Dietary plasticity of a understudied primate (*Sapajus cay*) in a biodiversity hotspot: applying ecological traits to habitat conservation in the Upper Paraná Atlantic Forest

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Abstract – One of the main threats to wild primates is habitat alteration, fragmentation and destruction. Therefore it is crucial to understand the ability of those species to adapt to human-induced habitat changes to prevent extirpation. Key to this is a species diet plasticity. In Paraguay over 91% of the Upper Paraná Atlantic Forest has been destroyed to expand agricultural land. We determined the diet composition of three *Sapajus cay* groups in degraded and near-pristine Atlantic Forest in eastern Paraguay to assess whether the diet composition of this species changes with habitat degradation. We accounted for diet variability associated with demographic traits and forest characteristics using multinomial linear models. Once the effect of age, sex, and season were accounted for, we found that the diet of capuchins was plastic and shifted to adapt to studied degraded forest conditions. The results showed that (as expected) the capuchins have a generalist and flexible diet, including opportunistically taking advantage of crop plants, particularly Slash Pine plantations, when the risks were lower. The capuchins ability to adjust their diet in different habitat fragments demonstrates that small islands of Paraguayan Atlantic Forest are valuable for their persistence. This insight can be used to create applied conservation strategies, such as using the existing Payment for Ecosystem Services (PES) legislation to provide an opportunity to begin reconnecting fragments using native trees bordered by Slash Pine plantations. Using the capuchins as an umbrella species would increase public support of the program, while compensation through the PES scheme and profiting from the timber would encourage landowner participation.

Keywords – conservation behaviour, ecological requirements, feeding behaviour, habitat degradation, Latin America, Paraguayan primates.

Introduction

The main threat facing wild primates is the alteration, fragmentation and clearing of their natural habitats to accommodate anthropogenic expansion (Estrada et al., 2017). This habitat fragmentation process results in a reduction in available habitat, an increase in the number of habitat patches and patch isolation and a decrease in patch size (Cristóbal-Azakarate and Arroyo-Rodríguez, 2007). Subsequent ecological constraints can affect diet, reproduction rates and potentially overall survival (Strier, 2006; Riley, 2007). Failure to adapt to a rapidly changing habitat means that a species would be extirpated (Isabirye-Basuta and Lwanga, 2008).

The Atlantic Forest of South America is a significant global ecoregion of which the

most near-pristine is recognised as a UNESCO World Heritage site (UNESCO, 1999). This forest is classified as one of the top five biodiversity hotspots for endemism. As late as the 1940's most of the original 86 000 km^2 of the Paraguayan Upper Paraná Atlantic Forest, hereafter BAAPA (*Bosque Atlántico del Alto Paraná*), remained intact but has since suffered from one of the highest global deforestation rates due to the expansion of industrial agricultures, particularly soybean monocultures, with less than 9% remaining (Cartes and Yanosky, 2003; Fleytas, 2007; Da Ponte et al., 2015; Da Ponte et al., 2017a; Da Ponte et al., 2017b) (supplementary fig. S1).

Understanding the effects of habitat fragmentation on the behaviour and ecology of native "umbrella" species can assist with the successful development and implementation of robust conservation strategies in threatened ecoregions like the BAAPA. An umbrella species is a species whose protection in turn protects a large number of other species (Roberge and Angelstam, 2004). The hooded capuchin (*Sapajus cay* Illiger 1815) is the only representative of its genus found in Paraguay (Lynch-Alfaro et al., 2012), where the largest part of its range is the remaining BAAPA (Stallings, 1985; Rylands et al., 2013) though it occurs in gallery forest in the Cerrado and parts of the humid Chaco (Stallings, 1985). Across its range (and like that of other Paraguayan primates), very little is known about this species diet, reproduction, movements and activity patterns, home range and social organisation (Pinto, 2006; Fernandes Jr., 2013; Rylands et al., 2013; Smith and Briggs, 2015; Fernandes Jr. et al., 2020) and their adaptability to habitat fragmentation. The hooded capuchin is currently classified as Least Concern (globally (Rimoli et al., 2021) and in Paraguay (Cartes et al., 2017)) though this status may require revision (Smith, 2021).

