DOI: https://doi.org/10.62015/np.2022.v28.347

ACTIVITY BUDGETS OF BLACK AND GOLD HOWLER MONKEYS LIVING IN URBAN AND NATURAL HABITATS IN SOUTHWEST PARAGUAY

Victoria Overbeck[1,2], Pamela Gonzalez[1], Wing Man Lau[1], Erica DesJardins[1,] Marco Alesci[1], Jake Wellian[1], John Kane[1,3], Melissa Henderson[1], Rachel Blood[1] and Rebecca L. Smith[1]

[1] Fundación Para La Tierra, Centro IDEAL, Pilar, Ñeembucú, Paraguay, Email: <rebecca@paralatierra.org>
[2] Swarthmore College, 500 College Ave, Swarthmore, Pennsylvania 19081, USA
[3] Department of Bacteriology, University of Wisconsin-Madison, Wisconsin, USA

Abstract

As urbanisation continues to encroach upon the natural habitats of wild primates, it is important to understand how species adapt to these anthropogenic changes by observing how they allocate time to different activities. This study investigated whether activity budgets of black and gold howler monkeys (*Alouatta caraya*) living in an urban habitat (located in the city of Pilar, Ñeembucú, southwest Paraguay) differed from black and gold howler monkeys living in the surrounding natural environment of the Ñeembucú Wetland Complex. We recorded 404.32 h of observation over 73 days – 360.07 h of observation in the Urban habitat over 67 days and 44.25 h of observation in the Natural habitat over 6 days. When comparing activity budgets across habitat types, there was no difference in time allocated to any of the four behavioural categories, which could suggest that the black and gold howler monkeys are adapting well to increased urbanisation. Among all age-sex classes and habitats, resting was the most prevalent activity (67.51%), followed by feeding (13.05%), travelling (12.74%), socialising (6.17%), and other (0.53%). Overall, adult males spent significantly more time resting (mean= 71.14%) and less time travelling (mean=8.86%) compared to immature males (mean = 46.10%, P = 0.038 for resting; mean=17.83%, P=0.026).

Key words: *Alouatta caraya*, behaviour, Central and South American primates, time budgets, urbanisation

Resumen

Mientras la urbanización continúa invadiendo los hábitats naturales de los primates silvestres, es importante entender cómo los primates se adaptan a estos cambios antropogénicos por observar cómo asignan sus tiempos a las diferentes actividades. Este estudio investigó si los presupuestos de actividad de los caraya (*Alouatta caraya*) que viven en un hábitat urbano (ubicado en la ciudad de Pilar, Ñeembucú, suroeste de Paraguay) difieren de los caraya que viven en el entorno natural circundante entorno del Complejo de Humedales de Ñeembucú. Anotamos 404,32 h de observación durante 73 días - 360,07 h de observación en el hábitat urbano durante 67 días y 44,25 h de observación en el hábitat natural durante 6 días. Al comparar los presupuestos de actividad entre los tipos de hábitat, no hubo una diferencia en el tiempo asignado a ninguna de las cuatro categorías de comportamiento, lo que podría insinuar que los caraya se están adaptando bien al crecimiento de la urbanización. Entre todas las categorías de edad-sexo y hábitats, a descansar fue la actividad más prevalente (67,51%), seguida de alimentarse (13,05%), translocar (12,74%), socializar (6,17%) y otras (0,53%). En general, los machos adultos pasaron significativamente más tiempo descansando (media = 71,14%) y menos tiempo viajando (media = 8,86%) en comparación con los machos inmaduros (media = 46,10%, P = 0,038 para descansar; media = 17,83 %, P = 0,026).

Palabras claves: *Alouatta caraya*, comportamiento, primates de Centro- y Sudamérica, presupuestos de actividad, urbanización

Ñemombyky

Urbanización oñemotenonde ohóvo umi ka'aguy ka'ikuera oikoha, tuicha mba'e oñentende mba'éichapa umi ka'i oikokuaa umi cambio antropogénico ndive rohecha chaicha mba'éichapa oiporu ijactividakuera. Ko estudio oinvestiga umi presupuesto actividad orekóva umi caraya (*Alouatta caraya*) oikóva peteî hábitat urbanope (Pilar, Ñeembucú, suroeste Paraguay) iñambuépa umi caraya oikóva ka'aguyhare pe estero tiuchakue Ñeembucúpe. Roregistra 404,32 aravo 73 árape - 360,07 aravo cuidape (67 árape) ha 44,25 aravo ka'aguype (6 árape). Oñembojojávo umi presupuesto caraya activida rehegua umi hábitat apytépe, ndaipóri diferencia umi tiempo oñeme'ẽvape ni peteĩva umi irundy categoríape hekove kuera rehegua, ikatúva ohechauka oiha diferencia, umi caraya ohechauka ojeadapta porãha la urbanización

ndive okakuaa haguã. Opaitechagua hábitat ha edad-sexo apytépe, opytu'u haẽ pe actividа ojeipysóva (67,51%), hapykuéri katu jekaru (13,05%), guata katu (12,74%), hapicha kuera apytepe (6,17%) ha ambue (0,53%). Opaiteicha umi machokuera kakuaáva hetave ohasa itiempo opytu'úvonde (media = 71,14%) ha sa'ive tiempo oguata (media = 8,86%) oñembojojávo machokuera inmaduros ndevi katu (media = 46,10%, P = 0,038 opytu'u haguã; media = 17,83%, P = 0,026).

