A life in fragments: the ecology, behavior, and conservation of the recently-described Parecis Plateau titi monkey (*Plecturocebus parecis*)

Abstract

While some South American primates are well-studied, many are poorly known to science. This makes reports of their ecology very valuable, especially when the region inhabited is threatened by human activities. Here we combined data from three independent field studies to provide a better understanding of the behavior, ecology, chemical composition of plant items consumed, and conservation of the Parecis Plateau titi monkey (*Plecturocebus parecis*), a recently-described species from the southern Amazonian Arc of Deforestation. Specifically, we collected behavioral data for 8 groups over 8 months and quantified the monkeys' activity budget. To analyze the chemical compounds in the plants eaten, we used vanillin to determine condensed tannin and alkaline precipitation to quantify total alkaloid content. We also determined the extent of forest loss and fragmentation from 2000 to 2019 within the known range of the Parecis Plateau titi monkey using satellite imagery. We found that group size ranged 2-6 individuals, and the monkeys spent 31% of the day foraging, 22% resting, 19% feeding, 14% moving, and 14% in other activities. The monkeys ate 50 plant species from 24 families and appeared to be unusually tolerant of dietary tannins but avoided alkaloids. Habitat modification within the species' range has been extensive: forest cover declined by 16.1% in 2000-2019; the largest areas of continuous forest were reduced by 37.5%, with mean fragment size decreasing 67.5% (from 421.0 to 136.9 ha). Forest loss and fragmentation were most significant in the northern half of the species' range and its southern border. Given the Parecis Plateau titi monkey's tolerance for toxic dietary species, the intense modification of its geographic range, and its capacity

to live in fragmented habitats, we recommend that future studies investigate these topics across all 37 species of titi monkeys. In addition, recordings of vocal repertoires will improve field surveys, and help with population estimates, especially for titi monkey species living in geographic regions that have been heavily modified by humans.

Keywords

Amazonia, Callicebiinae, Cerrado, Forest fragmentation, Habitat loss, South American primates

Introduction

Although it forms the cornerstone to understanding the biology of a species, studies of primate natural history have been sidelined in recent decades (Strum, 2019). Such data are often crucial to conservation planning (Belovsky *et al*., 2004; Bezanson & McNamara 2019; Tewksbury *et al*., 2014), yet the knowledge these studies generate is lacking for many primate species (Fernández *et al*., 2022). This lack becomes especially pertinent in cases where anthropic impacts are rapid, current, and widespread, as natural history information can provide an understanding of the ecological and ethological flexibility of a given species, and hence the likelihood of it successfully responding to environmental challenges. Such information can also inform appropriate conservation strategies and their implementation (Dayton, 2004; Greene *et al*., 1988; Phillips *et al*., 2014; Strum, 2019).

The most severe limitations on population survival in primates come from anthropic impacts. These may be direct, such as hunting (Shaffer *et al*., 2019) and habitat removal (Teichroeb *et al.*, 2019), or indirect, such as habitat fragmentation (Estrada & Coates-Estrada, 1996; Holmes *et al*., 2019) and the genetic consequences of population isolation (Farias *et al.*, 2015). Removal for pet-trade or medicinal purposes is also a threat in some areas (Alves *et al.,* 2010; Shanee *et al*., 2017). There may also be secondary effects, such as predation by domestic dogs (*Canis lupus familiaris*: Gould *et al*., 2007; Oliveira *et al.*, 2008) and cats (*Felis catus*: Brockman *et al*., 2008; Cäsar *et al*., 2012), and the transfer of diseases derived from humans (Dunday *et al.*, 2018), or from domestic animals (Gillespie & Chapman, 2006). Of these, in the Brazilian Arc of Deforestation (*sensu* Song *et al*., 2018), hunting, habitat loss, and habitat fragmentation are considered the greatest threats to primate populations (Ferronato *et al*., 2018;

Grande *et al*., 2020; Ochoa-Quintero *et al.*, 2017). Primates in this heavily impacted region include several species of titi monkeys.

Titi monkeys are a closely related clade of some 37 species of South American primates which together comprise the sub-family Callicebiinae (Opazo *et al.*, 2006; Veiga *et al*., 2013; Carneiro *et al*., 2018; Rengifo *et al.*, 2022). Formerly all placed in a single genus, *Callicebus* (van Roosmalen *et al.*, 2002), extant titi species were reallocated to three genera (*Callicebus*, *Cheracebus*, and *Plecturocebus*) by Byrne *et al*. (2016), based on molecular evidence. Collectively, titi monkeys occupy a wide variety of habitats, including montane forests (Shanee *et al*., 2013), lowland rainforests (Rodríguez & Rodríguez, 2018), mangroves (Beltrão-Mendes *et al*., 2011), seasonally-flooded swamps (Pinto *et al*., 2019), a variety of semi-arid habitats (Caatinga: Printes *et al*., 2011), and habitats with very marked seasonal patterns of annual rainfall (Cäsar *et al*., 2012). Titi monkey habitats include primary, natural secondary, and anthropogenically-disturbed habitats (Flesher, 2015; Heiduck, 2002), islands created by hydroelectric dams (Sampaio & Ferrari, 2005), and urban forest fragments (de Souza & Calouro, 2018). This high level of ecological tolerance is partially due to body size (adults of all three genera weigh approximately 1 kg: Ford & Davis, 1992; Norconk, 2011), small group sizes (2-7 individuals: Bicca-Marques & Heymann, 2003), simple social structure (generally an adult pair, offspring from the current year, and juveniles or adolescents from previous years: Souza-Alves *et al*., 2011), small home ranges (Bicca-Marques & Heymann, 2013), broad diets (*e.g.*, 159 plant species in the Caquetá titi monkey, *P. caquetensis*: Acero-Murcia *et al*., 2018; 198 fruit genera from 9 diet lists: Boyle *et al*., 2016), and high dietary flexibility (Souza-Alves *et al*., 2011, 2021).