Understanding a species behaviour is becoming more important in the design of conservation strategies (Tobais and Pigot, 2019) As habitat alteration leads to a reduction in availability of resources, animals may show flexibility in how they exploit the resources that are available (Maibeche et al., 2015) and understanding how animals respond to direct and indirect anthropogenic alterations is an integral bridge between behavioural ecology and conservation (Berger-tal et al., 2011). One method of investigating the response of non-human primates to anthropogenic habitat alteration is to examine dietary composition of different groups across areas that have experienced different levels of alteration (Wieczkowski, 2003; Isabirye-Basuta and Lwanga, 2008). Generalists tend to be less sensitive to reductions in patch size and habitat quality than specialists (Michalski and Peres, 2005; Devictor et al., 2008). Primates with more frugivorous diets can face challenges as habitat alteration can lead to a mismatch in the spatial and temporal distribution of their food resources (White et al., 1995; Donati et al., 2011). Species that are normally frugivorous, yet that are more adaptable to loss of resources, may show alterations in their diets such as an increase in consumption of "fallback foods" like mature leaves (Riley, 2007; Donati et al., 2011) or more difficult to access foods such as embedded insect larvae (Melin et al., 2014), or an increase in hard seeds or nectar (Terborgh, 1983). Habitat fragmentation and degradation can lead to a reduction in resources that may impact a species ability to meet their energetic requirements (Link et al., 2010). In some cases, species with particularly flexible behaviours or diets can benefit from human encroachment by supplementing their diets with anthropogenic resources such as agricultural crops (Freitas et al., 2008; Maibeche et al., 2015).

Capuchin monkeys (Genera: *Cebus* and *Sapajus*) are often described as generalists, opportunistic frugivorous-insectivores (Janson and Boinski, 1992; Fragaszy et al., 2004) with broad habitat requirements making them suitable umbrella species (Roberge and Angelstam, 2004). In general, most capuchin species appear thought to have diets mostly consisting of fruit and insects (Fragaszy et al., 2004). Although, information is available on the diets of hooded capuchins in the Argentinian Yungas

(Brown and Zunino, 1990) and Brazilian Cerrado (Pinto, 2006) no studies of the diet of this species in the BAAPA exist.

In this study, we compare the diets of three groups of Paraguayan hooded capuchins, two in a highly disturbed, isolated forest fragment and one in a near-pristine forest. We examined the effects of age, sex and season on the capuchins' dietary composition between the two sites to understand how capuchins adapt their feeding habits in response to fragmentation and degradation. As members of the genus *Sapajus* are known for their adaptability we hypothesised that the capuchins would be able to alter their diet in areas of different habitat quality and that age and sex would impact dietary diversity. As this study is part of a project that aims to use the hooded capuchin as an umbrella species for BAAPA conservation we discuss the implications of our results for BAAPA conservation in Paraguay.

Materials and methods

STUDY SITES

Data were collected from February 2016-February 2019 across two locations in the subtropical Oriental Region (Ervin and Gayoso de Ervin, 2019) in the Paraguayan BAAPA (supplementary fig. S1). Forests at both sites are characterised by deciduous, mesophytic, broadleaf plants (Lowen et al., 1996) but varied greatly in the level of anthropogenic alteration. Though Paraguay is sometimes considered to have only a Wet/Warm season and Cold/Dry season (Ervin and Gayoso de Ervin, 2019) in this study we are using a split of four seasons depending on rainfall and temperature. Rainfall in Paraguay varies greatly from year to year and is often not consistent throughout the seasons (Hill et al., 1984).

From February 2016-May 2017 the project was based in Rancho Laguna Blanca (RLB) in San Pedro department (23°49′52.0″S 56°17′42.2″W). During the study period RLB experienced an average temperature of 24°C (Spring: 24°C, Summer: 29°C, Autumn: 25°C, Winter: 19°C) with highs of 37°C and lows of 13°C. Mean rainfall varied throughout the study

period (Spring: 98 mm, Summer: 166 mm, Autumn: 130 mm, Winter: 22 mm) (TuTiempo, 2020; WorldWeatherOnline, 2020). RLB contained a 243 ha fragment of secondary BAAPA completely isolated from nearby fragments by soy fields treated regularly with pesticides, cattle ranches and human settlements. The forest fragment has a history of selective logging until 2010 when it was classified as a reserve. Reserve status formally ended in February 2015 when the property was put up for sale. During the study period human presence in the forest (apart from the researchers) was minimal. The hunting pressure on the monkeys was negligible as, though people from neighbouring communities did occasionally enter the reserve, monkeys were not their target. Domestic dogs were rarely sighted (either in person or on camera traps) inside the forest.

From May 2017-February 2019 data were collected at Nueva Gambach (NG), a property at the southern tip of San Rafael "National Park" in Itapúa department. San Rafael (26°62′62.5″S 55°66′52.2″W) is one only two areas of BAAPA in Paraguay with more than 50 000 ha. It consists of 60 privately-owned properties and while it is classed as "An Area to Become a National Park" has no formal protection. The NG property contained 150 ha of near-pristine forest surrounded on three sides by organic soy fields and connected to a 1.5 ha slash pine plantation on the western edge and at its northern border to the rest of San Rafael. With little to no primary or pristine Upper Paraná Atlantic Forest left in Paraguay (Da Ponte et al., 2017b) the forest of San Rafael is as close to near-pristine as remains and is of extremely high conservation importance. Outside of San Rafael and Reserva Natural Mbaracayu in Canindeyu department the majority of Paraguay's Atlantic Forest remains in small, degraded fragments, such as the forest fragment at RLB. This is why we have classified the NG forest as "Near-Pristine" in this study despite of its proximity to soy fields.

