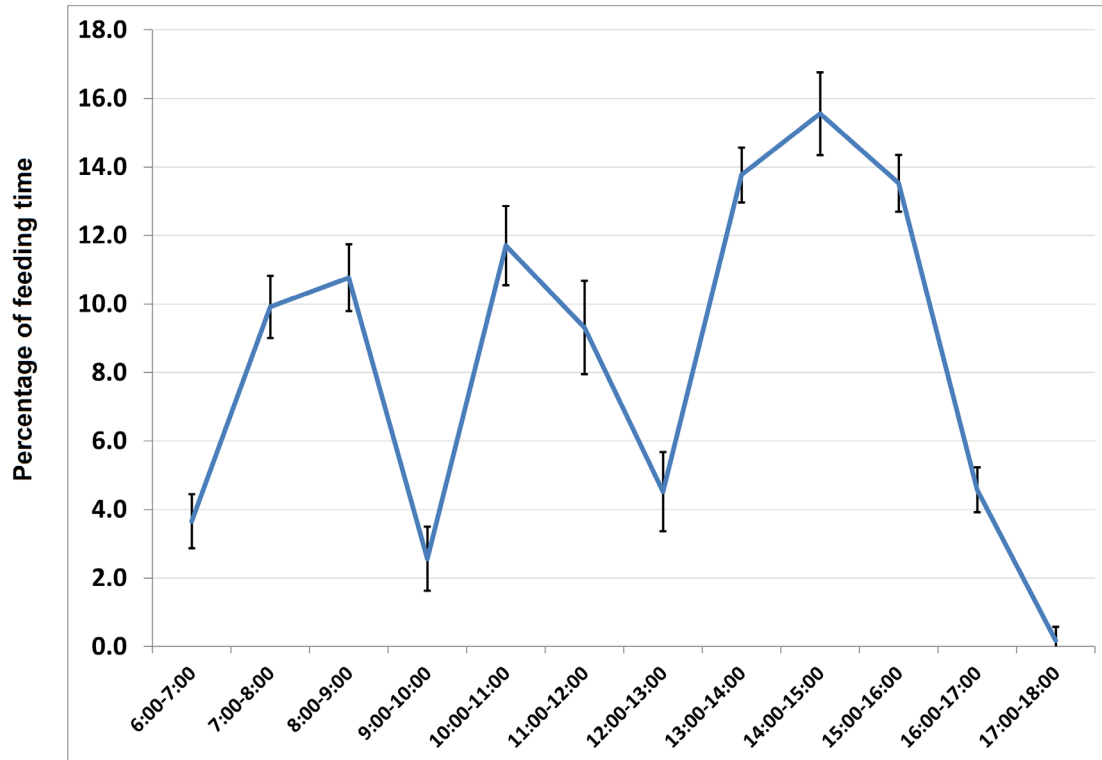


Figure 3. Average daily percentage of time investment in feeding during an annual cycle in urban tamarins. Bars denote the standard error of the mean.

We successfully identified specific food items 92% of the time spent feeding (Figure 4). Overall, 78% was based on food products from non-human sources. Tamarins dedicated almost half of the feeding time (47%) to consuming fruit pulp from natural sources. Animal products were the second most ingested food type in this list (14%), mainly represented by insects, bird eggs, and a single predation event on a turtledove chick. This was followed by other plant products such as leaves (8%), seeds (7%), and small proportions of gum and flowers (1% each). Altogether, tamarins fed on 32 different plant species, including 20 consumed during at least 1% of the feeding time (table 1). Five arboreal plants (*Psidium guajava*, *Mangifera indica*, *Inga* sp., *Melicoccus bijugatus*, and *Cecropia* sp.) accounted for 52% of this time. In addition to natural resources, tamarins appealed to anthropogenic food such as ripe bananas, processed sugar, and candies (12%), as well as baked goods such as cookies and crackers

in a smaller proportion (2%), either actively provided by people or opportunistically taken from accessible places like rooms or tables. Despite this human-associated behavior, tamarins rarely descended to the ground or explored trash cans on campus.