Ñe›ê clave: *Alouatta caraya*, Teko rehegua; Ka'ikuera Mbyteamérika ha Ñembyamérikagua, Actividа rehegua, Táva okakuava rehegua

Introduction

More than 60% of primate species are threatened with extinction and habitat loss that is driven by anthropogenic activities, including increasing urbanisation (Estrada 2009; Sol et al. 2013; Bicca-Marques 2017). The wide-scale alteration and fragmentation of natural habitats can lead to a decrease in natural food sources, an increase in noise, light, and chemical pollution, and increased opportunities for human-wildlife contact and potential conflict (Sol et al. 2013). To survive in this rapidly changing world, primate species must adapt to habitat alterations or risk becoming locally extirpated (Bicca-Marques 2017; Back et al. 2019).

Activity budgets are a measure of how primates allocate their time (Strier 1987) and are influenced by both environmental constraints (e.g., availability of food sources, sleeping sites, and water sources) and physiological constraints (e.g., individual energy requirements and thermoregulation) (Agetsuma and Nakagawa 1998; Hanya 2004; Doorn et al. 2010; El Alami et al. 2012). Behavioural flexibility in activity budgets could increase a population's chance of survival in these changing environments (El Alami et al. 2012). Examining the effect of urbanisation on a population's activity budget is the first step to understanding whether a given population (or species as a whole) can adapt to an increasingly anthropogenic world.

Age and sex are critical factors affecting primates' activity budgets as a result of the different energetic demands required at each stage of development (Strier 1987; Yanhong et al. 2014). For instance, adult black and gold howler monkeys (*Alouatta caraya*) in a seminatural forest located in Estância Casa Branca, Argentina allocated a greater proportion of time to resting (Bicca-Marques and Calegaro-Marques 1994), whereas subadult and juvenile black and gold howler monkeys socialised more often than other age classes, and infants spent the most time travelling (Prates and Bicca-Marques 2008).

Sociodemographic factors, such as group size, can influence primates' activity budget (Agostini et al. 2012). A large group of brown howlers (*Alouatta guariba clamitans*) in Misiones, Argentina spent more time moving, feeding, and less time resting than those in the smaller group; at the same site, in contrast, a larger group of black and gold howlers spent a significantly greater proportion of time travelling and socializing, and less time feeding than individuals in the smaller group (Agostini et al. 2012).

Howler monkeys (genus *Alouatta*) are folivorous-frugivorous primates found throughout Central and South America (Prates and Bicca-Marques 2008). The black and gold howler (*Alouatta caraya*) is found in Paraguay, Brazil, Bolivia, Argentina, and potentially northwestern Uruguay (Bicca-Marques et al. 2020). Activity budgets of black and gold howler monkeys in Argentina (Bravo and Sallenave 2003; Agostini et al. 2012; Pavé et al. 2016) and Brazil (Bicca-Marques and Calegaro-Marques 1994; Prates and Bicca-Marques 2008; Rímoli et al. 2008) have been conducted, but very few studies have looked at the ecology or activity budgets of black and gold howler monkeys in Paraguay (Stallings 1985; Pinkowski and Smith 2018; Kane and Smith 2020; Alesci et al. 2022; Duffy et al. 2022). Though previous studies of black and gold howler monkeys have shown that they are capable of coping with habitat alteration (Bicca-Marques 2003), no studies have examined the effects of living in an urban habitat on the activity budgets of black and gold howler monkeys. This study investigates whether black and gold howler monkeys living in a natural habitat allocate time differently compared to those living in an urban habitat in Ñeembucú Department, southwest Paraguay.

Methods

Study site

The study was conducted across two habitats (urban and natural) in Ñeembucú Department, southwest Paraguay. The City of Pilar (-26.85726, -58.30753)–the urban habitat in our study–is the capital of the Ñeembucú Department, with a population of about 33,000 people (DGEECC, 2020). The natural habitat, Estancia Santa Ana (-26.83612, -58.02426), is a 700-ha cattle ranch located 30 km east of Pilar in the Ñeembucú Wetland Complex. This habitat is a natural mosaic of humid Chaco, grassland, and gallery forest, that naturally exists in island-like fragments that have not been altered from this natural state despite the presence of low-impact cattle ranching.

