



Seasonal Ecological Flexibility of a Threatened Bolivian Endemic: Olalla's Titi Monkey (*Plecturocebus olallae*)

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Abstract

In the face of reduced food availability, primates must choose between expending energy to look for adequate foraging options, or saving energy by reducing activity and intake requirements. In a 1-year study of two groups of Olalla's titi monkey (*Plecturocebus olallae*) in the fragmented forests of the Llanos de Moxos, Bolivia, we assessed seasonal variations in behavior, ranging, and diet to examine their ecological flexibility. We observed groups in the wet and dry seasons, recording behavior with instantaneous group scan sampling (743.5 observation hours in the dry season and 733.0 hours in the wet season) and ranging and feeding data with all occurrence sampling. At the same time, we collected data on food availability via monthly phenology monitoring. The titi monkeys fed mainly on fruits and significantly reduced the time they spent consuming fruit during the dry season compared with the wet season while showing some (non-significant) increase in their consumption of leaves, and other foods (seeds, lichens, and fungi). Home ranges remained relatively constant, but titi monkeys spent less time moving in the dry season than in the wet season, although this difference was not significant. The observed shift in diet toward consuming alternative foods during the fruit lean period and reducing movement instead of expanding ranging behavior to look for higher-quality foods suggests that *P. olallae* follows an energy–area minimizing strategy that may enable these primates to inhabit fragmented forests. Nevertheless, deforestation and further fragmentation in the range of these endemic and Critically Endangered primates must be addressed, as they represent significant threats to the severely range-restricted *P. olallae* populations. Our study illustrates the relevance of understanding primate ecological flexibility in response to food reductions to the development of conservation actions, especially in the light of increasing forest degradation and loss in the study region.

Keywords Seasonality · Behavior · Ranging · Diet · Primate conservation

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Introduction

Increased threats to biodiversity, including primates, over the past two decades include natural habitat loss related to deforestation and forest fragmentation promoted by human activities (Boyle, 2014; Estrada *et al.*, 2017). Wildlife researchers recently highlighted the need for more information on natural history to better understand species' ecological flexibility, i.e., their ability to cope with changes in environmental conditions (Casse & Milhøj, 2013; Isaac & Cowlshaw, 2004; Hoffman and O'Riain, 2012; McLennan *et al.*, 2017; Nowak & Lee, 2013; Strum, 2019). This knowledge is necessary to develop effective conservation plans to preserve viable populations of threatened species (Boyle, 2014).

Variation in the availability of food resources determines the ecological flexibility of primate species, which can be reflected in their diet, behavior, and ranging patterns (Boyle & Smith, 2010; Eppley *et al.*, 2017; Nowak & Lee, 2013). Seasonal variation in food resources represents the most recurrent challenge that primates must cope with (Hemingway & Bynum, 2005; van Schaik *et al.*, 1993). Optimal foraging theory predicts changes in food choice due to decreases in the availability of main food types, leading to strategies based on a balance between the energy obtained and required to obtain and process alternative foods (Garber, 1987; Hemingway & Bynum, 2005; Krebs & Davies, 1993; MacArthur & Pianka, 1966; Pyke *et al.*, 1977). Thus, the dietary breadth of a primate species can expand or contract, and fall-back foods (food resources whose importance increase when principal food options are scarce) can be identified (Lambert, 2011; Marshall *et al.*, 2009; Schoener, 1971). During a scarcity of principal foods, primates can invest energy in searching for similar food options, which implies an increase in their use of space (energy and resource maximizing strategies), or save energy by switching the diet to alternative foods, reducing their use of space (energy and area minimizing strategies) (Mitchell & Powell, 2004; Schoener, 1971).

Fruit availability in tropical forests varies seasonally, and frugivorous species, such as primates, are sensitive to fruit shortages (van Schaik *et al.*, 1993). This is particularly the case for small species, due to their more limited movement possibilities and relatively higher energy demands than larger bodied species (Hemingway & Bynum, 2005; Lindset & Boyce, 1985). In addition, habitat degradation is likely to cause a meaningful reduction in food availability for primates, due to the low abundance of trees in disturbed or fragmented forests, that can cause a significant reduction in fruit availability (Baranga *et al.*, 2013; Boonratana, 2013; Estrada *et al.*, 2017). Moreover, shortages of food availability for species with small geographic distributions are especially challenging because these species may not be able to move to other areas (Boonratana, 2013; Boonratana & Le, 2013; Canale *et al.*, 2013).

The subfamily Callicebinae (the titi monkeys) is a diverse group of platyrrhines occurring mostly in continuous forest, although some species are apparently able to tolerate forest fragmentation as a result of their generalist ecology (Bicca-Marques & Heymann, 2013). Research on titi monkeys and forest fragmentation

has mainly focused on demographic variation related to the size and configuration of forest patches, but a wider variation in species' behavior, zoogeography, and physiological adaptations is related to their environment (Boyle, 2014; Costa-Araújo *et al.*, 2021; Ferrari, Jerusalinsky, *et al.*, 2013a; Gestich *et al.*, 2018). Thus, more information on titi monkey ecology is urgently required, because current forest fragmentation rates threaten the conservation of many of these species (Boyle, 2014; Costa-Araújo *et al.*, 2021; Ferrari, Jerusalinsky, *et al.*, 2013a).