The behavior and ecology of several titi monkey species have been studied extensively (Beni titi monkey, *P. modestus*, and Olalla brothers' titi monkey, *P. olallae*:

Martinez & Wallace, 2007; black-fronted titi monkey, *Callicebus nigrifrons*: Gestich *et al.*, 2019). However, for many other titi monkey species, little or no dedicated field work has been conducted. Importantly, changes in taxonomy can alter the patterns of apparent ecological knowledge. This is case with the titi monkeys in the Chapada dos Parecis (Parecis Plateau) region of Rondônia, Brazil (Alencar, 2011; Mattos, 2016), which, until very recently, were attributed to the ashy titi monkey (*Plecturocebus cinerascens*). However, Gusmão *et al*. (2019) revealed that these titi monkeys were a previously unknown species, the Parecis Plateau titi monkey (*P. parecis*) (Fig. 1). While little-known to science, ashy and Parecis Plateau titi monkeys have long been known to, and considered distinct by, the region's Apiaká indigenous inhabitants (Dario, 2018).

INSERT FIGURE 1 HERE

The Parecis Plateau titi monkey occupies the higher elevations in the transition zone between Amazonian forest and Cerrado savanna in southern Rondônia and western Mato Grosso, Brazil (Gusmão *et al*., 2019). The area includes part of the Parecis Plateau and extends into the Aripuanã/Juruena and Aripuanã/Roosevelt interfluves (Gusmão *et al*., 2019). The distribution of the Parecis Plateau titi monkey is of concern since it overlaps with the Arc of Deforestation (*sensu* Song *et al*., 2018) within the Amazon-Cerrado transition zone (Silva-Junior *et al.*, 2019). Here, native vegetation has been extensively removed or modified by agriculture, timber, and mining activities (Song *et al*., 2018), as well as human colonization, giving rise to an arc-shaped deforestation frontier (Levy *et al*., 2018). Forest loss and fragmentation in the region have been extensive and rapid (Aldrich *et al*., 2012; Herrera *et al*., 2019), radically altering the Amazon-Cerrado transition zone (Silva-Junior *et al*., 2019).

Our main objective was to describe the ecology, behavior, and habitat use of the Parecis Plateau titi monkey, to provide data to assist in the correct threat categorization for this species, recently recommended as Near Threatened by Gusmão *et al*. (2019), because much of its range occurs near the southern Amazon/Cerrado ecotone. Specifically, we addressed three research questions: 1) What is the activity budget of the Parecis Plateau titi monkey? 2) What does it eat? 3) To what extent do diet items contain tannins and alkaloids? and 4) How much forest cover has been lost and fragmented in its distribution since 2000?

Methods

Field Sites

We studied the ecology and behavior of the Parecis Plateau titi monkey in three independent field studies. The first two studies, Alencar site (Study 1) and Mattos sites (Study 2) (Fig. 2A) focused on the behavior and ecology of the species at the Rondon II Hydroelectric Power Plant (HPP) 11º58'07.1" S, 60º41' 47.3" W), Pimenta Bueno municipality, south-eastern Rondônia State, Brazil. Rondon II HPP lies in the south-western part of the species' range (Gusmao *et al*., 2019), some 590 km from the state capital, Porto Velho. Study 3 was a five-day field survey at a third site, Capa 120, Vilhena municipality, Rondônia State, Brazil (12°2'0" S, 60°25'12" W; Fig. 2B Gusmão and Silva-Diogo locations). This short census in unprotected but currently continuous forest aimed to further define the geographic distribution limits of the Parecis Plateau titi monkey.

Rondon II Hydroelectric Power Plant (HPP) field studies (Study 1 and Study 2)

Approximately 16,000 ha of legally preserved forest, which protects the watershed of the 7500-ha reservoir and associated regional wildlife (Rondônia, 2002), surrounded Rondon II HPP. Vegetation consisted of a transition zone among savannah and open ombrophilous forest, as well savanna and seasonal evergreen forest (RadamBrasil, 1978; IBGE, 2012), with areas of rocky outcrops, seasonally flooded zones, cerrado, gallery forests, and sub-montane forest. In the undisturbed forest, the canopy reaches 20 m, with a well-developed understory (F. S. Mattos, unpublished data). Highly-altered forests along roads and well-used trails had tree canopies reaching 15 m (F. S. Mattos, unpublished data). The canyons area (Fig. 2B Alencar site; Study 1) contained open, markedly stratified submontane rainforest, with the presence of *Phenakospermum guianense* (Musaceae), bamboo (*Merostachys multiramea*), and palms, interspersed within the tree-cover and dense vine thickets. Vegetation at the other Rondon II HPP study sites (Fig. 2B Mattos sites; Study 2) included open lowland rainforest, with patches of cerrado (*sensu stricto*, cerradão, gallery forest: Eiten, 1972).