Table 1. Average rainfall (mm) and temperatures (°C) in Ñeembucú Department, southwest Paraguay during the study observation periods (https://www.worldweatheronline.com/).

Month & Year	Temperature (°C)	Rainfall (mm)
August 2017	22	75.4
September 2017	25	59.9
October 2017	25	297.6
November 2017	26	177.2
June 2018	16	55.06
July 2018	17	30.1
August 2018	18	50
August 2019	19	18.4
January 2020	32	115.7
February 2020	30	61.6
March 2020	30	33.2

Paraguay has inconsistent rainfall that varies greatly each year throughout its "Wet and Dry" and "Hot and Cold" seasons (Hill et al. 1984; Duffy et al. 2022). Average rainfall (mm) and temperature (°C) for the study observation periods are shown in Table 1.

Study Subjects

Four groups of black and gold howler monkeys were sampled across the two different habitats. Within the urban habitat, we observed two groups (Factory and Police) of black and gold howler monkeys with highly fragmented, small home ranges (1.01 - 3.07 ha) that consist of a matrix of roads, buildings, and powerlines (Kane and Smith 2020; Duffy et al. 2022). Within the natural habitat, we observed two different groups (Swamp and Roadside) of black and gold howler monkeys with home ranges that are limited to the small areas of undisturbed gallery forest where there was little to no human interaction.

Across all four groups, there were 52 individuals. Individuals were identified by age and sex following the descriptions in Rumiz (1990). Demographics of the study groups are provided in Table 2.

Data Collection

Data were collected from 25th August to 28th November 2017, from 26th June to 6th August 2018, 20th – 27th August 2019, and from 20th January to 2nd March 2020 from 5:45am-10:45am and 13:45pm-17:45pm by 12 different observers (typically, 1-4 observer(s) collected data on a single group per day) (Table 3). The minimum time spent per day with a given group over the entire study period was 15 minutes, and the maximum time spent per day with a given group over the entire study period was 10 hours. On average, an observer spent about 4.4 hours with one group per day over the entire study period. We recorded 404.32 h of observation (170.06 h with Factory group, 190.01 h with Police group, 22.50 h with Roadside group, and 21.75 h with Swamp group) over 73 days. We excluded records with insufficient behavioural

Table 2. Demographics of the black-&-gold howler monkeys by habitat and groups within each habitat. Numbers varied through immigrations, emigrations, births and deaths during the observation period; all individuals observed in the groups during the study period are included here in the tally. Subadult, juvenile, and infant males and females were classified as 'Immature' males and females.

	Habitat & Groups				
	Urban		Natural		
Age-Sex	Factory	Police	Swamp	Roadside	TOTAL
Adult male	2	5	2	2	11
Adult female	2	6	2	4	14
Immature male	4	5	3	1	13
Immature female	1	11	1	1	14
TOTAL	**9**	**27**	**8**	**8**	**52**

Table 3. Observation months/years for each study group over the entire study period.

Study Group	Observation Period
Factory	August – October 2017 June – August 2018
Police	October – November 2017 June – August 2018 August 2019 January – February 2020
Swamp	January & March 2020
Roadside	August 2018 January & March 2020

Table 4. Number of behavioural records observed for each age-sex class in the urban and natural habitats over the entire study period.

	Habitat		
Age-Sex	Urban	Natural	Total
Adult male	961	412	1373
Adult female	1209	767	1976
Immature male	806	423	751
Immature female	841	266	586
TOTAL	**3817**	**1868**	**5685**

description, and/or that were missing age/sex information, leaving a total of 5685 behavioural records (Table 4).

We used scan sampling (Altmann 1974) to record the behaviour of all visible individuals every 30 minutes. We reduced the potential for bias in the sampling effort by randomly sampling when doing visual scans in the field. In each scan, we recorded: (a) the time and area location of the group; and for the visible black and gold howler monkeys, we recorded: (b) identity, (c) sex, (d) age, (e) behaviour, and when applicable, (f) tree location, (g) height above the ground, (h) proximate individuals, and (g) any other relevant information. The behaviour was classified into one of the following categories, using similar definitions as Rímoli et al. (2012) and Schreier et al. (2021): feeding (i.e., when the animal was observed biting, chewing, ingesting, and/or manipulating food or water with its hands, feet, mouth), resting (i.e., when the animal remained in one location, was inactive, lying down, or asleep), social (i.e., when the animal was observed engaged in social interactions including grooming, playing, aggression, submission), travelling (i.e., moving any sort of distance) and other (i.e., any behaviour not mentioned above).