Olalla's titi monkey (*Plecturocebus olallae*) is Critically Endangered, 1 of the 25 world's most threatened primate species, and endemic to Bolivia with a small population (ca. 2,850 individuals) restricted to a 383 km² region in the upper part of the Yacuma river (Martinez & Wallace, 2010, 2016, 2019, 2021a, 2021b; Wallace *et al.*, 2013). The entire range of *P. olallae* occurs within the Llanos de Moxos ecosystem, consisting of naturally fragmented forests embedded in a grassland matrix, a fragile habitat type further threatened by forest loss (Martinez & Wallace, 2007, 2010, 2016, 2019, 2021a, 2021b; Porter *et al.*, 2013; Wallace *et al.*, 2013). In addition to the spatial restriction, fragmented forests also may be a low-quality habitat for *Plecturocebus* due to limitations in the availability of fruits and other food resources (Baranga *et al.*, 2013; Boonratana, 2013), which can be even more scarce during the dry season. Moreover, cattle ranching on the natural grasslands increases risks to the forest as ranchers use fire as part of seasonal pasture management, while improvements to a major road that passes through the region may promote unplanned intensive farming or new human settlements (Martinez & Wallace, 2010, 2016, 2019, 2021a; Siles *et al.*, 2019). Marked ecological changes to seasonal changes in food availability might be expected in *P. olallae* considering the limited fruit availability of the fragmented forests they inhabit. The forest fragmentation in their distribution gives rise to questions of how these primates cope with variation in food resource availability, and how ecologically flexible they are.

We studied two groups of *P. olallae* for 1 year to assess how seasonal variation in food availability affects their diet, behavior, and ranging patterns and improve our behavioral and ecological knowledge of this Critically Endangered species. We hypothesized that reductions in fruit availability would affect the consumption of other food types and the foraging strategy of *P. olallae*. We predicted a direct relationship between fruit availability and its consumption, and an inverse relationship with the consumption of other food types. If *P. olallae* are energy–resource maximizers, we predicted similar fruit consumption levels in both wet and dry seasons, and an increase in energy expending activities, and use of a larger area by groups during the dry season of fruit scarcity. Conversely, if *P. olallae* are energy–area minimizers, we predicted an increase in consumption of alternative foods in the lean period, accompanied by a reduction in energy expending activities and reduction in range use.

Methods

Study Site and Groups

We conducted our study at La Asunta cattle ranch, in the southwest of Beni Department, Bolivia (14°14'32.28"S, 66°58'39.91"W; Fig. 1). This site is in the Llanos

de Moxos ecosystem, which is composed of a matrix of lowland grasslands where seasonal flooding has shaped the landscape so that forest patches occur at higher elevations and are interspersed within the surrounding grassland matrix (Hanagarth, 1993). The flora is dominated by members of Fabaceae (e.g., *Tabebuia* sp., *Inga* sp.), as well as Moraceae (*Ficus* spp.), Arecaceae (e.g., *Attalea* sp., *Mauritia* sp.) in the forest patches, while a variety of Poaceae species are found in the grasslands (Killen *et al.*, 1993; WCS unpublished data).

The local economy is based on cattle ranching, with natural grasslands managed as pastures whose regrowth is promoted by traditional annual burning (Martinez & Wallace, 2007, 2010, 2016, 2019, 2021a, 2021b; Wallace *et al.*, 2013). Ecotourism is another important activity due to the wildlife observation opportunities available along the Yacuma River and led the Santa Rosa del Yacuma Municipality to create the Pampas del Yacuma Protected Area (Natural Area of Integrated Management category) in 2007 (HCMSRY, 2007). With similar goals, the Reyes Municipality recently created the Rhukanrhuka protected area (HCMR, 2019). *P. olallae* is considered a conservation priority for both protected areas. Approximately 20% of the range of the endemic *P. olallae* lies within Pampas del Yacuma protected area, including our study site.

Gallery forest along the Yacuma River and more isolated forest islands were the two main habitat types for *P. olallae* at our study site. Mean forest patch

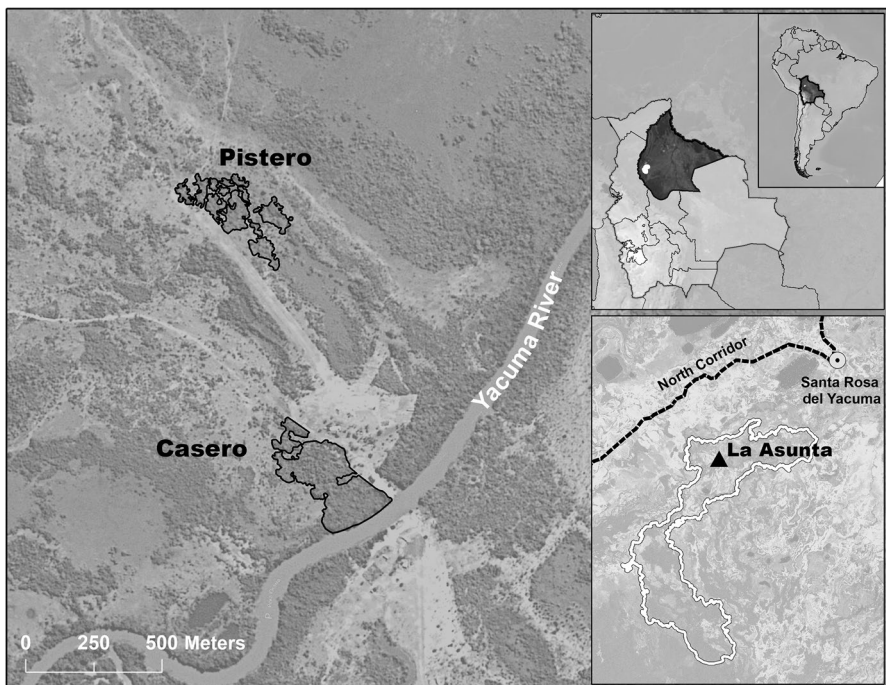


Fig. 1 Location of two study groups of *Plecturocebus olallae* at La Asunta cattle ranch, Bolivia. Casero group in gallery forest, and Pistero group in fragmented forest.