The local climate at Rondon II HPP is *Aw* (Köppen), which is warm, moist, and tropical, with a dry season in the austral winter (Alvares *et al*., 2014; Kottek *et al*., 2006), and marked dry (Jun-Aug) and rainy seasons (Sept-May) (IBGE, 2002). Dry season rainfall is below 50 mm/month, and there may be a moderate water deficit. Total annual rainfall varies between 1,400 and 2,600 mm (Rondônia, 1999, 2002).

Rondon II HPP became a Legal Reserve in 2011, immediately following completion of the dam. Before dam construction, the area was public land where unlicensed selective extraction of timber and firewood occurred (Rondonia, 2002), and so should be considered a secondary forest formation. The study areas within Rondon II HPP (Study 1 and Study 2) have a long history of human disturbance, including resource exploitation and from visitors to the canyons and other geological formations of the Legal Reserve´s Monumento Natural Apertado da Hora (Fig. 2A).

Vilhena field survey (Study 3)

The vegetation in Vilhena, where we conducted the five-day survey, is composed of an open ombrophilous forest with Cerrado enclaves (RadamBrasil, 1978), with a mean annual temperature of 23°C and a mean annual rainfall of 2,200 mm (Alvares *et al.*, 2014). The forest was relatively intact at the time of the study, but the region is targeted for intensive agricultural development, which is expected to impact the native vegetation heavily.

INSERT FIGURE 2 HERE

<u>Study 1 (2010-2011): behavior and ecology</u>

We studied one group of Parecis Plateau titi monkeys for 15 days/month from June 2010 to January 2011 (8 months) in a 94-ha forest fragment at Rondon II HPP (Fig. 2A). During the 3 months prior to the study we spent 228 hours on initial surveys and habituation and walked 420 km of trails. Trails formed a grid separated by 50 m, and were marked with coded tape to facilitate researcher orientation. The data presented in this manuscript represent 469 observation hours over 120 field days.

For 15 days/month, we recorded behavioral data using group scans every five minutes during daylight hours (NRC, 1981; Ferrari & Rylands, 1994). Behavioral categories included resting (sitting or recumbent without movement), locomotion (movement of short or long distance, by an individual or as a group), foraging (manipulating or procuring food items; visually scanning the immediate environment), eating (biting, chewing, or swallowing food), and other (any other behavior not listed;

Alencar, 2011). When there was an infant in the group, we noted which group member (e.g., adult female, adult male) carried the infant.

During each behavioral scan we also recorded the GPS location of the group centre, and estimated their strata use (in 5 m intervals from the ground). When the animals were feeding, we collected the food samples, recorded the items they were eating, and tagged the trees with field tape for later identification. We then collected samples from tagged trees and dried them for later identification at Acre Federal University botany laboratory using Miranda (2000), regional technical reports (Rondônia, 1999, 2002), and Veloso *et al*. (1991).

Study 2 (2015-2016): feeding ecology and plant chemical analysis

We collected data from May 2015 to April 2016 (12 months) at Rondon II HPP (Fig. 2A). We walked 408 km of trails during 700 hours on 100 field days. The study sites consisted of degraded or disturbed forest, and there had been frequent human transit in the area, leading to habitatuation of the titi monkeys. We studied seven groups of Parecis Plateau titi monkeys in seven forest fragments for 9 days/month. These seven sites were separated by a distance approximating to Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) home range (6.7-8.3 ha: Souza-Alves *et al.*, 2021), a species which initial studies (F. S. Mattos, unpublished data) suggested are ecologically similar to Parecis Plateau titi monkeys.

When we detected a titi monkey group feeding, we scan sampled (Altmann, 1974) all members of the group every five minutes for 20 minutes. During the scans we noted the time and GPS location of the group in the tree that they were feeding, food items eaten, and forest strata used (in 5-m intervals from the ground). We tagged feeding sites with numbered tape and revisited the sites as soon as possible following observation to collect plant-derived food specimens (leaves, branches, fruits and flowers) from the individual plants on which animals fed. We also collected food parts rejected or partially-eaten by the titi monkeys from beneath feeding trees. Collections followed standard protocols (Queensland Herbarium, 2013). We identified collected material with the help of regional literature (Pennington, 1990; Ribeiro et al., 1999; van Roosmalen, 1985) and the help of botanical experts.

Study 3 (2020): Field survey

During the 5-day survey (6-10 August, 2020) we used linear transects (Buckland *et al*., 2010) adapted to include call playback (Gestich *et al.*, 2019), with a portable amplifier (20 Hz, 40W RMS) attached to a cell phone to emit Parecis Plateau titi monkey territorial vocalizations. These transects consisted of two trails (lengths: 5 km and 3 km). In 39 hours of sampling effort, we walked 27 km of trails (15 km in *terra firme* Amazon Forest, 12 km in Cerrado) (Fig. 2B). We conducted playbacks every 500 m, and waited for 3 min for any response from the animals. We directed the amplifier to both sides of the trail, and we recorded every movement in the vegetation or calls associated with titis monkeys. When we saw a group of animals, we counted the number of individuals in each group, and recorded sex and age class for each individual.