Data analysis

We pooled data for the different age-sex classes into four total classes to provide sufficient data for analysis (Table 2; similar to Rímoli et al. 2012 and Jaman and Huffman 2013). Similar to Prates and Bicca Marques, (2008), we did not include behaviours accounting for <1.5% of records among any of the age-sex classes in our analyses. Activity budgets were calculated similarly to Agostini et al. (2012). First, we combined all data for each day of observation for each age-sex class. We then calculated the time allocated to each activity for each day of observation and each age-sex class as the proportion of scanned individuals engaged in each activity type. Using these proportions, we calculated an overall activity budget and activity budgets for each age-sex class within each group and habitat. Activity budgets were expressed as the time allocated to each activity divided by the total amount of time sampled overall, for each age-sex class, and within each group and habitat. One-way ANOVA was used to compare the time allocated to each of the behavioural activities for the four age-sex classes, the groups within each habitat, and the two habitats. Tukey's *post hoc* test was used for the pairwise comparisons of the respective proportions. All statistical analyses were done using RStudio 2022.07.1+554. Each analysis was 2-tailed with significance set at $p < 0.05$.

Results

Overall, resting was the most prevalent activity (67.51%), followed by feeding (13.05%), travelling (12.74%), socialising (6.17%), and other (0.53%).

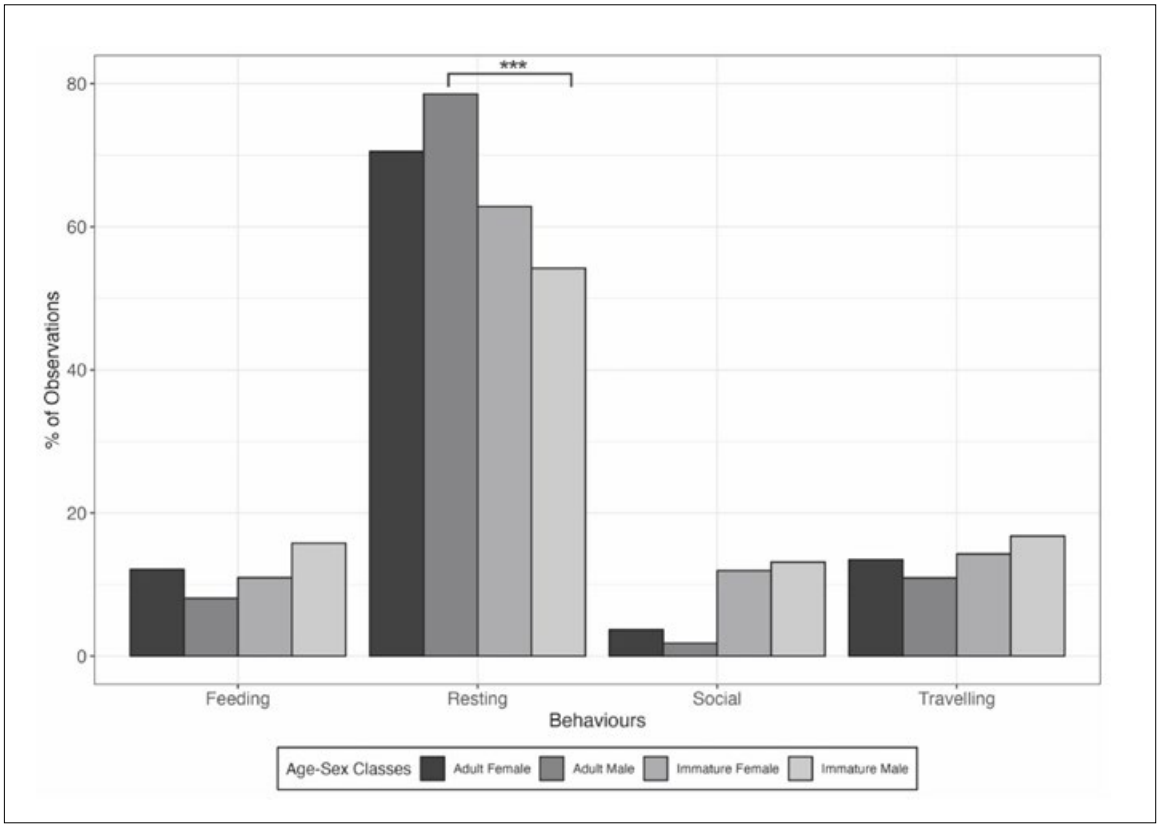

Figure 1. Activity budgets between the different age-sex classes.