Whereas fruit pulp was the main food source year-round, it showed two peaks, one during February and March (78 and 74%, respectively), and another one in September (63%) (Figure 5). The trend exhibited by SiD was exactly the opposite, reaching its lowest values during these two time periods. There was a particularly high diversity in the diet in May marked by the consumption of all the potential food sources, both natural and human supplied. Consequently, months when tamarins most relied on fruit pulp were those with the lowest diversity in diet. When the lowest proportion of fruit pulp was consumed, tamarins tended to rely on a wider variety of food sources.

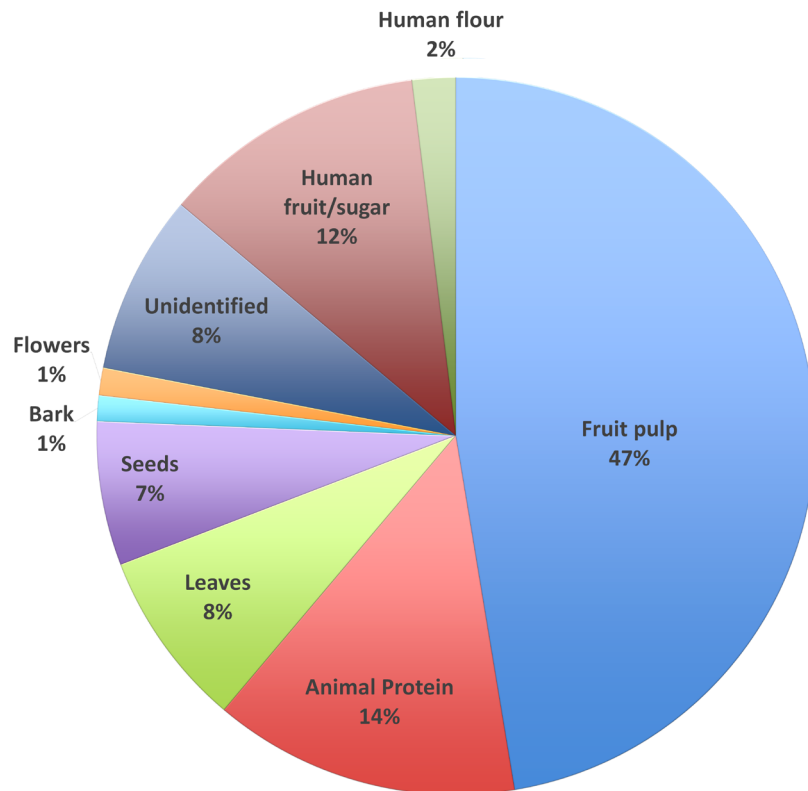


Figure 4. Overall percentage of time *Oedipomidas leucopus* spent feeding on different food sources during a one-year period (effective feeding time of 18 hours and 45 minutes).

Predated animals were more frequently eaten during the second part of the year, becoming the second most consumed source between June and October. Interestingly, anthropogenic food remained a secondary resource throughout the year despite its availability.

Time model

As a result of a Stepwise Regression, the model with the lowest BIC includes the monthly standard deviation of humidity (SDH) as the only variable that explains the variation in the diet diversity ($SiD = 5.98 - 0.32 \cdot SDH$, adjusted $R^2 = 0.25$, $p = 0.055$), with the errors of the model following a normal distribution ($W = 0.88$, $p = 0.097$). A Box-Cox transformation of SiD improved the relationship between the two variables. The optimal value of the lambda parameter of the transformation was $-38/99$ (~ -0.3838), which yielded the best approximation of a normal distribution curve for the data and maximized the likelihood function of the response variable. Thus, the transformed model is given by the function $((1 - \widehat{SiD}(-0.3838)))/0.3838 = 1.56 - 0.08 \cdot SDH$ (adjusted $R^2 = 0.39$, $p = 0.018$).