Behavioral and Ecological Analyses

We calculated the activity budget of the titi monkey group in Study 1 using the percentage of behavioral scans during these eight months for each of the noted behavioral categories. We tallied all feeding records and calculated the percentage of feeding records that represented fruits, flowers, buds, leaves, and invertebrates. We also calculated the percentage of scans when the monkeys were at each forest strata level.

For Study 2, we calculated the calculated the percentage of feeding records that represented fruits, flowers, buds, leaves, and invertebrates.

Chemical Analyses

In Study 2, we recorded tannins for all plant species used as food by the titi monkeys. We assayed the alkaloid content of the fruit samples using the alkaline precipitation method described by Harborne (1973). We divided the diet material into eaten and non-eaten parts (*e.g.*, for *Inga*: sarcotesta [eaten], seed [not-eaten]), and performed analyses in triplicate to provide a mean alkaloid concentration (Manikpuri & Jain, 2015). The Harborne method is a semi-quantitative method involving the gravimetric measurements of precipitated nitrogen-containing compounds. For this, we extracted 2 g of crude material in Erlenmeyer flasks with 80 ml of 20% acetic acid in methanol for 4 hours. Then, we filtered the solid material, and concentrated the solution until 10 ml remained. We then added 1 ml of ammonium hydroxide and observed the resulting alkaloid-based precipitate. Next, we filtered the solution and weighed the material using an analytical balance (0.001 g precision, Shimadzu) to determine the total alkaloid mass.

We assayed tannin compounds using a modified version of the method described by Burns (1971). For this, we combined equal volumes of 8% hydrochloric acid (HCl) in methanol and 4% of vanillin in methanol, then prepared a standard curve by adding 10 mg of catechin to 5 ml methanol, using various dilutions to construct a standard curve (ranging from 1 to 1000 μg/ml). Once we had prepared 10 dilutions (20 tubes), we quickly added 5 ml of vanillin-HCl reagent to each, to ensure the elimination of interferent compounds in the data. Substracting the blank analysis allowed us to plot transmittance against catechin concentration with a spectrophotometer (model

SpectraMax 384 plus, Molecular Devices), operating at 500 nm for 20 minutes, using vanillin-HCl for the 100% transmittance blank. We extracted 1 g of raw ground fruit material in Erlenmeyer flasks with 50 ml of methanol and let it settle for 48 hours. Then, we filtered and dried the solvent under a stream of nitrogen gas to obtain a crude extract. Next, we dissolved 1 mg of this extract in the same solvent as the standard curve at 20 mg/ml and directly assayed the mix as described above.

We compared chemical values from eaten and non-eaten parts of each diet item. We analysed each part in triplicate to provide mean values (Manikpuri & Jain, 2015).

Forest Loss and Fragmentation

We examined regional forest loss and fragmentation by quantifying forest cover changes in the Parecis Plateau titi monkey geographic range between 2000 and 2019. We conducted all treatments and image processing in ArcGIS 10.7. We defined range limits based on 14 localities noted by Gusmão *et al*. (2019), and two additional localities (12°02'0"S, 60°25'12"W; 12° 32'44"S, 60°21'41"W: A. Gusmão and O. Silva-Diogo, unpublished data; one of these records were from roadkill).

We downloaded forest cover data from the year 2000, then the extent to which forest cover was lost between 2000 and 2019, using the Global Forest Change 2000-2019 data set (Hansen *et al*., 2013, which is updated annually and has a spatial resolution of approximately 30 m). We classified a pixel as forested if the forest cover in that pixel was 50% or greater. Using the two data sets (forest cover in 2000 and forest loss from 2000-2019), we calculated forest cover for 2019. We then quantified the number of independent forest fragments and calculated the area of each forest fragment for the range defined by Gusmão *et al*. (2019), and the additional two sites. For our forest loss and fragmentation change analysis, we focused on forest fragments 0.5 ha and larger so that single pixels of forest cover (area of a single pixel is approximately 0.09 ha) would not overrepresent the fragmentation results. Overall, we quantified the area of forest cover in 2000 and 2019, percent of forest cover lost, the number of forest fragments 0.5 ha and larger in 2000 and 2019, the largest area of continuous forest in 2000 and 2019, and mean size of forest fragments 0.5 ha and larger in 2000 and 2019.

Ethical Note

We conducted procedures in our study without animal manipulation; therefore we did not require licenses. We declare no conflict of interest.

Data Availability

All data are in the authors' possession and will be made available upon reasonable request.

Results

Group Size and Composition

In Study 1, there were five individuals in Group 1, the focal study group for the behavioral study: an adult male and female, a sub-adult male, a juvenile female, and a juvenile male. In June/July a female infant was born, and the sub-adult male dispersed from the group. A second group, Group 2, was present in the Study 1 forest fragment but it was not the focus of this study. Group 2 contained six individuals: an adult male and female pair, two sub-adult males, a juvenile female, and a juvenile male.

In Study 2, which consisted of surveys of seven forest fragments, maximum group size was six individuals, with a mode of four and a minimum of two individuals (N = 7 groups). These values remained constant during the 2015-2016 survey period. We observed copulations in July 2015, and observed infants (N = 3) 13 times at the end of the dry season/start of the wet season (September and December 2015 and April 2016).

In Study 3, we encountered seven groups of Parecis Plateau titi monkeys. Although sampling effort was greater in the Amazon rainforest habitat, we observed all groups in Cerrado habitat. All sightings were in response to call playback sampling.