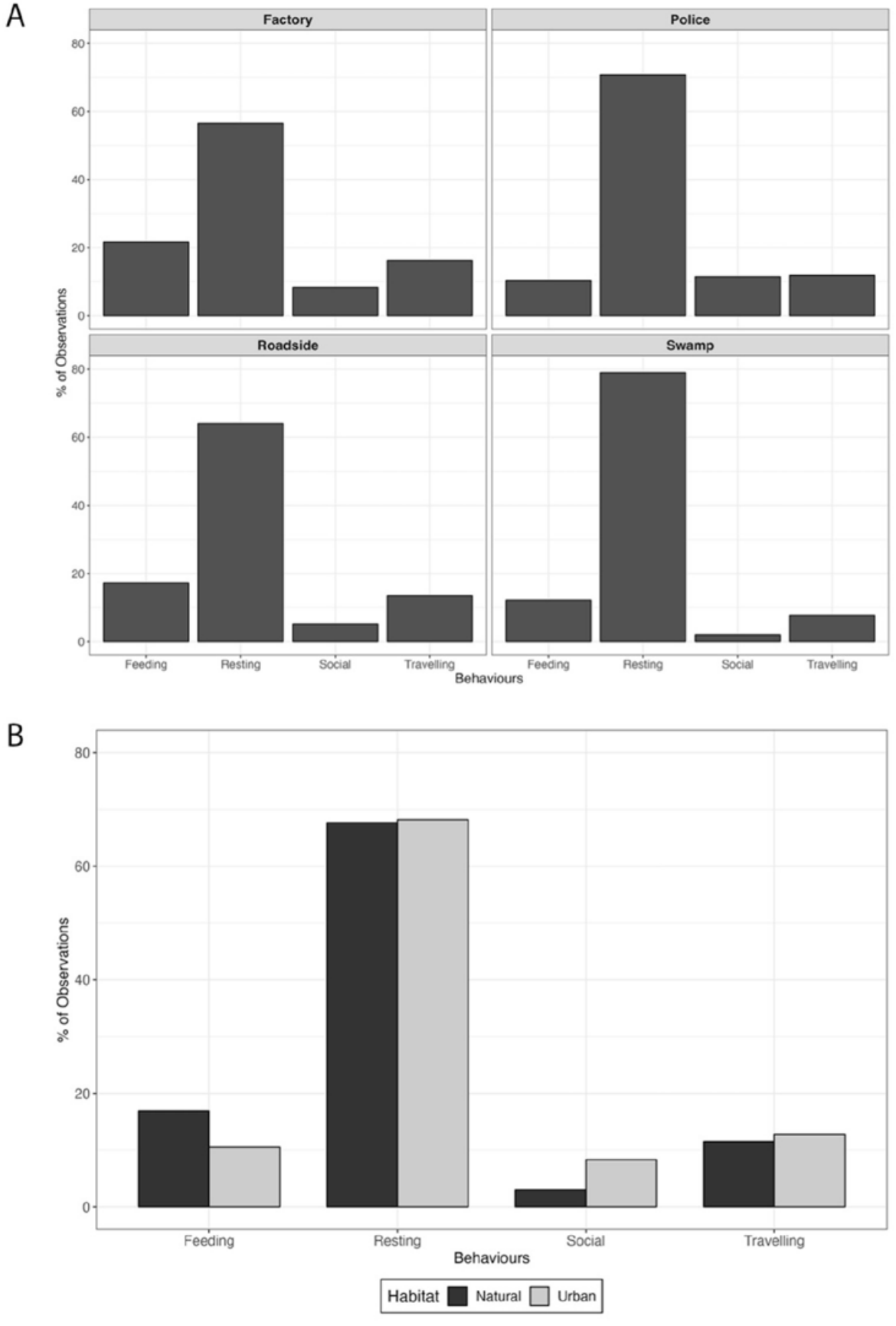

Figure 2. (A) Activity budgets between the different groups within each habitat (Urban = Factory and Police; Natural = Roadside and Swamp). (B) Activity budgets between the different habitats.

Table 5. Comparison of activity budgets across the genus *Alouatta*.

Species	Location	% of Time Allocated to Each Activity					Reference
		Resting	Feeding	Travelling	Social	Other	
Alouatta caraya	Ñeembucú Wetland Complex, Paraguay	66.65	16.60	11.34	4.28	1.12	This Study
Alouatta caraya	Pilar, Paraguay	67.93	11.32	13.41	7.10	0.24	This Study
Alouatta caraya	Estabelecimento Nossa Senhora da Conceição, Alegrete, Rio Grande do Sul, Brazil	56.5	14.9	23.4	3.9	-	Prates and Bicca-Marques (2008)
Alouatta caraya	Flooded forest, Brasilera Island, Northeastern Argentina	56.5	18.9	16.5	8.0	-	Bravo and Sallenave (2003) (Mean annual values)
Alouatta caraya	Aquidana River, Mato Grosso do Sul, Brazil	64.7	10.1	18.5	4.4	2.3	Rímoli et al. (2012)
Alouatta caraya / Alouatta guariba clamitans	El Piñalito Provincial Park, Misiones, northeastern Argentina	57.0-65.0	12.0-15.0	11.0-15.0	3.0-5.0	1.0-2.0	Agostini et al. (2012)
Alouatta seniculus	Colombian Andes	63.0	22.0	10.0	-	4.0	Palma et al. (2011)
Alouatta seniculus	Colombian Andes	78.5	12.7	6.2	2.0	0.5	Gaulin and Gaulin (1982)
Alouatta palliata	Los Tuxtlas, Mexico	80.0	17.0	3.0 (includes traveling and social behavior)		-	Estrada et al. (1999)
Alouatta palliata	Los Tuxtlas, Mexico	61.9	26.4	10.5	-	1.2	Asensio et al. (2007)
Alouatta belzebuth	Paranata, MT, Brazil	58.7	20.0	18.2	2.1	-	Pinto (2002)
Alouatta guariba	Araucaria Pine Forest, southern Brazil	57.6	19.0	18.8	-	-	De Marques (1996)