Space model

The tamarins occupied 15 of the 24 quadrats in the study area, with an average of 6.67%, 95% CI [4.66, 8.68] of time invested in each quadrat. The best model as given by the Brute Force Algorithm analysis included a positive effect of TD, and the abundance of seven plant species, namely sp2 (*Citrus nobilis*) and sp15 (*Bahuinia kalbreyeri*) with a positive coefficient, and sp3 (*Ficus benjamina*), sp4 (*Fraxinus uhdei*), sp14 (*Annona muricata*), sp18 (*Cariniana pyriformis*) and sp21 (*Ceiba pentandra*) with a negative coefficient (BIC = -98.6, adjusted $R^2 > 0.99$, $p < 0.01$) (supplementary tables 1 and 2). Besides, there are alternative models with BIC values < -90 that reiterate the influence of TD and highlight the influence of the SiS and the abundance of sp7 mango (*Mangifera indica*), sp9 guava (*Psidium guajava*), sp22 orange (*Citrus x sinensis*), sp24 coral bean (*Erythrina fusca*) and sp27 almond (*Terminalia catappa*) (Supplementary tables 1 and 2). Among these plant species, the effect of sp24 is ambiguous given its negative and positive signs on models 2 and 3, respectively.

Table 1. Plant species consumed by *Oedipomidas leucopus* and percentage of time invested in feeding on each source.

Family	Species	Local name	% Feeding time	Part eaten*
Myrtaceae	<i>Psidium guajava</i> L.	Guayabo	14.8	P
Anacardiaceae	<i>Mangifera indica</i> L.	Mango	10.8	P, L
Fabaceae	<i>Inga</i> sp.	Guamo	10.5	S, L, P
Sapindaceae	<i>Melicoccus bijugatus</i> Jacq.	Mamoncillo	9.8	P, G, L
Urticaceae	<i>Cecropia</i> sp.	Yarumo	6.1	S, G, P
Malvaceae	<i>Pseudobombax septenatum</i> (Jacq.) Dugand	Ceiba verde	5.5	P
Fabaceae	<i>Inga edulis</i> Mart.	Guamo Bejuco	5	P
Malvaceae	<i>Ochroma pyramidale</i> (Cav. ex Lam.) Urb.	Balzo	4.6	P
Lythraceae	<i>Lafoensia speciosa</i> (Kunth) DC.	Guayacán de Manizales	3.9	S, L
Bignoniaceae	<i>Crescentia cujete</i> L.	Totumo	3.5	P
Malpighiaceae	<i>Malpighia glabra</i> L.	Huesito	2.9	L
Oleaceae	<i>Fraxinus uhdei</i> (Wenz). Lingelsh.	Urapán	2.1	L
Rutaceae	<i>Citrus x sinensis</i> (L.) Osbeck	Naranja	1.9	L, P
Fabaceae	<i>Leucaena leucocephala</i> (Lam.) de Wit	Leucaena	1.7	S, F
Arecaceae	<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Palma de azúcar	1.5	P
Moraceae	<i>Ficus elastica</i> Roxb. ex Hornem.	Falso caucho	1.2	P
Combretaceae	<i>Terminalia catappa</i> L.	Almendro	1.2	S
Myrtaceae	<i>Eugenia malaccensis</i> L.	Pomarrosa	1.1	P
Rutaceae	<i>Casimiroa edulis</i> La Llave	Mango matasano	1	P
Malvaceae	<i>Pachira aquatica</i> Aubl.	Cacao de monte	1	G
Bignoniaceae	<i>Spathodea campanulata</i> P. Beauv.	Miona	0.8	P
Fabaceae	<i>Bauhinia kalbreyeri</i> Harms	Casco de vaca blanco	0.7	F
Salicaceae	<i>Flacourtia indica</i> (Burm. f.) Merr.	Cerezo del gobernador	0.4	P
Arecaceae	<i>Aiphanes caryotifolia</i> (Kunth) H. Wendl.	Palma corocito	0.3	L
Annonaceae	<i>Annona muricata</i> L.	Guanábano	0.3	P
Arecaceae	<i>Bactris gasipaes</i> Kunth	Palma chontaduro	0.3	L
Fabaceae	<i>Erythrina fusca</i> Lour.	Búcaro	0.3	S
Fabaceae	<i>Bauhinia variegata</i> L.	Casco de vaca orquídea	0.1	L
Moraceae	<i>Ficus lyrata</i> Warb.	Pandurata	0.1	G
Malvaceae	<i>Hibiscus tiliaceus</i> L.	Majagua	0.1	L
Sapindaceae	<i>Sapindus saponaria</i> L.	Chumbimbo	0.1	P
Rosaceae	<i>Eriobotrya japonica</i> (Thunb.) Lindl.	Níspero	0.1	P
-	Unidentified species	-	6.4	-