Activity patterns

In Study 1, based on 22,081 total scan records for the focal study group (Group 1), the monkeys spent 31% (N = 6846 scans) of these scans foraging, followed by resting (22%; N = 4858 scans), feeding (19%; N = 4195 scans), locomotion (14%; N = 3091 scans) and other activities such as social play, grooming, tail twining, offspring care, vigilance, and territorial defense (14%; N = 3091 scans). When an infant was present, the adult male carried the infant in approximately 90% of the behavioral scans.

In both Study 1 and Study 2, we recorded bouts of territorial vocalizations. These were most often given before leaving the sleeping site (05:40h-06:20h). The monkeys often performed such vocalizations as a duet of the adult female and adult male, at which time the duetting adults frequently entwined tails. The monkeys also emitted territorial calls in response to vocalizations of neighboring groups and, far less frequently, before sleeping.

Diet composition

The titi monkeys in the Study 1 focal study group had a varied diet that included 38 plant species in 20 families (Table I) and three insect Orders (total of 3,729 feeding records). In Study 2, feeding records for seven groups of titi monkeys represented 12 plant species from 11 families (total of 65 feeding records; Table I). We recorded a total of 50 taxa in 22 families across both studies (Table I); two species overlapped between the two studies. For the single group in Study 1, the mean time spent feeding at a single plant source was 25 min (range: 15-60 min). Overall, for this single titi monkey group, fruits represented 67% of the diet (N = 2,720 records), leaves 21% (N = 853 records), insects 8% (N = 325), and flowers 4% (N = 162 records). For the seven groups in Study 2, their combined diet records represented fruits (77% of diet records; N = 45), followed by 14.6% invertebrates (spiders, winged termites, and other insects; N = 8 records), and 8.5% flowers and buds (N = 5 records).

Table I. Parecis Plateau titi monkey (*P. parescis*) plant diet items, Rondonia State, Brazil.

Plant	**Growth form[1]**	**Plant parts recorded[2]**	
		Study 1 (2010-2011)	**Study 2 (2015-2016)**
Anacardiaceae			
Anacardium giganteum	T	Fruit	-
Annonaceae			
Annona paraensis	T	Fruit, leaves	-
Guatteria duckeana	T	Fruit, leaves	-
Arecaceae			
Oenocarpus bataua	P	Leaves, fruit	-
Maximiliana maripa	P	Fruit, flowers, leaves	-
Mauritia flexuosa	P	Fruit, leaves	-
Burseraceae			
Protium heptaphyllum	S	-	Pulp
Caryocaaceae			
Anthodiscus amazonicus	T	Fruit	-
Cecropiaceae			
Cecropia concolor	T	Fruit	-
Pourouma bicolor	T	-	Pulp
Chrysobalanaceae			
Hirtella racemosa	S	-	Fruit
Licania incana	T	Fruit	-
Clusiaceae			
Clusia cf *planchoniana*	E	Fruit, flower	-
Rheedia brasiliensis	T	Fruit	-
Rheedia macrophylla	T	Fruit	-
Vismia cayannensis	T	Fruit	-
Euphorbiaceae			
Mabea angustifolia	T	Fruit	-
Unidentified 1	T	Fruit	-

Unidentified 2	T	Fruit	-
Fabaceae (Caes.)			
Hymenaea palustris	T	Fruit, flowers	-
Fabaceae (Mim.)			
Enterolobium contortisiliquum	T	Fruit	-
Inga alba	T	-	Sarcotesta
Inga ingoides	T	Fruit, leaf	-
Inga nitida	T	Fruit	-
Inga rubiginosa	T	Fruit	-
Inga velutina	T	Fruit	-
Inga sp.	T	-	Seed (sarcotesta)
Parkia panurensis	T	Flower, fruit	-
Parkia pendula	T	Fruit	-
Fabacee (Pap.)			
Cavanalia grandifolia	V	Leaves	-
Malphigiaceae			
Amorimia (*Mascagnia*) *rigida*	S	-	Seed
Malvaceae			
Theobroma speciosum	T	Leaves, fruit	-
Melastomataceae			
Bellucia grossularioides	T	Fruit, flower, leaf	Fruit
Miconia chrysophylla	T	Leaf, flower	-
Miconia tomentosa		Leaf, flower	-
Mouriri acutiflora	S		Aril
Moraceae		-	
Ficus trigona	T	Fruit/flower	-
Maquira guianensis	T	Fruit/flower	-
Myrtaceae			
Calyptranthes cebra	S	Fruit	-
Unidentified	T	Fruit, flower	-
Passifloraceae			
Passiflora coccinea	V	Fruit	Seeds, pulp, husk
Rubiaceae			
Genipa americana	T	Fruit	-
Sapindaceae			
Matayba guianensis	T		Seed (testa)
Sapotaceae		-	
Micropholis cyrtobotria	T	Fruit	-
Pouteria ramiflora	T	-	Pulp
Solanaceae			
Solanum lycocarpum	S	Fruit	-
Vochysiaceae			
Qualea paraensis	T	-	Pulp
Vochysia vismiifolia	T	Flower, fruit	-

[1]Growth forms included epiphyte (E), palm (P), shrub/small tree (S), tree (T), and vine (V).
[2]When there was more than one item. The order reflects relative importance in the diet.