size was 5.1 ha ($N = 30$), and ranged between 0.1 and 100.4 ha, with the largest patches (16.5 and 100.4 ha) corresponding to gallery forest, while the rest consisted of forest patches of less than 10 ha at a distance from the river. We selected one group of *P. olallae* in each vegetation type. The gallery forest group (Casero) was composed of four individuals (adult pair, juvenile, and infant) inhabiting a forest patch of 16.5 ha, and the forest island group (Pistero) had five members (adult pair, subadult, juvenile, and infant) in an area of 6.9 ha, which included 11 forest patches whose size ranged between 0.1 and 0.9 ha (Fig. 1).

Data Collection

To measure food resource availability, we installed 10 permanent vegetation plots (50 m x 20 m; Baraloto *et al.*, 2013; Gentry, 1982) in each habitat type (gallery forest and forest islands), marking all 2,828 plants with a Diameter at Breast Height greater than 2.5 cm. We collected voucher plant specimens that we subsequently deposited in the Herbario Nacional de Bolivia in La Paz city for species identification and storage. We monitored the phenology of each marked plant monthly, recording the abundance of leaves, flowers, and fruits using a score from zero to five (0 = absence, and each integer value equivalent to 20%; Wallace & Painter, 2003).

We observed *P. olallae* between July 2007 and December 2008, dedicating the first 6 months to habituation and the next 12 months to data collection. Two observation teams followed groups simultaneously 10 d/mo for approximately 10 hours per day between 06:30 and 18:30 h (depending on seasonal variation in daylight duration). In total, we followed groups for 743.5 observation hours in the dry season (April–September) and 733.0 hours in the wet season (October–March).

To record primate behavior, we used instantaneous group scan sampling every 10 minutes (Altmann, 1974), synchronizing the sampling of both monkey groups at preestablished times (i.e., 07:00, 07:10, etc.). We recorded six behavioral categories: Moving (travelling/locomotion); Feeding (manipulation and ingestion of food); Resting (individual inactive, not performing any other behavior); Social Interactions (affiliative or aggressive interactions, such as playing, grooming, or fighting); Territorial Call (emission of titi monkeys' distinctive vocalizations); and Other (any other behavior).

We collected data on feeding and ranging patterns using all occurrence sampling of feeding and moving (3,501 and 6,981 events, respectively; Altmann, 1974). We recorded the start and finish time of feeding and the species and food type consumed, such as leaves, flowers, fruits, and others (e.g., invertebrates). We recorded the time at a resolution of seconds. We labeled all plant food sources for subsequent sample collection and identified species at the Herbario Nacional de Bolivia in La Paz city. For movement, we recorded the time when groups arrived at or left a tree. We recorded group location based on estimated distance and compass bearing to georeferenced reference points including the largest trees, food source plants, and trail cross points.

Data Analysis

We estimated monthly variation in the availability of fruits, flowers, and leaves for each habitat type using a Food Abundance Index (FAI; Guo *et al.*, 2007). We calculated monthly means of the phenology scores per food type across all the sampled individuals of each plant species and multiplied them by the species density (individuals/ha, from the combined area of plots for each habitat). Then, we summed the resulting values for each food type across species to obtain the monthly FAI estimates for each food type. We calculated the duration of feeding observations from the start and finish times recorded, and obtained the accumulated consumption time for each food species and monthly consumption percentages for each food type. We used Spearman rank correlation tests to assess the relationship between fruit availability and the consumption of fruits, flowers, and leaves and between the monthly availability of each food type and their consumption.

We superimposed the recorded locations on a 25-m x 25-m grid to estimate monthly home ranges for each group of monkeys from the number of cells they occupied (1 cell = 0.0625 ha, grid count method; De la Torre *et al.*, 2013; Thorington, 1981). We calculated the length of daily routes from the centroids of consecutive grid cells visited by monkeys (Quantum Gis®, plugin: Poin2One, UTM projection, zone: 19 South; minimum distance approach; Ostro *et al.*, 1999; Thorington, 1981), divided them by the daily hours of observation to obtain standardized daily path length (distance-per hour) estimates, then calculated the monthly mean (Boyle *et al.*, 2009).

To assess the foraging strategy of *P. olallae*, we compared the variety of species consumed between seasons. We used Generalized Linear Mixed Models (GLMM) to assess seasonal variation in the monthly percentage consumption of fruits, flowers, and leaves; monthly percentages of Moving, Feeding, and Resting; and monthly home ranges and standardized daily path length, setting each of these variables as dependent variables in separated tests (we tested the residuals for normality). To select the family and fit function of the dependent variables for GLMMs, we tested Normal, Gamma, and Inverse Gaussian Family with Logit or Identity links and selected the model based on the lowest Akaike Information Criterion (Field, 2009). We used Normal family fit with Logit link for feeding, resting, and for consumption of fruits, flowers and leaves, and Inverse Gaussian – Logit for moving, home range and standardized daily path length. For all models, we set season and group as fixed factors, and month as a random effect (Field, 2009). We performed tests in SPSS (v. 24) with a significance level of 0.05 for GLMM, and 0.017 for multiple Spearman correlations, because we used the same dataset for each food type (fruits, flowers, and leaves).