* F: Flowers; G: Gum; L: Leaves; P: Fruit pulp; S: Seeds.

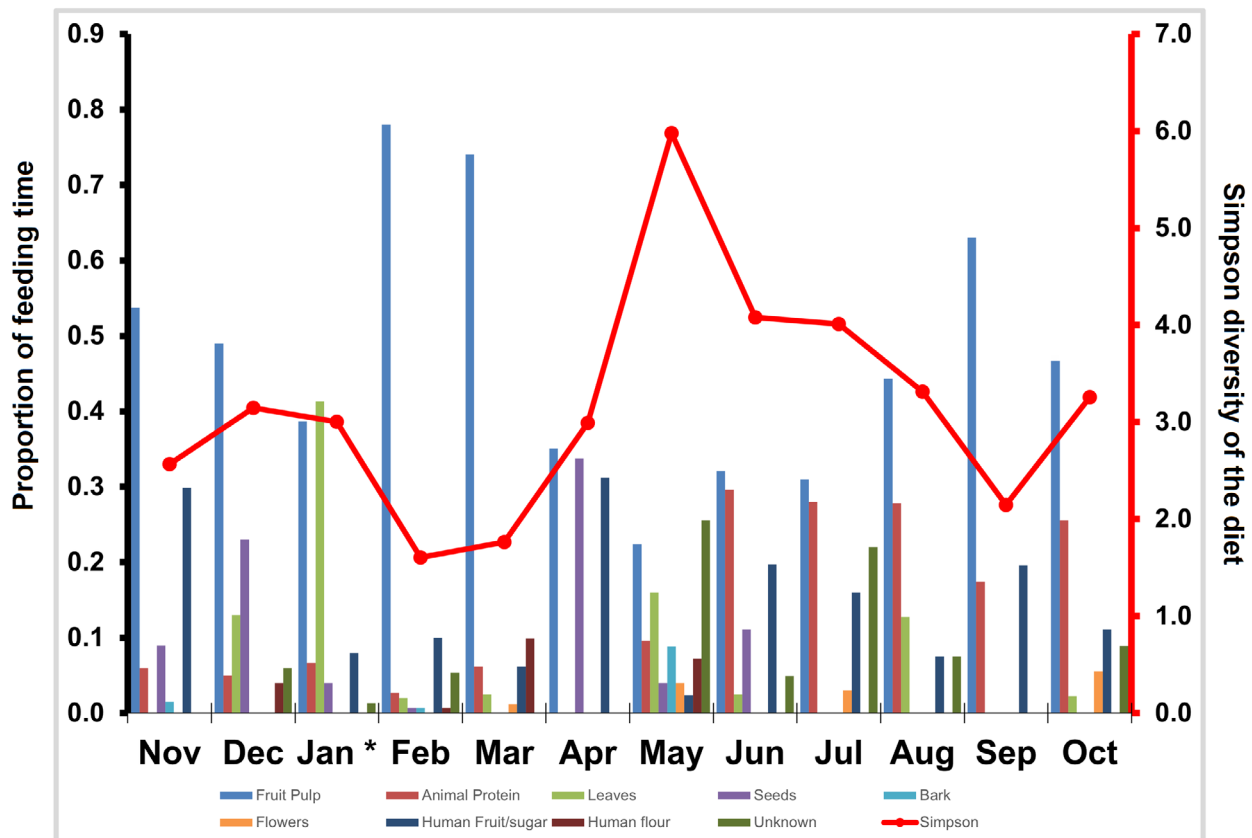


Figure 5. Monthly variation in fraction of time invested in feeding from different sources between November 2013 and October 2014. The proportion of time (color bars) and the Simpson diversity of Diet (red line) are represented by the left and right y-axes, respectively. *January data were collected in 2015 instead of 2014.