During the study period NG experienced a mean temperature of 24°C (Spring: 22°C, Summer: 26°C, Autumn: 23°C, Winter: 17°C) with a maximum temperature of 39°C and a minimum temperature of 1°C. Mean rainfall at NG was

Table 1. Demographics of study groups across the study period. Throughout the study, group sizes at both sites varied because of births, disappearances and immigrations.

Group/Site	Adult male	Adult female	Subadult	Juveniles	Infants	Total
O Group/RLB	3*	5-6	5-7	4-6	1-3	18-25
F Group/RLB	3-4	5-6	7-9	1-4	0-3	19-23
CC Group/NG	3-4	5-6	7-9	6-8	1-4	26-31

*In O Group three resident adult males were ousted in a takeover by three incoming adult males in August 2016.

slightly higher during the study period than during the study period at RLB (Spring: 235 mm, Summer: 175 mm, Autumn: 132 mm, Winter: 77 mm) (TuTiempo, 2020; WorldWeatherOnline, 2020).

STUDY SUBJECTS

RLB was home to two groups of semi-habituated hooded capuchins (table 1). As the two groups had overlapping home ranges (Smith, unpubl. data), the data for these groups was pooled. The NG property is home to four groups of capuchins. Only one group, the habituated CC Group (table 1) was included in the study as the others were completed unhabituated to human presence and their home ranges extended beyond the property border into areas with high levels of poaching. Adults of all focal groups were differentiated based on facial mask colouration, tuft shape and features such as scars (Smith and Briggs, 2015).

DATA COLLECTION

Data were collected six days/week at RLB and 15 days/month at NG. The capuchins were followed for as long as possible between dawn until dusk (typically between 3-8 hours per day). Data was collected at both sites using one-minute scan sampling (Altmann, 1974). One-minute samples were used to capture behavioural dynamics and to maximise the amount of data collection given the difficulties of remaining with the groups for long periods of time in the dense environment. The behaviour was recorded for every visible individual using a dictaphone. As it was not always possible to identify the species of plant, insect or vertebrate that an individual was feeding on, the item was classified as Bark, Crops, Fruit, Flowers, Grass, Galls, Leaves, Insects, Roots, Seeds or Vertebrates. The category Insects included insects and other invertebrates as it was not possible to discriminate between species in the field. The term Insects is used for brevity. It was not possible in the field to determine whether Gall consumption involved the complete gall or just the insect they contained. Crops were defined as non-native plants that had been cultivated by people for human use and include soy, maize and slash pine. Grass only contained two species of bamboo *Chusquea ramosissma* (Pocaece) and *Guadua chacoensis* (Poaece), both native to the BAAPA. The category Roots only contained the species *Philodendron bipinnatifidum* (Aracaeae).

Due to personnel and budget restrictions full phenological surveys of both sites were not possible. Habitat surveys were conducted at both sites using the quarter-point method (Ganzhorn et al., 2011). At RLB 20 × 20 m plots were used and the results extrapolated to give results per hectare (Smith et al., 2018a). At NG 100 × 100 m plots were used. Diameter at breast height (DBH) was calculated using a measuring tape to give the circumference and dividing by pi to give the diameter. Heights of all trees with a DBH of above 10 cm were measured using a clinometer. Length of borders with crop field (an indication of availability of crop access) was measured using Google Earth. For full description of the habitat survey method, see Smith et al. (2018a).

DATA ANALYSIS

Using Microsoft Excel (version 16.45) we first collated the observed dietary diversity of the capuchins at each site (separated by age,

sex and season). We used the frequency method (feeding observations per category/total feeding observations)*100) to determine the percentage of the diet composed of each category.

Using R Studio (version 1.3.1093) we used a data mining approach to estimate the influence of age, sex, season and site on the diets of the capuchin. Site is used as a variable to qualify habitat (degraded or not) and we recognise the lack of replication (two sites) for this variable in the interpretation of estimated effects. We anticipated that diet would vary depending on dietary requirements driven by demographic classes and seasonal fluctuations. We used these variables (Age, Sex and Season) to determine whether, given those potential effects, site was still influencing the diet, and whether potential site differences varied by demographic factors.