Ethical Note

We used standard observational methods with no capture of individuals and the National Biodiversity Directorate of Bolivia approved and granted us research permits. The authors declare that they have no conflict of interest.

Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

The phenology data revealed that fruits and flowers were more abundant during the wet season than in the dry season, while leaf abundance varied little (Fig. 2). We found that the consumption of fruits, leaves, and flowers was not significantly related to the availability of fruits (Spearman correlation: fruits $r_s = 0.36$, $N = 24$, $P = 0.090$; leaves $r_s = -0.37$, $N = 24$, $P = 0.072$; flowers $r_s = -0.10$, $N = 24$, $P = 0.645$). Flower consumption was significantly and positively related to flower abundance ($r_s = 0.688$, $N = 24$, $P < 0.001$), but this was not the case for leaves ($r_s = 0.08$, $N = 24$, $P = 0.728$).

Our observations show that *P. olallae* primarily fed on fruits and secondarily on leaves, while the activity budget consisted mainly of resting, moving and feeding (Fig. 3). Of 45 plant species, the 3 most consumed were *Machaerium latifolium*, *Coccoloba* sp., and *Tabebuia nodosa* (44.5% of feeding time), which provided fruits, flowers, and leaves (Table I). Fruit consumption of *P. olallae* on Fabaceae vines *M. latifolium*, *Diphysa carthagenensis*, and *Machaerium hirtum* consisted of seeds, accounting for 13.2% of the total feeding time and 24.2% of the fruit consumption time (Table I). The monkeys complemented their diet with insects (Cicadidae and Formicidae), fungi, lichens, and water. The nonweaned infant of Pistero group also nursed (Table I).

Thirty-one plant species, including the three most consumed, provided food for titi monkeys in both seasons (69% of recorded species), with the same number of species consumed in both periods (38 species). Time spent consuming seeds was higher in the dry than the wet season, with the most notable increase for *D. carthagenensis* (Table I). Lichen and fungi were present only in the dry season diet, and *P.*

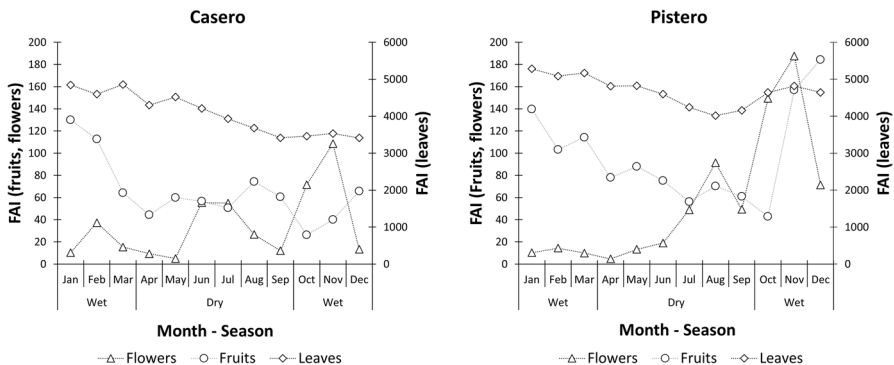


Fig. 2 Variation in abundance of fruits, flowers and leaves, according to Food Abundance Index estimates (left axis for fruits and flowers, right axis for leaves) for the habitat of two groups of *Plecturocebus olallae* (Casero: gallery forest; Pistero: forest islands) observed during 2008 in La Asunta Cattle ranch, Bolivia.

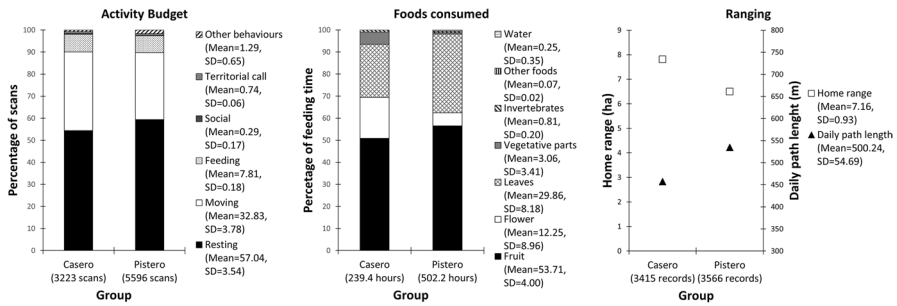


Fig. 3 Behavioral, dietary, and ranging parameters for two groups of Olalla's titi monkey (*Plecturocebus olallae*) observed during 2008 in La Asunta Cattle ranch, Bolivia.

olallae consumed more vegetative parts in the dry season, whereas they only consumed insects and water in the wet season (Table I). Titi monkeys consumed significantly more fruit in the wet than in the dry season (Fig. 4; Table II). Leaf consumption, time spent resting, time spent feeding, and home range size were all higher in the dry season than the wet season, but these differences were not statistically significant. Estimates of flower consumption, time spent moving, and standardized daily path length were higher in the wet season than in the dry season, but again none of these differences were statistically significant (Fig. 4; Table II).