DISCUSSION

The rapid growth of human populations and urbanization conflicts with the concentration of biodiversity hotspots and primate ranges in developing countries (DESA, 2018). An unavoidable consequence of this juxtaposition is the increase in human-primate interactions, which have been mainly studied in Old World primates (McLennan et al., 2017). In this study, we assessed the spatial and temporal patterns of habitat use of the White-footed tamarin *O. leucopus* in an urban environment in north-western Colombia during one annual cycle. Although this study is based on a single social group and our conclusions are obtained from an urban forest with a unique combination of landscape features, it provided us with an opportunity to understand human-primate interactions, and primate adaptation to anthropogenic habitats. It also allowed us to gather empirical evidence of the relative relevance of several landscape features on the habitat use of urban animal species such as tamarins.

Even though resting was the most prevalent behavior of the target tamarin group, its quantification may be an underestimation since we failed to identify specific activities when tamarins were lying on the building roofs and food resources were likely unavailable. Therefore, we expect that the time budget devoted to resting or other social interactions be even higher than observed. This differs from tamarins in rural areas where feeding and moving are the most prevalent behaviors (De Luna et al., 2016; Rueda-Campiño et al., 2011; Zorrilla Aguirre and Ospina Serna, 2014). Likewise, urban macaques are known to spend more time grooming and playing than feeding due to reduced need of effort and time to seek food or easy access to provisioned food (Jaman & Huffman, 2013).

The interplay of multiple factors may explain this behavioral difference between rural and urban tamarins. Provisioned food (bananas and processed carbohydrates) was largely underrepresented in the diet of urban tamarins, but it is highly caloric and accessible year-round. Moreover, the lack of

competition with other tamarin groups and the high availability of fruit pulp from trees such as mangoes and guavas may reduce the need to seek food. This abundance of food resources results in reduced physical activity and as previously shown, an increased body weight and cholesterol levels (Soto-Calderón et al., 2016). Trash can exploration or receiving food from people are frequent in capuchin monkeys in Brazil (Sabbatini et al., 2006; Saito et al., 2010) and macaques in Gibraltar (Klegarth et al., 2017), and these behaviors were occasionally recorded in tamarins in this study. This trend toward exploring human resources is even more common in tamarins rescued from illegal trade recently released in UA (data not shown), revealing a role of learning derived from human interaction in these behaviors. Also, educational constraints induce begging behaviors in tamarins since entertainment by luring them with food or the misconception that urban wildlife is starving motivates people to keep providing food to primates and other vertebrates (Leite et al., 2011; Rodrigues & Martinez, 2014; Sabbatini et al., 2006). In addition to nutritional issues, the transmission of infectious diseases, and opportunistic capture of primates for illegal trade are other potential consequences of food exchange with primates and other vertebrates in urbanized environments.

We recognized both daily and seasonal variations in feeding behaviors of *O. leucopus*. Three distinct peaks of daily feeding activity were identified in *O. leucopus*. This consistency in feeding times persisted despite seasonal changes in food availability, indicating a robust daily feeding schedule for this species. While we were unable to investigate whether this pattern is common across other tamarin populations or the extent to which it may vary with environmental factors such as temperature or rainfall, similar patterns of daily feeding activity have, nonetheless, been documented among populations of the same primate species, including *Eulemur fulvus* and *Lemur catta* (Sussman, 1977).