We determined whether diet, represented as a multinomial variable composed of eight categories (Bark, Crops, Fruit, Flowers, Grass, Leaves, Insects and Seeds) varied between sex, age class, season, and site. The rare categories Roots, Galls and Vertebrates were excluded from the modelling process. Seasons were defined as Spring – September to November, Summer – December to February, Autumn – March to May and Winter – June to August based on temperature and rainfall. The ages of individuals were determined according to Smith and Briggs (2015). Individuals were categorised as "adults" (adult individuals) and "non-adults" (subadults and juveniles). Subadults and juvenile were combined as the ages of individuals were unknown and the distinction between subadults and juveniles is harder to determine. Sex of individuals was determined by observation of genitals or extended nipples indicating lactation (Smith and Briggs, 2015). Observations of infants (individuals always carried by an adult or a subadult) and individuals of undetermined sex were excluded from the analysis. Infants were excluded because of the difficulty to observe them and also because milk would likely consistent of part of their diet and not the diet of any other age class. Multinomial log-linear models were fitted using the multinom function (Wood et al., 2006) in R Studio 1.3.1093 and we used a semi-supervised AIC-driven model selection approach (MuMIn dredge function (Barton, 2018) in R).

Feeding was recorded as a state during which individuals carried out feeding events and that was separated in time by prolonged periods of other behaviour. A single feeding event was defined as an individual ingesting a food item during a scan. We therefore assumed that we could deal with these observations as independent samples of diet. We determined whether this assumption was violated by inspecting the distribution of the residuals of our final models. The final model was interpreted after model validation was ascertained.

Results

FOOD AVAILABILITY

Habitat surveys indicated that the abundance of fruiting plants differed between sites. Forest structure differed between the two sites (likely as a result of the history of selective logging at LB) with a mean canopy height of 16.4 m (maximum tree height of 29.5 m) at RLB and 18.3 m (maximum tree height 31.2 m) at NG. The diversity of fruiting tree species (species indicated by Paraguayan forest guards to produce fleshy fruit rather than hard seeds) did not differ greatly between the sites with 31 species recorded at NG and 35 recorded at RLB. At RLB a mean of 110 trees/ha (Diameter at breast (DBH) height >25 cm) were recorded and the forest was dominated by the fruit producing species *Chrysophyllum gonocarpum*, *Inga marginata* and *Inga uruguensis*. NG had a mean of 90 trees/ha (Diameter at breast (DBH) height >25 cm) but no single species dominated the forest. However, at NG mean basal area was 42.4 m^2/hectare, while at RLB the mean basal area was only 3.2 m^2/hectare as the forest was dominated by smaller, younger trees. Fruit production increases with increasing basal area (Stevenson et al., 1998), therefore, there are indications that the abundance of fruit differed between sites, fruits having the potential to be more abundant at NG. Across the Atlantic Forest, fruit is available throughout the year but it is more abundant in the

summer months (Cardoso et al., 2018; More-latto et al., 2000) which was consistent with observations made at both sites. Insect abundance was not considered in this study but previous studies have shown that insect activity is higher in this region during the warmer, wetter months (Wolda, 1978; Coutinho-Silva et al., 2017; Smith et al., 2017). At both sites the capuchins' home ranges had direct contact borders with crop fields (RLB: 4.96 km / NG: 4.44 km) that were planted year-round on rotations including soybeans and maize. At the NG site there was a 1.5 ha slash pine (*Pinus elliottii*) plantation bordering the forest. RLB did not have a pine tree plantation. Native bamboo stands of *Chusquea ramosissma* (Pocaece) and *Guadua chacoensis* (Poaece) dominated 33% of the forest in RLB and 28% of NG.

Observed dietary diversity

A total of 12 013 observations of feeding were recorded during the study period: 5013 at RLB (2625 observations with confirmed age and sex of individual) and 7000 at NG (5592 observations with confirmed age and sex of individual) (shown in fig. 1A, B and supplementary table S1). There were items in the capuchins' diets unique to a site at both study sites. Roots were only observed being consumed at NG even though this species was available at RLB. Galls were only observed being consumed from one infected tree by O Group at RLB, although galls were available at NG. Vertebrates were consumed at both sites, the very small numbers of observations indicated that this was an opportunistic rare behaviour mainly involving stealing of birds' eggs and chicks from nests. The capuchins were observed feeding on parts of 43 different plant species (not only trees) from 24 families across both sites (supplementary table S2).

Influences of age, sex, season and site

The number of available observations permitted testing for more complex interactions among explanatory variables. The best fitting model included a 3-way interaction of age, sex and site and two-way interactions of season with

the other terms (table 2, supplementary figs S2-S6). The residuals of this model were not auto-correlated (supplementary figs S7-S8). All models close to the best fitting model (ΔAICc <10) had similar structures (table 2). The predicted effects of site alone on the diet are shown in fig. 2. The predicted composition of the diet when the interactions between sex, age and site are accounted for are shown in fig. 3 and the predicted seasonal differences are shown in fig. 4.