The standardized daily path length was significantly shorter in Pistero group (small forest patch) than in Casero (large forest patch) (Fig. 4; Table II). We found higher values for Pistero than Casero for fruit, flower, and leaf consumption, as well as for time spent resting and feeding, whereas we observed the opposite for time spent moving and home range size (Fig. 4; Table II), although none of these differences were statistically significant. The focal groups showed similar seasonal variation, but in the dry season Casero spent less time feeding and increased its home range compared with the wet season, while we observed the opposite in Pistero (Fig. 4).

Discussion

Like other titi monkeys (Bicca-Marques & Heymann, 2013), *P. olallae* are mainly frugivorous. We predicted that fruit consumption for this species would depend directly on its availability, which also would negatively influence the consumption of other food types (Hemingway & Bynum, 2005; Pyke *et al.*, 1977; van Schaik *et al.*, 1993), but our results showed no statistically significant correlation between these variables. Instead *P. olallae* fed on all the most consumed species (>1% of feeding time) in both seasons, which suggests a relatively stable diet. Nevertheless, the observed reduction in fruit consumption in the dry season when fruits were less available, accompanied by an increase in leaf consumption, suggests that fruit availability influences the diet of *P. olallae*.

Table 1 Species consumed by Casero and Pistero groups of *Plecturocebus ollatae* (741.6 hours of total feeding time) during 2008 in La Asunta Cattle ranch, Bolivia

Family	Species	Total feeding time (hours)	% feeding time	Casero (hours of feeding time)												Pistero (hours of feeding time)																	
				Dry season						Wet season						Dry season						Wet season											
				Fruit	Flower	Leaf	Root	Trunk	All	Fruit	Flower	Leaf	Root	Trunk	Abdomen	Fruit	Flower	Leaf	Root	Trunk	All	Fruit	Flower	Leaf	Root	Trunk	Entire body	All					
Fabaceae	<i>Maeharium latifolium</i>	145.7	19.6	23.95	-	11.71	-	-	-	-	-	13.40	-	7.67	-	0.02	-	-	-	-	-	-	14.91	-	54.07	0.03	0.05	-	9.69	0.58	9.57	-	-
Polygonaceae	<i>Coccoloba</i> sp.	109.7	14.8	0.05	-	0.23	-	-	-	-	-	46.62	1.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	60.98	0.33	-	-	-	
Bignoniaceae	<i>Tabebuia nodosa</i>	74.8	10.1	0.01	-	9.23	-	-	-	-	-	-	1.28	0.63	-	-	-	-	-	-	-	-	4.29	9.64	23.3	-	-	5	3.24	18.13	-	-	
Salicaceae	<i>Casearia aculeata</i>	48.8	6.6	1.12	0.07	0.2	-	-	-	-	-	5.52	-	1.5	-	-	-	-	-	-	-	-	9.63	0.02	6.38	-	-	17.7	-	6.71	-	-	
Fabaceae	<i>Diphyssa carthagensis</i>	35.7	4.8	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	28.94	-	2.53	-	-	3.7	-	0.22	-	-	
Rubiaceae	<i>Randia armata</i>	28.6	3.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.76	-	0.87	-	-	0.17	-	-	-	-	
Combretaceae	<i>Combretum lanceolatum</i>	26.8	3.6	4.7	21.61	-	-	-	-	-	-	0.45	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
Polygonaceae	<i>Coccoloba cujibensis</i>	25.6	3.5	1.85	0.18	-	-	-	-	-	-	3.45	0.22	3.03	-	-	-	-	-	-	-	-	2.23	1.5	1.35	-	-	8.18	-	3.6	-	-	
Piperaceae	<i>Piper arboreum</i>	24.1	3.3	0.02	-	0.37	10.44	-	-	-	-	-	-	-	0.05	2.44	0.08	-	-	-	-	-	1.87	-	2.11	-	-	1.8	2.66	2.32	-	-	
Fabaceae	<i>Maeharium hirtum</i>	23.7	3.2	2.87	-	1.19	-	-	-	-	-	-	11.04	0.84	-	-	-	-	-	-	-	-	0.23	0.93	3.62	-	-	0.03	0.34	2.61	-	-	
Araceae	<i>Acrocomia aculeata</i>	23.5	3.2	-	-	-	-	-	-	-	-	0.62	-	-	-	-	-	-	-	-	-	-	20.88	-	0.22	-	-	1.26	0.5	0.04	-	-	
Bignoniaceae	<i>Tabebuia impetiginosa</i>	22.2	3	-	2.27	0.05	-	-	-	-	-	0.26	-	2.95	-	-	-	-	-	-	-	-	-	0.75	14.83	-	-	-	-	1.1	-	-	
Fabaceae	<i>Swarzella jorori</i>	19.5	2.6	-	-	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19.48	-	-	-	-	-	

Table 1 (continued)