In Study 1, the most common diet species were: *Maximiliana maripa* (Arecaceae: 10.8%), *Inga ingoides* (Fabaceae-Mimosoideae: 9.6%), *Hymenaea palustris* (Fabaceae-Caesalpinioideae: 9.0%) and *Theobroma speciosum* (Malvaceae: 8.6%). Fabaceae (32.4%), Arecaceae (12.3%), and Myrtaceae (10%) were the most common families. In Study 2, the most commonly eaten plant species were *Bellucia grossularoides* (Melastomataceae) and *Inga* spp. (Fab-Mim); Melastomataceae and Fabaceae were the most common families in Study 2.

In Study 1, 8% of the diet records were insects representing three Orders: Lepidoptera (larvae), Orthoptera, and Hymenoptera (ants). Of these records when titi monkeys ate insects, 43% of the records occurred during insect-specific terrestrial foraging; such terrestrial foraging for insects primarily occurred when the group as a whole was otherwise resting (12:30h-13:30h).

Chemical composition of plants eaten

While differences in tannin concentration values for eaten and non-eaten fruit parts differed substantially in some cases (by up to 2,600% in *Mouriri acutiflora*, Melastomataceae), they were only lower in the eaten parts for *Amorimia* (*Mascagnia*) *rigida* (Malphigiaceae) (Table II). For the remaining 10 species, tannin concentration in the eaten part was higher than or very similar to the uneaten part (Table II). We recorded alkaloids in the non-eaten parts only in *A.* (*M.*) *rigida* and *Inga* sp. fruits (Table II), with their levels being lower than for tannins.

Table II. Tannin and alkaloid content of the Parecis Plateau titi monkey (*P. parescis*) plant diet items (ND = not detected) in Rondonia State, Brazil (2015-2016).

	Fruit tannin Concentration	**Fruits alkaloid concentration**

Plant Name	Part eaten	Part not eaten	(mg CE/100 g fwb ± SD)		(mg TA/g fwb ± SD)	
			Eaten part	Non-eaten part	Eaten part	Non-eaten part
Amorimia (Mascagnia) rigida	Seeds	Winged part	4.16 ± 0.67	23.72 ± 4.18	N.D.	1.02 ± 0.15
Bellucia grossularioides	Half fruit	Half fruit	74.11 ± 8.76	74.11 ± 8.76	N.D.	N.D.
Hirtella racemosa	Whole fruit	---	3.45 ± 0.57	---	N.D.	N.D.
Inga alba	Testa	Seeds	3.55 ± 0.58	3.67 ± 0.50	N.D.	N.D.
Inga sp.	Testa	Seeds	12.65 ± 2.71	3.83 ± 0.50	N.D.	1.51 ± 0.21
Matayba guianensis	Testa	Seeds	19.12 ± 3.12	3.15 ± 0.53	N.D.	N.D.
Mouriri acutiflora	Aril	Seeds	84.20 ± 9.21	3.22 ± 0.51	N.D.	N.D.
Passiflora coccinea	Seeds	Seeds and Pericarp	4.55 ± 0.65	4.14 ± 0.62	N.D.	N.D.
Pouteria ramiflora	Testa	Seeds	9.28 ± 1.88	4.03 ± 0.60	N.D.	N.D.
Pourouma bicolor	Testa	Seeds	5.02 ± 0.73	4.19 ± 0.64	N.D.	N.D.
Protium heptaphyllum	Testa	Seeds	6.61 ± 1.25	4.49 ± 0.90	N.D.	N.D.
Qualea paraensis	Seeds	Winged part	6.13 ± 0.76	5.81 ± 0.62	N.D.	N.D.

Habitat Spatial Use

In Study 1, the titi monkeys used mostly low- and medium-level vegetation (less than 5 m from ground: 23% of records; 5-10 m above ground: 25%; 10-15 m: 30%; 15-20 m: 14%; and 20-25 m: 8%; N = 22,081 scan records). In Study 2, groups were noted primarily in the lower canopy, with 72.8% of scans occurring when the monkeys were less than 5 m from the ground (range: 0 - 20 m from ground). Both studies recorded terrestrial activity, all of which were foraging-associated.

Forest Loss and Fragmentation

Most of the recorded land cover change occurred in a wide area covering the Mato Grosso state municipalities of Aripuanã, Colniza, Cotriguaçu, Juruena, Castanheira, and the northeastern area of Juína. This region constitutes approximately half the Parecis Plateau titi monkey range (Fig. 3). In the southern part of their range, additional areas that experienced high levels of change stretched from Pimenta Bueno to Vilhena in Rondônia state to the western region of Comodoro in Mato Grosso.

INSERT FIGURE 3 HERE

Between 2000 and 2019, the Parecis Plateau titi monkey range lost 16.1% of its forest cover, and the largest area of contiguous forest decreased by 37.5%. The number of forest fragments 0.5 ha and larger increased 2.6-fold, while mean fragment size decreased by 67.5% (from 421.0 ha to 136.9 ha). Forest loss and fragmentation were extensive throughout the range (Fig. 4A), especially in the northern half (Fig. 4B), except for the Escondido Indigenous Land. The southern range boundary also experienced forest loss and fragmentation (Fig. 4C). Although the middle of the range has been less heavily impacted than the northern and southern sectors, forest loss and fragmentation will likely continue along the highway BR-174, which connects Juína to Vilhena; a clear line of deforestation already links these two highly impacted areas (Fig. 4D). Although there are several protected areas on the western and eastern sides of the highway BR-174, there has been forest loss and fragmentation in some of these since 2000 (Fig. 4D).