Discussion/conclusion

The diet of the capuchins differed between the two sites, with the main differences between the highly disturbed and near-pristine BAAPA sites being in the consumption of roots, galls and crops. O Group (RLB) were observed to eat insect galls from the infected leaves of a single *Balfourodendron riedelianum* tree. Neither F Group (RLB) or CC Group (NG) were ever observed to eat galls, although many other plant species were infected with galls at both sites. It is possible that the gall-eating behaviour observed by O Group capuchins was a group-specific tradition group tradition or something else. All age and sex classes were observed to feed on galls. Root feeding was observed by two subadult individuals at NG on a single occasion potentially indicating that an opportunistic experimentation of a new food source. Exploratory foraging allows the incorporation of new items into the diet and younger capuchin monkeys have been shown to be more willing to investigate and try novel food source than older individuals (Visalberghi et al., 2003).

As fruit production increases with increasing basal area (Stevenson et al., 1998) suggesting that NG had greater availability of fruits than RLB. However, the forest at RLB was dominated by smaller trees, likely as result of the history of selective logging for charcoal production, most of which were soft-wood, fruiting producing species. The observations and model predictions show that there is no noticeable difference in overall fruit consumption between the two sites. This could be a result of the capuchins using the smaller fruiting trees at RLB but it may also be a result of the NG capuchins access to the pine plantation. During

Observed Dietary Diversity of Hooded Capuchins in Reserva Laguna Blanca, San Pedro, Paraguay

	Adult Male				Adult Female				Non-Adult Male				Non-Adult Female			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Bark	0.00	6.32	3.30	7.10	0.00	0.72	1.87	9.41	0.00	7.06	0.00	0.00	0.00	7.87	0.56	0.00
Crops	0.00	0.00	0.00	0.55	0.00	0.00	0.00	0.59	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Flowers	0.00	0.00	0.90	0.00	8.00	0.72	1.12	0.00	0.00	0.00	0.60	0.00	0.00	0.00	1.12	0.00
Fruit	8.33	59.77	41.14	13.66	8.00	65.94	40.93	8.82	14.29	46.47	42.26	0.00	0.00	62.92	31.46	0.00
Galls	33.33	0.00	0.00	0.00	64.00	0.00	0.75	0.00	0.00	0.00	11.90	0.00	0.00	0.00	3.37	0.00
Grass	2.08	14.94	5.71	42.62	16.00	12.68	7.66	56.47	0.00	22.35	16.37	100.00	0.00	12.36	33.71	97.44
Insects	52.08	16.09	9.61	10.93	4.00	15.22	11.40	0.00	71.43	20.00	5.95	0.00	80.00	14.61	5.62	0.00
Leaves	4.17	2.87	21.62	15.85	0.00	4.35	18.88	22.94	14.29	4.12	3.57	0.00	20.00	2.25	2.81	2.56
Seeds	0.00	0.00	16.82	9.29	0.00	0.00	17.20	1.76	0.00	0.00	19.35	0.00	0.00	0.00	21.35	0.00
Roots	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vertebrates	0.00	0.00	0.90	0.00	0.00	0.36	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Age, Sex and Season

Observed Dietary Diversity of Hooded Capuchins in Nueva Gambach, San Rafael, Itapúa, Paraguay

	Adult Male				Adult Female				Non-Adult Male				Non-Adult Female			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Bark	5.14	0.00	0.00	0.00	0.00	0.79	0.39	0.00	0.00	1.71	0.00	0.00	0.00	0.71	0.00	0.00
Crops	5.14	69.44	65.24	7.30	0.39	58.27	43.05	1.73	0.32	52.00	37.29	0.91	2.92	42.86	29.02	2.79
Flowers	0.79	0.00	0.00	0.00	0.00	4.72	0.00	0.00	0.00	0.00	0	0.00	0.00	5.00	0.00	0.37
Fruit	69.57	18.75	8.02	63.27	87.40	22.83	8.49	63.11	52.38	11.43	9.32	68.41	55.44	19.64	5.88	52.60
Galls	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Grass	1.98	2.08	17.83	19.91	7.87	4.72	44.79	30.93	13.02	1.71	41.53	25.23	20.16	3.57	57.65	40.15
Insects	15.42	4.86	6.77	9.51	4.33	7.87	1.93	4.24	28.57	21.71	6.36	4.32	12.20	22.14	7.45	3.90
Leaves	1.58	4.86	1.96	0.00	0.00	0.79	1.35	0.00	2.86	8.00	1.69	0.91	5.04	4.29	0.00	0.19
Seeds	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.22	3.43	3.81	0.23	2.92	1.79	0.00	0.00
Roots	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	1.33	0.00	0.00	0.00
Vertebrates	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Age, Sex and Season

Figure 1. A) The observed dietary composition of the capuchins of Reserva Laguna Blanca according to age, sex and season. The observations of F and O Group were pooled. B) The observed dietary composition of one capuchin group of Nueva Gambach, San Rafael according to age, sex and season.

the two warmest seasons, Summer and Autumn, the capuchins' diets at RLB were dominated by fruits, whereas the capuchins' diets at NG were dominated by crops (pine seeds). This confirms that this group of hooded capuchins are adaptable enough to switch to a another, potentially higher quality food source when available, even if it is of anthropogenic origin.