Apocynaceae	<i>Forsieronia amblybasis</i>	13.8	1.9	-	0.62	0.77	-	0.09	-	0.72	1.75	1.09	-	-	1.58	0.28	3.76	-	-	1.28	1.84	0.02	-	-
Myrtaceae	<i>Psidium guineense</i>	13.5	1.8	0.23	-	-	-	-	-	-	0.08	-	-	-	1.47	-	2.98	-	-	7.59	-	1.15	-	-
Bignoniaceae	<i>Arrabidaea</i> sp.	9.1	1.2	4.46	-	2.1	-	-	-	0.05	-	2.17	-	-	-	-	0.3	-	-	-	-	-	-	-
Lauraceae	<i>Ocotea diospyrifolia</i>	8.4	1.1	-	-	-	-	-	-	-	-	-	-	-	0.1	-	0.05	-	-	2.67	1.43	4.18	-	-
Cactaceae	<i>Cereus hankcunus</i>	6.3	0.8	-	-	-	-	-	-	0.09	1.38	-	0.02	-	0.47	-	-	2.36	-	0.58	0.67	-	0.71	-
Boraginaceae	<i>Cordia alliodora</i>	6	0.8	2.4	0.97	-	-	-	-	-	-	-	-	-	1.8	0.78	-	-	-	-	-	-	-	-
Cucurbitaceae	<i>Melolhria warmingiana</i>	5.7	0.8	-	-	-	-	-	-	-	-	-	-	-	-	-	1.77	-	-	3.98	-	-	-	-
Myrtaceae	<i>Psidium guajava</i>	4.3	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.28	-	-	-	-
Passifloraceae	<i>Passiflora ligularis</i>	3.8	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6	-	-	-	1.21	0.03	-	-
Clusiaceae	<i>Clusia</i> sp.	3.8	0.5	0.38	0.13	0.03	-	-	-	-	-	2.05	-	-	1.16	0.05	-	-	-	-	-	-	-	-
Bombacaceae	<i>Ceiba samauana</i>	3.5	0.5	-	-	0.92	-	-	-	1.33	0.78	0.37	-	-	-	-	0.05	-	-	-	-	-	-	-
Insecta	Insecta undetermined	3.4	0.5	-	-	-	-	-	-	-	-	-	-	2.03	-	-	-	-	-	-	-	-	-	1.36
Urticaceae	<i>Cecropia</i> sp.	3.3	0.4	-	-	-	-	-	-	0.03	-	-	-	-	0.05	-	0.1	-	-	3.08	-	-	-	-
Annonaceae	<i>Oxandra</i> sp.	2.9	0.4	-	-	-	-	-	-	2.31	-	-	-	-	-	-	-	-	-	0.62	-	-	-	-
Water	Water	2.5	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.5
Insecta	Formicidae	2	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.02

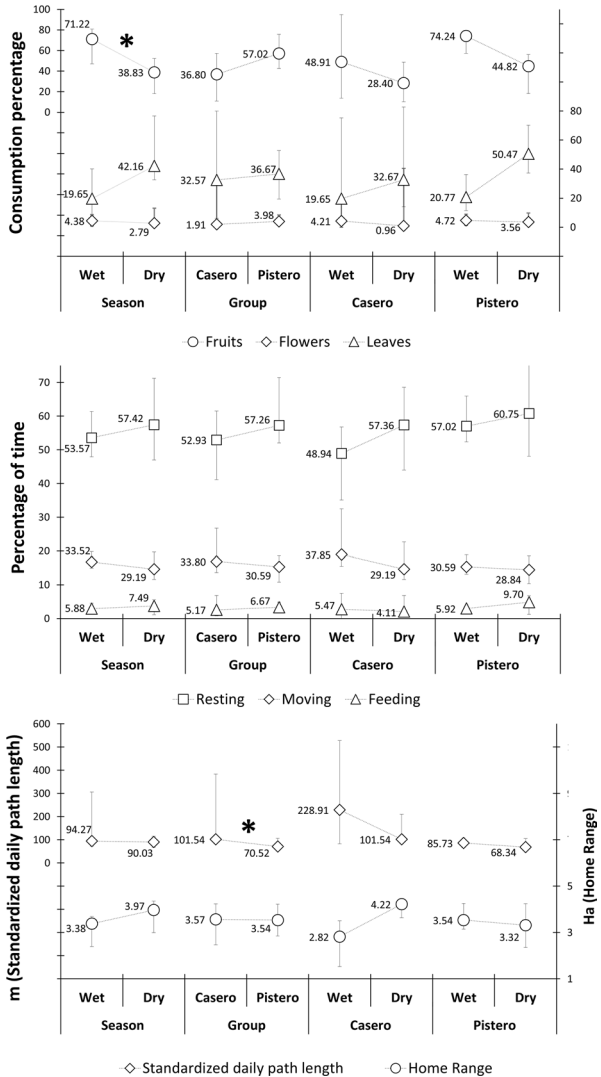
Table I (continued)

Moraceae	<i>Ficus pertusa</i>	1.9	0.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bignoniaceae	<i>Tabebuia aurea</i>	1.7	0.2	0.52	-	-	-	-	-	-	0.88	-	-	-	-	-	-	0.33
Araceae	<i>Mauritiella</i> sp.	1.5	0.2	0.22	-	-	-	-	-	-	-	1.32	-	-	-	-	-	-
Celastraceae	<i>Salacia elliptica</i>	1.1	0.1	1.1	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
Cannabaceae	<i>Celtis ehrenbergiana</i>	1.0	0.1	0.01	1.03	-	-	-	-	-	-	-	-	-	-	-	-	-
Fabaceae	<i>Acacia</i> sp.	1.0	0.1	0.24	0.09	-	-	-	-	-	0.63	-	-	-	-	-	-	-
Rutaceae	<i>Zanthoxylum petiolare</i>	0.9	0.1	-	-	-	-	-	-	-	-	-	0.67	-	-	-	-	0.2
Peitiveriaceae	<i>Seguiera</i> sp.	0.8	0.1	-	0.79	-	-	-	-	-	-	-	-	-	-	-	-	-
Combretaceae	<i>Combretum</i> sp.	0.6	0.1	0.4	-	-	-	-	-	-	0.2	-	-	-	-	-	-	-
Fabaceae	<i>Inga</i> sp.	0.6	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.24	0.34
Cactaceae	<i>Pracereus</i> sp.	0.5	0.1	-	-	-	-	-	-	0.45	-	-	-	-	-	-	-	-
Polygonaceae	<i>Coccoloba</i> cf. <i>peruviana</i>	0.3	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.32	-
Lichen	Lichen undetermined	0.3	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.15	-
Insecta	Cicadidae	0.2	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.23	-
Fungi	Fungi undetermined	0.2	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	0.17	-
Rubiaceae	<i>Genipa americana</i>	0.2	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.17