Variation in Activity Budgets between Age-Sex Classes

There was no difference in time allocated to feeding or socialising between any of the age-sex classes ($F_{[3,27]} = 1.504$, $P = 0.24$ for feeding; $F_{[3,27]} = 0.358$, $P = 0.784$ for socialising). There was a difference in time allocated to resting and travelling between at least two of the age-sex classes ($F_{[3,27]} = 3.274$, $P = 0.036$ for resting; $F_{[3,27]} = 3.61$, $P = 0.026$ for travelling). Adult males allocated significantly more time to resting (mean= 71.14%) and significantly less time to travelling (mean=8.86%) compared to immature males (mean = 46.10%, $P = 0.038$ for resting; mean=17.83%, $P=0.026$). There was no difference in time allocated to resting or time allocated to travelling between any other age-sex classes (Figure 1).

Variation in Activity Budgets between Groups within each Habitat

There was no difference in time allocated to any of the behavioural categories between the two groups (Factory and Police) in the urban habitat (F [1,6]=1.713, P=0.238 for feeding; F [1,6]=2.515, P=0.164 for resting; F [1,6]=2.02, P=0.205 for travelling; F [1,6]=0.996, P=0.357 for socialising) or between the two groups (Roadside and Swamp) in the natural habitat (F [1,2]=0.345, P=0.616 for feeding; F [1,2]=1.212, P=0.386 for resting; F [1,2]=1.65, P=0.328 for travelling; F [1,2]=14.95, P=0.0609 for socialising) (Figure 2A).

Variation in Activity Budgets between Habitats

There was no difference in time allocated to any of the behavioural categories between the two habitats (F [1,7]=3.402, P=0.108 for feeding; F [1,7]=0.149, P=0.711 for resting; F [1,7]=0.016, P=0.903 for travelling; F [1,7]=1.718, P=0.231 for socialising) (Figure 2B).

Discussion

The differences between age-sex classes in both habitats were consistent with previous observations of this species, with older individuals spending more time resting and less time socialising (Bicca-Marques and Calegaro-Marques 1994). In our study, adult males spent more time resting than immature males. This could be because adult male black and gold howler monkeys tend to eat at a faster rate than others in the group, and are capable of monopolising food sources, which means less time required for travelling to get food sources. Less time required for travelling and feeding allows for more time for resting. Another possible explanation for why adult male black and gold howler monkeys spent more time resting compared to younger, more active males is due to their limited energetic requirements (Bicca-Marques and Calegaro-Marques 1994).

The amount of time spent feeding is inversely related to the nutrient content of the food consumed (Strier 1987). Even though black and gold howlers in the urban and natural habitats spent similar times feeding (11.32% vs. 16.6% respectively; Figure 2A), there are differences in the diets of the primates between these two habitats. Black and gold howler monkeys in the urban habitat have access to higher quality food sources from neighbouring gardens or rubbish piles scattered throughout their home range. The urban black and gold howler monkeys were observed consuming fewer leaves and had easier access to high energy fruit, including mangoes and avocadoes (Para La Tierra, unpublished data), which could enable them to spend less time feeding, while still fulfilling their energetic needs. Compared to previous studies of *Alouatta* species, the black and gold howler monkeys in the urban habitat spent a higher proportion of time engaged in social activities (7.1%; Table 5). Further studies of the diets and activity budgets in other areas where howler monkeys have colonised urban habitats are required to confirm whether the low level of social interactions once thought to be characteristic of this genus are related to diet or habitat quality.

Habitat can impact the behaviour of different age-sex classes differently (Li and Rogers 2003). However, this did not appear to be the case with the howler monkeys in the two habitats in Ñeembucú, which supports previous findings of the phenomenal adaptability of black and gold howler in other areas (Bicca-Marques 2003). Behavioural flexibility to changing habitats may increase a species' chance of survival, but not all behaviours are necessarily beneficial. Primates' use of agricultural crops and other behaviours can negatively impact their coexistence with people, and lead to people perceiving the primates as pests (McLennan et al. 2017). The long-term survival of the Pilar black and gold howler monkeys not only depends on their ability to adapt behaviourally, but also on the humans' tolerance of their presence. Fortunately, in Pilar, the black and gold howler monkeys are not considered a pest to people (Alesci et al. 2022); the local people's tolerant attitudes towards the black and gold howler monkeys may be due to their high levels of daily inactivity.