Though capuchins at both sites were observed to eat crops, crop foraging at RLB was rare (2 occurrences out of 5013 observations, both of which were soybeans). A large proportion of the (NG) CC Group diet consisted

Table 2. Model selection outcomes from MuMIn dredging function with models ranked by increasing AIC. We provide details for the 10 best models and the terms they contain (+) or not (n).

Model	A	S	Sx	Si	A:S	A:Sx	A:Si	S:Sx	S:Si	Sx:Si	A:S:Sx	A:S:Si	A:Sx:Si	df	AICc	Δ	w
1	+	+	+	+	+	+	+	+	+	+	n	n	+	140	19498.1	0	0.49
2	+	+	+	+	+	+	+	+	+	+	+	n	+	161	19500.6	2.5	0.14
3	+	+	+	+	+	+	+	+	+	+	+	n	n	154	19501.0	3.0	0.11
4	+	+	+	+	+	+	+	+	+	+	n	+	+	161	19501.2	3.1	0.11
5	+	+	+	+	+	+	+	+	+	+	n	n	n	133	19502.5	4.4	0.05
6	+	+	+	+	+	+	+	+	+	+	+	+	n	175	19502.9	4.8	0.05
7	+	+	+	+	+	+	+	+	+	+	+	+	+	182	19503.0	4.9	0.04
8	+	+	+	+	+	n	+	+	+	+	n	+	n	154	19504.8	6.7	0.02
9	+	+	+	+	+	n	+	+	+	+	n	n	n	126	19519.7	21.6	0.00
10	+	+	+	+	+	+	+	+	+	+	n	+	n	147	19520.6	22.5	0.00
χ^2	314.5	2408.9	200.3	2425.6	297.3	30.1	52.4	136.0	786.6	38.7			22.2				
df	7	21	7	7	21	7	7	21	21	7			7				
p	***	***	***	***	***	***	***	***	***	***			**				

A: age category (adult or not), S: season, Sx: Sex, Si: site, ':' denotes an interaction. AIC: corrected AIC, Δ: difference in AIC between the model and the best model, w: weight of evidence for the model given its AICc and the AICc of other models. The significance of the effects for model 1 is given below the models ranked (χ^2 with associated df and *p*-value: *** <0.0001, ** <0.001).
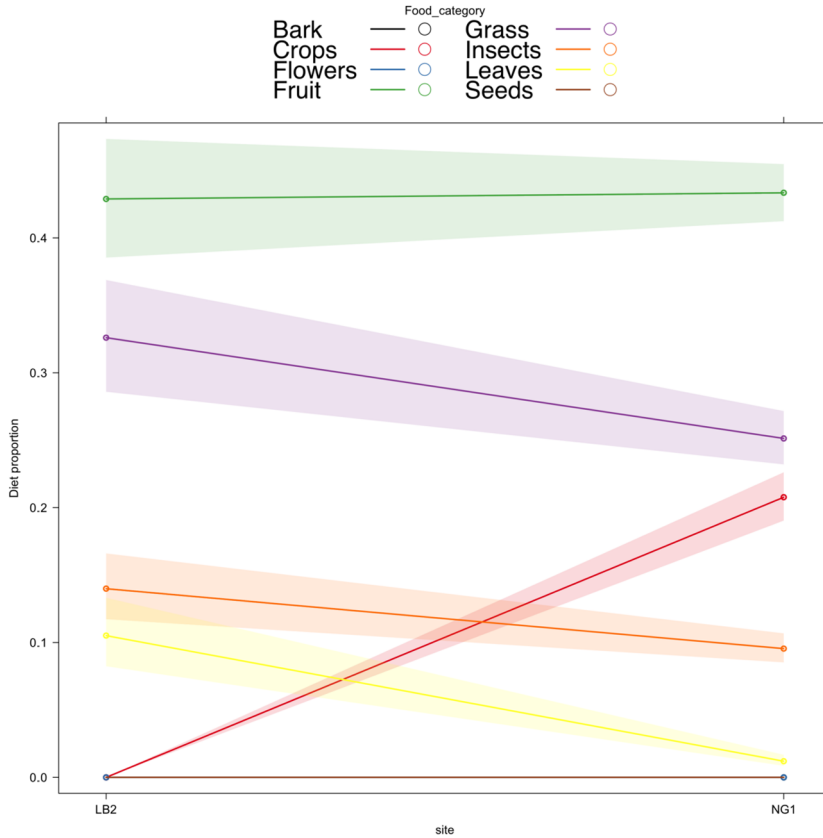
Figure 2. Predicted partial effect of site (model 1-table 2) on the diet composition of capuchins. Bands are 95% confidence intervals.