INSERT FIGURE 4 HERE

Discussion

We found that the Parecis Plateau titi monkey spent approximately half of the daytime activity budget foraging and eating, followed by resting. Of the nine groups noted, group size ranged from two to seven individuals, and infants were present in multiple groups. The titi monkeys ate plants from a variety of species, and a majority of their diet records were for fruit. These fruits that the monkeys ate often had notably higher levels of tannins than the fruit items the titi monkeys did not eat; however, for most of the diet records alkaloids were not detectable in the tested samples. Overall, habitat modification has been extensive throughout the geographic range of the Parecis Plateau titi monkey. Between 2000 and 2019, there was 16.1% loss of forest cover, the largest area of continuous forest decreased in size by 37.5%, and the mean size of forest fragments decreased by 67.5%.

Behavior and Ecology

The ecology of the Parecis Plateau titi monkey appears to follow that of other members of the genus *Plecturocebus* (Bicca-Marques & Heymann, 2013), in the composition of its diet, including the extent to which the monkeys eat fruits, and the dominant plant families. However, the apparent tolerance to tannins is notable. Tannin concentrations in three of the species eaten (*Mouriri acutiflora,* Melastomataceae; *Matayba guianensis*: Sapindaceae, and *Pouteria ramiflora*: Sapotaceae) were much higher in the parts consumed than in those discarded. This is unusual since tannins and alkaloids are widely considered anti-herbivore defenses (Wink, 2003), with avoidance of plant parts containing them being a common feature of primate diet selectivity (Chapman & Chapman, 2002). It may be that the Parecis Plateau titi monkey tolerates tannins, given the levels we found in eaten fruits. In Atlantic Forest titi monkeys (*Callicebus melanochir*), tannins had no apparent influence on food selection (Heiduck

1997). Therefore, tannins may not function widely in anti-herbivore defense in titi monkey foraging.

The situation was different for alkaloids, which we recorded as present in only two diet plant species (*Amorimia [Mascagnia] rigida* and *Inga* sp.). In both species, alkaloid levels in eaten parts were far lower than tannin levels, a surprising finding since alkaloids commonly occur in plants at levels higher than tannins (Jung *et al*., 1979). Although present at low levels, the alkaloids were found in fruit parts rejected by feeding titis in both species (*A.* [*M.*] *rigida* fruit wings, *Inga* sp. seeds) (Fig. 5). This apparent avoidance matches the behavior of other primate species (*e.g.*, black colobus: *Colobus satanas*, McKey *et al*., 1981; olive baboon: *Papio anubis*, Barton & Whiten, 1994). Avoiding *A.* (*M.*) *rigida* fruit wings is highly adaptive as they contain sodium monofluoroacetate. This lethally toxic organic salt blocks cell respiration once ingested (Tokarnia *et al*., 2002), and is known to kill cattle, sheep, goats, and rabbits (Becker *et al*., 2013; Duarte *et al*., 2013; Lee *et al*., 2014; Peixoto *et al*., 2010).

INSERT FIGURE 5 HERE

Our findings suggest that the Parecis Plateau titi monkey has adapted to a diet of local tannin-rich plants, while behaviorally avoiding alkaloids and a lethal organic salt. The characteristically broad titi monkey diet is essentially opportunistic (*e.g.,* Heiduck, 1997). While this allows the monkeys to minimize foraging distance and adopt an energy minimizing strategy (Nagy-Reis & Setz, 2017), it also means that ingested volumes of each food plant are likely to be small, minimizing the overall toxicity profile (Provenza *et al*., 2007). Thus, the broad and generalist diet commonly seen in titis (Souza-Alves *et al.*, 2011, 2021), may allow the exploitation of otherwise dangerous species, including those with high tannin levels, a common feature of many pioneers and secondary forest species, especially on poor soils (Krause *et al*., 2003).

The high tannin levels, presence of sodium monofluoroacetate, and the general absence of alkaloids in food items may reflect local soil and climatic characteristics since water stress, nutrient availability, and high insolation can affect secondary metabolite production (Gershenzon, 1983; Waterman *et al*., 1984), and this can be facultative within a species (*e.g.*, Vrieling & van-Wijk, 1994: *Senecio jacobaea*, Asteraceae). The soils of the southern-most part of the Amazon Basin where HPP Rondon II is located are notably poor (IBGE, 2006), and the dry season is protracted (IBGE, 2002). Under such circumstances, regional plant defensive profiles would be expected to be tannin-rich but low in alkaloids, whose N-rich nature makes them more expensive to make on nutrient-poor soils (Cunningham *et al*., 1999; Mali & Borges, 2003). Sodium monofluoroacetate is also frequently associated with poor soils (Eisler, 1995; Oriens & Milewski, 2007).