Table I (continued)

Nyctaginaceae	<i>Neea</i> sp.	0.2	<0.1	-	0.07	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	
Breast milk	Breast milk	0.1	<0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1
Clusiaceae	<i>Garcinia brasiliensis</i>	0.1	<0.1	0.02	-	-	-	-	0.07	-	-	-	-	-	-	-	-	-	-	-
Bixaceae	<i>Cochlospermum vitifolium</i>	<0.1	<0.1	-	-	-	-	-	-	-	-	-	-	0.03	-	-	-	-	-	-
Bignoniaceae	Undetermined	11.8	1.6	0.13	-	0.48	-	-	-	0.02	-	-	-	-	-	-	-	-	-	11.14
Fabaceae	Undetermined	15.5	2.1	-	0.03	1.94	-	-	-	2.99	-	-	-	0.1	1.64	6.68	-	-	-	1.54 0.42 - 0.13
Hippocrataceae	Undetermined	0.2	0	-	0.05	-	-	-	-	0.15	-	-	-	-	-	-	-	-	-	-

Fig. 4 Seasonal variation in diet, behaviour and ranging parameters (monthly median values and interquartile range) for Olalla's titi monkeys (*Plecturocebus olallae*) observed during 2008 in La Asunta Cattle ranch. Seasonal estimates for each focal group are also provided. *Significant differences (based on results of Generalized Linear Mixed Models).



P. olallae also consumed more vegetative parts and fungi and lichens in the dry season than in the wet season. Similar expansions of dietary breadth involving increased leaf consumption when fruits were scarce were observed in *Callicebus coimbrai* and *Plecturocebus brunneus* (Lawler et al., 2005; Souza-Alves et al., 2011). Another titi monkey response to fruit scarcity is increased seed consumption, as observed in *Cheracebus lugens* (Palacios et al., 1997), *Callicebus melanochir* (Heiduck, 1997), and *Callicebus nigrifrons* (Nagy-Reis & Setz, 2016). We found a similar increase in seed consumption by *Plecturocebus olallae*, especially in *Diphysa carthagenensis*, but also in the other species that provided this food type (*Machaerium latifolium* and *M. hirtum*). Overall, our observations, suggest flexibility in the dietary breadth of *P. olallae* in response to reductions in fruit availability.

Table II Results of Generalized Linear Mixed Models used to assess seasonal and intergroup variation in monthly percentage consumption of fruits, flowers, and leaves; monthly percentages of Moving, Feeding, and Resting; and monthly home ranges and standardized daily path length for two groups of Olalla's titi monkey (*Plecturocebus olallae*) observed during 2008 in La Asunta Cattle ranch, Bolivia.

Response variable		Predictor	Estimate (β)	St. Error	t	P
Foods consumed	Fruit ($\chi^2 = 9.120$; df = 2; P = 0.010)	Intercept	-4.246	0.157	27.086	<0.001
		Season	-0.549	0.205	-2.680	0.014
		Group	-0.278	0.218	-1.274	0.217
	Flower ($\chi^2 = 0.544$; df = 2; P = 0.762)	Intercept	1.756	0.419	4.192	<0.001
		Season	-0.587	1.137	-0.517	0.611
		Group	0.320	0.601	0.533	0.600
	Leaves ($\chi^2 = 3.202$; df = 2; P = 0.202)	Intercept	3.394	0.324	10.478	<0.001
		Season	0.540	0.306	1.766	0.093
		Group	-0.097	0.295	-0.329	0.746
Activity budget	Resting ($\chi^2 = 4.788$; df = 2; P = 0.091)	Intercept	-4.053	0.067	60.451	<0.001
		Season	0.095	0.090	1.062	0.300
		Group	-0.170	0.089	-1.913	0.070
	Moving ($\chi^2 = 5.742$; df = 2; P = 0.057)	Intercept	3.475	0.106	32.645	<0.001
		Season	-0.158	0.133	-1.184	0.250
		Group	0.279	0.134	2.083	0.050
	Feeding ($\chi^2 = 0.924$; df = 2; P = 0.630)	Intercept	1.897	0.288	6.575	<0.001
		Season	0.251	0.261	0.960	0.348
		Group	0.018	0.375	0.047	0.963
Ranging	Home range ($\chi^2 = 2.252$; df = 2; P = 0.324)	Intercept	1.131	0.103	10.987	<0.001
		Season	0.165	0.110	1.492	0.151
		Group	0.017	0.105	0.162	0.873
	Daily path length ($\chi^2 = 16.698$; df = 2; P < 0.001)	Intercept	4.549	0.179	25.465	<0.001
		Season	-0.271	0.216	-1.256	0.223
		Group	0.914	0.235	-3.889	0.001

This feature may allow titi monkeys (Callicebinae) to occupy a diversity of habitats, including fragmented forests (Bicca-Marques & Heymann, 2013).