of seeds from pines of the Slash Pine (*Pinus elliotti*) plantation bordering the forest. Pine seeds have a high lipid content of the mature the pines seeds (∼21% of seed weight) (Barnett, 1976), higher than the lipid content (2-8%) of the fleshy fruit species found in the Atlantic Forest (Galetti et al., 2011). Pine seeds may therefore be a better source of lipids. Sex and age impacted the amounts of pine seeds in the diet. Males consumed more pine seeds than the females and adult capuchins were observed consuming pine seeds almost twice as frequently than non-adults. This could be due to the differences in metabolic requirements between ages. The metabolic requirements of adult *Sapajus macrocephalus* in Peru were 60% higher than those of juveniles (1674 kJ vs ∼ 1000 kJ (Nicolosi and Hunt, 1979). Another reason may be the accessibility of the seeds. The seeds are

encased in a hard, spiky shell requiring significant manipulation to open. Adult male *Sapajus* have greater attachments for the *M. temporalis* muscle (Silva Jr., 2001) and the *M. masticator* muscle contributing to increased bite force (Frazgaszy et al., 2004), potentially making it easier for adult males to access the seeds than females or younger individuals. Pine maturity peaked during Autumn and Summer and the capuchins appeared to take advantage of this high-quality food source as the proportion of this food item in their diet increases concurrently. Crops did not form an important part of the diet at RLB. There was no pine plantation at RLB and the capuchins had access to maize and soy beans, both crops that required descending to the ground to access. It is possible that the risk involved with foraging on terrestrial crops was higher. We can hypothesise that capuchin's
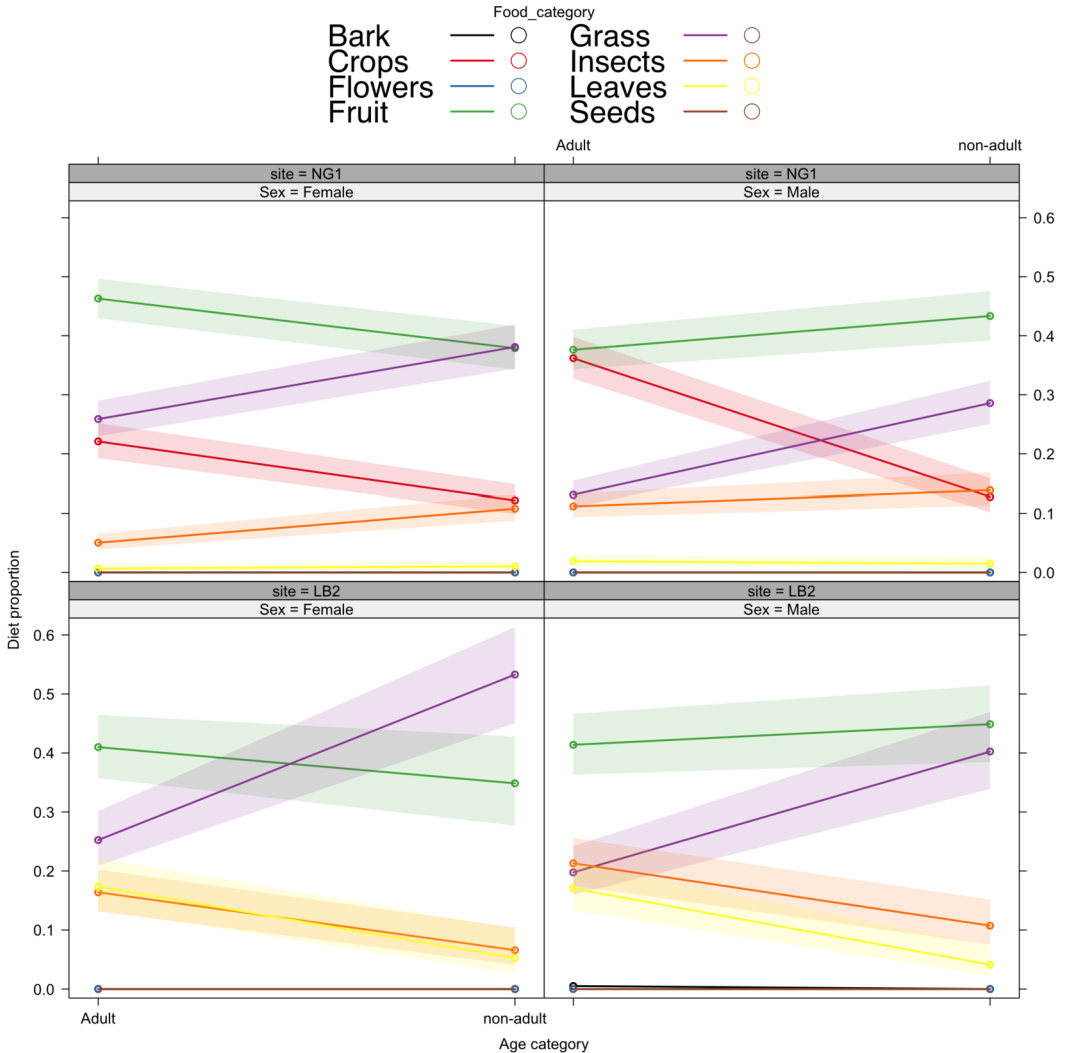
Figure 3. Predicted effect of Sex, Age and site on the diet composition of capuchins. Bands are 95% confidence intervals.

diet is flexible enough to take advantage of high-reward food items when they become available and the cost of acquiring them is not too high.