We also observed a prevailing proportion of fruit pulp in the diet followed by invertebrates, and then other plant products from over 30 species/genera. In other studies, at least twelve of these plants have been reported as part of the *O.*

leucopus diet (Gómez-Ruiz, 2014; Poveda and Sánchez-Palomino, 2004; Rueda-Campiño et al., 2011; Sánchez-Londoño et al., 2013). These include four of the most consumed arboreal species which together account for 42.2% of the feeding time, namely *M. indica*, *P. guajava*, *Inga* sp., and *Cecropia* sp. These are cultivated species common at low and intermediate elevations in Colombia. Whereas *M. indica* and *P. guajava* are highly consumed and traded by local communities and represent reliable food sources for frugivorous or omnivorous animals, *Cecropia* sp. is also highly consumed by other mammals such as owl monkeys (*Aotus lemurinus*) (Bustamante-Manrique et al., 2021) and phyllostomid bats (Castaño et al., 2018) in urban settings of the northern Andes.

Likewise, *M. indica* and *P. guajava* are the most abundant species of tree in the study area (251 and 72 plants, respectively), while there are only nine specimens of *Inga* sp. (the third most consumed), indicating that the selection of plant species for feeding may be determined by both abundance and preference. The omnivorous diet of *O. leucopus* is highly variable, and varies with space and time, thus endowing this species with an intrinsic ability to adapt to urban matrices (De Luna et al., 2016; Poveda & Sánchez-Palomino, 2004).

SiD exhibited a gradual variation during the study period and an inverse relationship with the within-month SDH. Despite the significant relationship between these two variables, the R² explained under 50% of the SiD variation, and it is likely that other unconsidered factors also affect the diet variability of tamarins throughout the year. The consumption of fruit pulp decreases as alternative sources such as insects and other plant products increase, and it also varies with SDH so that there is a reduced reliance on fruit when humidity is more homogenous.

In lowland forests of the Colombian Andes, where our study area is located, most fruit types are available during the dry season, although several plant species have peaks of fruit production in both the wet and dry seasons (Gómez Restrepo, 2018). In contrast, a phenological review of tropical forests has pointed out that fruit preferred by primates usually peaks in the wet season (van Schaik & Pfannes, 2005). However, we found no

relationship between SiD and the average monthly humidity, and a more detailed analysis of the relevance of climatic and phenological factors on diet will be a matter of interest for future studies.

High TD in the areas occupied by *O. leucopus* stands out in the models, regardless of the plant species diversity and composition. This indicates that tree cover plays a significant role in space use in these areas, facilitating traveling and providing shelter. The individual abundance of tree species with a positive effect in the models was found to be important in areas of the campus where they may improve connectivity or facilitate access to roofs. Several of these tree species in the first model may also serve as alternative food sources, including *Bahuinia kalbreyeri* (sp15) and *Citrus x sinensis* (sp22), while species such as *P. guajava* (sp9) and *M. indica* (sp7), which are present in models 2 and 3 respectively, are the main components of the diet of tamarins in the university campus. Therefore, planting these species may be an effective way to connect corridors while providing food sources. On the other hand, the effect of certain tree species that appear in the models with negative coefficients may be interpreted in terms of their location, rather than an intrinsic repulsion of the tamarins towards these species. Most of these trees are in peripheral zones of the campus close to developed areas or roads in the urban matrix whose use by tamarins is scarce or null (e.g. *Ficus benjamina*) or are in spots isolated from effective tree corridors (e.g. *Ceiba pentandra*).

Our models reveal the importance of both vegetation composition and structure in urban settings for the conservation of biodiversity. The high consumption of several tree species, such as mango and guava, and their role at the bottom of the trophic chain, indicate that they are keystones in the preservation of urban wildlife. Likewise, the structure of tree communities is essential to guarantee access to food resources as well as connectivity and dispersal among forest patches. The latter is particularly challenging in fragmented and rapidly changing urban forests, but it is necessary to prevent the deleterious effect of isolation, inbreeding, and extinction due to random demographic changes of small populations. Moreover, although our temporal model partially explains the seasonal variation in habitat use of

urban tamarins, it is necessary to support further ecological research in cities to better understand the habitat requirements in these environments.