This study provides this first evidence that living in the urban habitat does not significantly alter how black and gold howler monkeys in southwest Paraguay allocate their time in different activities. These results provide the foundation for future research into the extent of the adaptability of this species, which is essential to understand as urbanisation continues to alter Paraguay's last remaining wild areas.

Acknowledgments

All authors are grateful to the staff, interns and volunteers of Fundación Para La Tierra. We express our immense gratitude to the Pilar community for their incredible hospitality and friendliness that made this research possible. R. L. Smith is grateful to the PRONII program of Conacyt. Thanks to Dr. David Lusseau for guidance with data analysis. Thanks to Jorge Damián Ayala Santacruz and Paul Smith for checking the grammar of the Guaraní and Spanish abstracts. Fundación Para La Tierra is grateful to the estate of Don Julio Contreras for their continued support of PLT's activities. Special thanks to Don Oberon Barrios for allowing the team to use his property of Estancia Santa Ana. V. Overbeck is grateful for the Natural Sciences Summer Research Grant (2020) from Swarthmore College, which funded her research opportunity with Fundación Para La Tierra. Thanks to Jessica Lynch and the anonymous reviewers for their efforts and helpful comments.

References

Agetsuma, N. and Nakagawa, N. 1998. Effects of habitat differences on feeding behaviors of Japanese monkeys: Comparison between Yakushima and Kinkazan. *Primates* 39: 275–289.

Agostini, I., Holzmann, I. and Di Bitetti, M. S. 2012. Influence of seasonality, group size, and presence of a congener on activity patterns of howler monkeys. *J. Mammal.* 93: 645–657.

Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. *Behaviour* 49: 227–267.

Asensio, N., Cristobal-Azkarate, J., Dias, P. A. D., Vea, J. J. and Rodríguez-Luna, E. 2007. Foraging habits of *Alouatta palliata mexicana* in three forest fragments. *Folia Primatol.* 78: 141–153.

Back, J. P., Suzin, A. and Aguiar, L. M. 2019. Activity budget and social behavior of urban capuchin monkeys, *Sapajus* sp. (Primates: Cebidae). *Zoologia* 36: 1–10.

Bicca-Marques, J. C. and Calegaro-Marques, C. 1994. Activity budget and diet of *Alouatta caraya*: an age-sex analysis. *Folia Primatol.* 63: 216–220.

Bicca-Marques, J. C. 2003. How do howler monkeys cope with habitat fragmentation? In: *Primates in Fragments*, L. K. Marsh (ed.), pp.283–303. Springer, Boston.

Bicca-Marques, J. C. 2017. Urbanization (and primate conservation). In: *The International Encyclopedia of Primatology*, A. Fuentes, M. Bezanson, C. J. Campbell, A. F. Di Fiore, S. Elton, A. Estrada, J. Yamagiwa (eds.), pp.1-5. Wiley, New York.

Bicca-Marques, J., Alves, S. L., Boubli, J., Cornejo, F. M., Cortes-Ortíz, L., Jerusalinsky, L., Ludwig, G., Martins, V., de Melo, F. R., Messias, M., Miranda, J., Rumiz, D. I., Rímoli, J., Talebi, M., Wallace, R., da Cunha, R. and do Valle, R. R. 2020. *Alouatta caraya*. The IUCN Red List of Threatened Species 2020.

Bravo, S. P. and Sallenave, A. 2003. Foraging behavior and activity patterns of *Alouatta caraya* in the northeastern Argentinean flooded forest. *Int. J. Primatol.* 24: 825–846.

De Marques, A. A. B. 1996. Ecology and behavior of brown howlers in Araucaria Pine Forest, southern Brazil. *Neotrop. Primates* 4: 90–91.

DGEEC 2020. Dirección General de Estadística, Encuestas y Censos. Website: https://www.ine.gov.py/publicacion/2/poblacion. Accessed 5th December 2020.

Doorn, A. C., O'Riain, M. J. and Swedell, L. 2010. The effects of extreme seasonality of climate and day length on the activity budget and diet of semi-commensal chacma baboons (*Papio ursinus*) in the Cape peninsula of South Africa. *Am. J. Primatol.* 72: 104–112.

Duffy, P. X., Wellian, J. and Smith, R. L. 2022. Use of space by black and gold howler monkeys (*Alouatta caraya*) in an urban environment in Paraguay. *Urban Ecosyst.* 25: 1777–1786.

El Alami, A., Van Lavieren E., Rachida, A. and Chait, A. 2012. Differences in activity budgets and diet between semiprovisioned and wild-feeding groups of the endangered barbary macaque (*Macaca sylvanus*) in the central high Atlas Mountains, Morocco. *Am. J. Primatol.* 74: 210–216.