Habitat Use

Parecis Plateau titi monkey habitat use appears to be flexible. At Rondon II, animals used two types of forest, lowland rainforest and sub-montane forest, both in states of regeneration, while at Vilhena, all records came from Cerrado, despite rainforest being available. While this may indicate habitat-use flexibility, other causes are possible since, at the Vilhena site, the Parecis Plateau titi monkey overlaps with the Prince Bernhard’s titi monkey, *Plecturocebus bernhardi* (Gusmão *et al*., 2019). Given that the latter prefers taller and more closed forests (Lopes, 2016; van Roosmalen *et al*., 2002), Parecis Plateau titi monkeys may reduce interspecific competition by occupying the Cerrado in such areas (Schreier *et al*., 2009).

Playback-based surveys indicated a strong preference by the species for Cerrado over more humid forest types. Modification of the existing land cover is widespread throughout most of the known range of the Parecis Plateau titi monkey (Sampaio *et al*., 2012). Consequently, its presence in areas known to have undergone past disturbance (such as Rondon II) gives us hope that the species is disturbance-tolerant to some degree. If so, this is likely linked to the need to cope with vegetation dynamics in the Cerrado, a habitat where non-anthropic dry season fires and a consequence, vegetation mosaic at different regeneration stages form a crucial feature of the biome (Kaufman *et al*., 1994; Ferreira & Huete, 2004).

Habitat Loss and Conservation Concerns

We found that forest loss and fragmentation are extensive in the distribution of the Parecis Plateau titi monkey. Furthermore, one of the range-defining occurrence records we used came from a road-killed individual (highway BR-364). Given the degree to which this species' range has been transformed, and the indications that such transformation will continue (Fig. 4), the Parecis Plateau titi monkey should be considered a species of conservation priority.

Recommendations for Future Research

Our knowledge of Parecis Plateau titi monkey behavior and ecology is patchy. Furthermore, the species' geographic range has undergone extensive transformation. Accordingly, we suggest the following research priorities:

1) *Record the entire vocal repertoire of Parecis Plateau titi monkeys*: Titi species generally have some 10-13 distinct vocalizations (Cäsar *et al*., 2012). Use of

vocalizations, both via playback and passive monitoring devices, can act as highly effective and rapid survey methods (Bastos *et al*., 2019; Bezerra *et al*., 2010), and have been used in this way in surveys of several titi species (*e.g*., Rio Mayo titi monkey, *Plecturocebus oenanthe*, Aldrich *et al*., 2008; Rio Beni titi monkey, *Plecturocebus modestus*, López-Strauss & Wallace, 2015; Prince Bernhard's titi monkey, *Plecturocebus bernhardi* and the Olalla brothers' titi monkey, *Plecturocebus olallae* Silva-Diogo *et al*., 2018). Knowledge of the complete Parecis Plateau titi monkey vocal repertoire would greatly enhance passive monitoring survey species recognition (Kalan *et al*., 2015).

2) *Habitat preferences and fragmentation tolerance*: Although appearing highly tolerant of perturbation, titi species have well-defined preferences for both natural and anthropic vegetation (Flesher, 2015). The geographic range of the Parecis Plateau titi monkey lies within the Amazon/Cerrado biome transition zone, so the vegetation is highly heterogeneous. Superimposed on this are various land-use histories that differ temporally and in intensity (Fearnside, 2005), resulting in a palimpsest landscape of varying suitability for Parecis Plateau titi monkeys. Future population surveys for titis should include vegetation type and fragment size, and the landscape use history for each area surveyed (Gouveia *et al*., 2016; Costa-Araújo *et al*., 2021). Such a program might also allow the identification of suitable, but currently unpopulated, areas into which reintroductions might be made (Allgas *et al*., 2017).

3) *Population estimates*: Once preferred habitats and minimum viable fragment sizes have been identified, field surveys should be conducted to assess the presence of Parecis Plateau titi monkeys in remaining regional forest cover, in both protected and non-

protected areas. In addition, comparisons of DNA samples from museum specimens would provide an estimate to the true extent of species´ historical population decline (Rosenbaum *et al*., 2000; Storz *et al*., 2002; Wandeler *et al*., 2007; Chaves *et al*., 2011).

4) *Long-term ecological studies*: Forests surrounding Rondon II hydroelectric dam could serve as a focus for social and dietary ecology studies, as the site is sufficiently large and well-protected for the population to be viable, safe, and given the infrastructure associated with dam maintenance access, relatively easily studied. Findings would provide a reference against which the ecology of populations in more precarious situations could be compared.

Conclusions

This study brings together all currently available information concerning the behavior, ecology, and conservation of the Parecis Plateau titi monkey. Such information on basic ecology can be used to promote effective conservation, in association with ecological niche modeling (Gusmão *et al*., 2021), and thus identify critical areas for future conservation actions. This is especially important given the long-term threats of climate change to this ecotonal region of Brazil (Javeline *et al*., 2013), and the more immediate ones from agribusiness-driven removal of native vegetation cover (Sauer, 2018). Our study also showed that Parecis Plateau titi monkeys have a possible tolerance for high levels of dietary tannins, which is unusual and should be the focus of future studies. Specifically, we propose that additional studies include an analysis of specific proteins in the saliva linked to tannin tolerance (Espinosa-Gómez *et al*., 2020; Mau *et al*., 2011; Prinz & Lucas, 2000; Shimeda, 2006), and focus on the capacity of Parecis Plateau titi monkeys to interact flexibility with other primate species and to alter foraging strategies in habitat patches of different size and botanical composition.

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