Monitoring an urban social group of wild tamarins for an entire year allowed us to better understand the mechanism of adaptation to an urban landscape. Given the plasticity of the tamarin diet, these primates rely on a wide range of food resources including those provided by humans and exhibit a notable seasonal variation in feeding habits. In addition, their isolation prevents competition for territory and resources with other tamarins, likely associated with the observed reduced physical activity. This scenario may explain their trend toward a metabolic disorder and their low parasite diversity, likely derived from the disruption of some parasite transmission cycles (Soto-Calderón et al., 2016; Werner & Nunn, 2020).

Whereas climate (and likely plant phenology) partially explained the seasonal diet variation, other variables such as tree abundance, distribution of specific food sources, and the location of certain trees account for habitat use. Together, these factors guided the preference for specific areas where wild animals may find food, shelter, and effective corridors between suitable forest patches.

Future conservation actions include education to promote healthy human-wildlife interactions, avoiding for instance the offer of food scraps or the use of wildlife feeders, frequently employed to attract charismatic animals such as birds, but also primates. Also, the conservation of urban biodiversity confers multiple benefits to local communities (Dearborn & Kark, 2010); it provides opportunities for environmental education, and in doing so, it promotes healthier interactions between humans and wildlife, reduces the risk of parasite transmission and nutritional imbalances, and discourages wildlife trade as factors that jeopardize the sustainability of wild populations in urbanized areas. Education itself can also be regarded as an opportunity to instill ethical principles around the interaction with urban wildlife (e.g. discouraging wildlife trade) (Dearborn & Kark, 2010).

Integration of wildlife into land-use and development plans (e. g. Planes de Ordenamiento Territorial), and restoration of functional corridors

between forest reserves and urban parks is necessary to prevent isolation and local extinction of urban fauna. Involving local governments and stakeholders through the integration of wildlife into development plans of urban areas is key to guarantee the preservation of urban wildlife refuges and continuation of conservation practices in those areas.

Finally, complementary studies should also address the impact of noise and air pollution, predation, and epidemiological dynamics to better understand the challenges that wildlife face in urbanized habitats.

CONCLUSIONS

- This study shows that urban tamarins rely on a wide range of food resources including those provided by humans, and exhibit a notable seasonal variation in feeding habits. The exploitation of a wide range of potential food resources seems to be key in the adaptation of white-footed tamarins to disturbed environments including urban and peri urban forests.

- Whereas climate (and likely plant phenology) partially explained the seasonal diet variation, other variables such as tree abundance, distribution of specific food sources, and the location of certain trees accounted for the habitat use. Together, these factors guided the preference for specific areas where tamarins may find food, shelter, and effective corridors between suitable forest patches.

- A daily feeding pattern with three distinct activity peaks—two in the morning and one in the afternoon—was identified in the white-footed tamarin. Whether this behavior is an intrinsic characteristic of the species or varies in response to ecological factors remains an important topic for future research.

- Future conservation actions include education to promote healthy human-wildlife interactions, integration of wildlife into land-use plans, and restoration of functional corridors between forest reserves and urban parks to prevent isolation and local extinction of tamarins and other small species, and research to investigate the impact of pollution, noise, and accidentality on the survival and viability of urban populations.

- The results from this study are preliminary and restricted to a single tamarin group; therefore, caution has to be taken in their extrapolation to other populations or species in urbanized areas.

ACKNOWLEDGMENTS

This research received no external financial support and was conducted with funds of the research laboratory. We are grateful to Andrea Hinek for proofreading and polishing this manuscript. All the co-authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTION

IDSC: Conceptualization, methodological design, data curation, formal analysis, organization of fieldwork, original investigation design, project administration, and document writing. AMPE: Methodological design, data curation, formal analysis, and document writing. TAM: Data collection, data curation, formal analysis, and organization of fieldwork. AMJG, VDV and VMA: Data collection, data curation and organization of fieldwork. CCHG: Formal analysis, document writing, and editing.

CONFLICT OF INTEREST AND ETHICS STATEMENT

The authors declare no conflicts of interest in any step of this study. This research adhered to the legal requirements of the Colombian government. The National Authority of Environmental Licenses (ANLA; permit #268, February 1, 2013) and the Committee on Ethics and Animal Research at the University of Antioquia (May 3, 2013) authorized all animal-handling protocols to the first author.

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