The observed increase in the consumption of leaves and seeds by *P. olallae* in the dry season may reflect an attempt to balance nutrient intake when fruits are less available. Most of the leaves and seeds consumed by *P. olallae* were from *M. latifolium* (Fabaceae) in the dry season, making this species the overall top consumed species. Leaves and seeds contain high levels of protein (Lambert, 2011; Nagy-Reis & Setz, 2016), and high nitrogen concentrations in the leaves of leguminous species are linked to high protein content (Dasilva, 1994). Thus, *M. latifolium* is probably a good source of protein for *P. olallae*. From our observations, leaves and seeds can be considered as fall-back foods for *P. olallae*, because their consumption increased when the main food resource (fruits) were less available (Lambert, 2011; Marshall *et al.*, 2009). This finding also emphasizes the relevance of *M. latifolium* as the main source for those food types in the dry season.

Our observations of a more varied diet in the season when less fruit was available suggest that *P. olallae* follows an energy minimizing foraging strategy (Mitchell & Powell, 2004; Schoener, 1971). If this is the case, we also predicted other changes in titi monkey behavior when fruits were less available. Although these differences were not significant, we observed a reduction in time spent moving, an increase in resting, and lower standardized daily path length in the dry season than in the wet season. However, there also was an unexpected increase in monthly home range size in the dry season, due to Casero group, which also reduced its daily path length. Similar changes in the use of space were observed for *Callicebus nigrifrons* as a response to more patchily distributed feeding sites in the dry season, with the monkeys presumably trying to reduce energy expenditure on moving (Nagy-Reis & Setz, 2016). Although specific study is required to better understand how *P. olallae* responds to the spatial distribution of food, our results suggest that feeding sites may have been more dispersed in the dry season for Casero group, making them use a larger area. However, we observed a reduction in time spent moving and standardized daily path length by this group, which suggest they also may have tried to increase their moving efficiency.

We found intergroup differences in monthly standardized daily path length, with lower values in Pistero in the small forest patch habitat, although its monthly home range was quite similar to Casero in gallery forest. Although the differences between the groups were not significant, Pistero invested less time in moving, but more time feeding and resting than Casero group, both in general and in the dry season. Pistero group inhabited a highly fragmented forest area that may have limited group movements, as suggested by forced ground displacements to reach separated forest patches when looking for food (Martinez & Wallace, 2011). This group also showed a more pronounced increase in the consumption of leaves and seeds in the dry season than the group in the gallery forest. Thus, although Pistero group may try to use energy efficiently and reduce movements, the fragmented habitat may represent an additional challenge due to a low offer of food (Baranga *et al.*, 2013; Boonratana, 2013). Effects of forest fragmentation on food availability have been observed in other Callicebinae, promoting ecological adjustments in diet or ranging patterns (Ferrari *et al.*, 2013a, b; Nagy-Reis & Setz, 2016; Souza-Alves *et al.*, 2011), but despite the generalist attributes assumed for these group of primates (Bicca-Marques & Heymann, 2013; Ferrari, Boyle, *et al.*, 2013b), their tolerance and resilience generally remain unknown. The study of forest fragmentation effects on primates is complex, and guidelines have been suggested to improve assessments by refining landscape metrics criteria and incorporating ecological, behavioral, and genetic patterns (Ferrari, Boyle, *et al.*, 2013b; Marsh *et al.*, 2013). More research on the effects of forest fragmentation is required to understand how it affects the survival of *P. olallae*, which is restricted to this habitat type. This study provides a basis from which to design further specific research on this topic (Costa-Araújo *et al.*, 2021; Ferrari, Boyle, *et al.*, 2013b).

The entire distributional range of *P. olallae* is in an area that experiences seasonal floods (Martinez & Wallace, 2021a; Siles *et al.*, 2019). Flood regimes contribute to riverine forest soil fertility by providing a regular supply of nutrients, making these forests more productive in terms of fruit availability than drier forests (Camaratta *et al.*, 2017; Haugaasen & Peres, 2005; Jung *et al.*, 2015). Flooding also promotes

more rapid regrowth of plant leaves, increasing young leaf abundance, and reducing their concentration of toxic compounds, thus turning them into more suitable food than leaves in unflooded forests (Haugaasen & Peres, 2005). Our observations also suggest that *P. olallae* found enough food across seasons. The presence of offspring also suggests no serious limitations in forest carrying capacity for these primates, despite forest fragmentation levels (Boyle *et al.*, 2013). These considerations suggest that some habitat features, combined with the ecological flexibility of *P. olallae*, may help them to survive in these fragmented forests. Nevertheless, the fragility of fragmented habitats to threats (Boyle, 2014; Estrada *et al.*, 2017) suggests that this is a delicate scenario and underlines the need for conservation actions for these endemic, range-restricted, and threatened primates.

In summary, and with the caveat that we observed only two groups, *P. olallae* seems to respond to reductions in fruit availability by showing ecological flexibility through the adoption of an energy–area minimizing strategy and increasing their dietary breadth (Mitchell & Powell, 2004; Schoener, 1971). Considering the endemism, extreme range restriction to fragile fragmented forests, the threatened status of *P. olallae* (Martinez & Wallace, 2021b), and the threats they currently face (Martinez & Wallace, 2019, 2021a, 2021b), we provide valuable knowledge to inform research and conservation actions to reduce threats and increase awareness about these threatened primates and their habitat.

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