Estrada, A. 2009. Primate conservation in South America: the human and ecological dimensions of the problem. In: *South American Primates.* P. A. Garber, A. Estrada, J. C. Bicca-Marques, E. W. Heymann, K. B. Strier (eds.), pp.463–505. Springer, New York.

Estrada, A., Juan-Solano, S., Martínez, T. O. and Coates-Estrada, R. 1999. Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *Am. J. Primatol.* 48: 167–183.

Gaulin, S. and Gaulin, C. 1982. Behavioral ecology of *Alouatta seniculus* in Andean cloud forest, Colombia. *Int. J. Primatol.* 3: 1–32.

Hanya, G. 2004. Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. *Am. J. Primatol.* 63: 165–177.

Jaman, M. F. and Huffman, M. A. 2013. The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates* 54: 49–59.

Kane, J. and Smith, R. L. 2020. *Bertiella* sp. (Meyner, 1895) infection of *Alouatta caraya* (Humbolt, 1812) in urban and natural environments in Ñeembucu, southwest Paraguay. *Am. J. Primatol.* 82: e23166.

Li, Z. and Rogers, E. 2003. Habitat quality and activity budgets of white-headed langurs in Fusui, China. *Int. J. Primatol.* 25: 41–54.

McLennan, M. R., Spagnoletti, N. and Hockings, K. J. 2017. The implications of primate behavioral flexibility for sustainable human-primate coexistence in anthropogenic habitats. *Int. J. Primatol.* 38: 105–121.

Palma, A. C., Vélez, A., Gómez-Posada, C., López, H., Zárate D. A. and Stevenson, P. R. 2011. Use of space, activity patterns, and foraging behavior of red howler monkeys (*Alouatta seniculus)* in an Andean Forest fragment in Colombia. *Am. J. Primatol.* 73: 1062–1071.

Pavé, R., Kowalewski, M. M., Zunino, G. E. and Leigh, S. R. 2016. Sex differences in the behavior of wild *Alouatta caraya* infants. *Primates* 57: 521–532.

Pinkowski, D. and Smith, R. L. 2018. Activity Budgets of Urban Dwelling Paraguayan Howler Monkeys in Pilar, Paraguay. Poster Presentation, International Primatological Society Conference, Nairobi, Kenya. DOI: 10.13140/RG.2.2.22808.14083

Pinto, L. P. 2002. Diet, activity, and home range of *Alouatta belzebuth discolor* (Primates: Atelidae) in Paranaíta, northern Mato Grosso. *Neotrop. Primates* 10: 98–99.

Prates, H. M. and Bicca-Marques, J. C. 2008. Age-sex analysis of activity budget, diet, and positional behavior in *Alouatta caraya* in an orchard forest. *Int. J. Primatol.* 29: 703–715.

Rímoli, A. O., Valdivino, E. M., Rímoli, J., and Ferrari, S. F. 2008. Behavior patterns of a group of black howler monkeys *Alouatta caraya* (Humboldt, 1812) in a forest

fragment in Terenos, Mato Grosso do Sul: a seasonal analysis. *A Primatologia no Brasil* 9: 179–191.

Rímoli, J., dos Santos Nantes, R. and Júnior, A. É. L. 2012. Diet and activity patterns of black howler monkeys *Alouatta caraya* (Humboldt, 1812, Primates, Atelidae) in ecotone Cerrado-Pantanal in the left bank of Aquidauana River, Mato Grosso do Sul, Brazil. *Oecologia Australis*. 16: 933–948.

Rumiz, D. I. 1990. *Alouatta caraya*: Population densities and demography in Northern Argentina. *Am. J. Primatol*. 21: 279–294.

Schreier, A. L., Bolt, L. M., Russell, D. G., Readyhough, T. S., Jacobson, Z. S., Merrigan-Johnson, C. and Coggeshall, E. M. 2021. Mantled howler monkeys (*Alouatta palliata*) in a Costa Rican Forest fragment do not modify activity budgets or spatial cohesion in response to anthropogenic edges. *Folia Primatol*. 92: 49–57.

Sol, D., Lapiedra, O. and González-Lagos, C. 2013. Behavioural adjustments for a life in the city. *Anim. Behav.* 85: 1101–1112.

Stallings, J. 1985. Distribution and status of primates in Paraguay. *Primate Conserv*. 6: 51–58.

Strier, K. 1987. Activity budgets of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *Am. J. Primatol*. 13: 385–395.

Yanhong L., Li, D., Ren, B., Hu, J., Li, B., Krzton, A. and Li, M. 2014. Differences in the activity budgets on Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) by age-sex class at Xiangguqing in Baimaxueshan nature reserve, China. *Folia Primatol.* 85: 335–342.