Capuchins at both sites consumed insects most often in Spring, possibly resulting from an increase in insect activity in warming weather. Non-adults at RLB consumed less insects than at NG. The crop fields surrounding NG produce organic soy and do not use chemical pesticides (Hostettler, pers. comm., 2019). At RLB the crop field bordering the forest was regularly sprayed with pesticides. The use of pesticides

on crop fields significantly reduces insect abundance compared to organic fields (De Snoo and De Leeuw, 1996; Krauss et al., 2011). When the crop field at RLB was sprayed the effects of the pesticide (burning eyes and throat) could be felt strongly throughout the forest (Smith, pers. obs.), indicating that the pesticides were permeating the whole fragment. It may be that the size of the insect community was affected by crop spraying resulting in the non-adult capuchins consuming less than non-adults at NG. Sustainable forest/crop management may require a
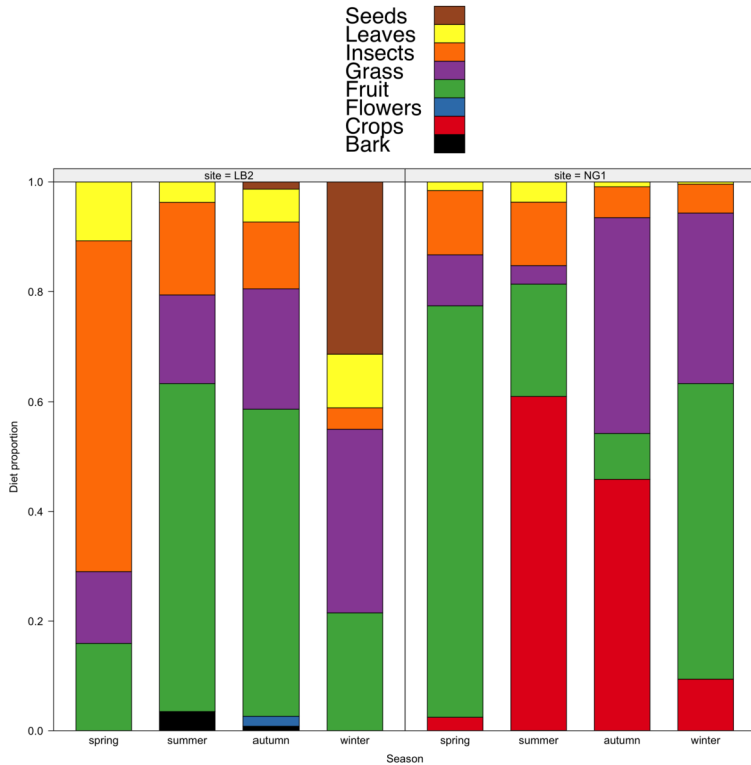
Figure 4. Predicted seasonal change in diet composition (model 1-table 2) across both sites.

minimum forest patch size, and ideally reducing the use of harmful pesticides, to allow insect communities to be sustained in the forest and not jeopardise the diet of resident insectivorous animals.

At both sites non-adult capuchins consumed more than twice as much Grass as adults. *Chusquea ramosissima* has roughly the same nutrient content as rice or wheat (Janzen, 1976), which contain 5.7-7.4% protein and 2.4-2.8% fat (Heinemann et al., 2005). The consumption of grass peaked in winter for all of the age-sex classes at LB and in autumn and winter for all age-sex classes at NG. This could potentially indicated that bamboo are a fall back food that supplements the diet when fruit or insects are less prevalent.

IMPLICATIONS FOR BAAPA CONSERVATION

Natural habitats, particularly the BAAPA, have been disappearing at a fast rate in Paraguay. Paraguay is the country forecasted

to be the first in the world to see a total disappearance of its moist primary forests (European Commission, 2019). In the late 1990's, Paraguay was experiencing the second highest rate of deforestation in the world, the government introduced reforestation incentives with little success due to lack of clear regulations (Da Ponte et al., 2017b). The Zero Deforestation Law (Law 2524/2004) implemented in 2004 makes it illegal to transform or convert any of the remaining forested land in the BAAPA region. Landowners with more than 20 hectares of land are required to keep 25% of their land forested and keep 100 m forested on either side of watercourses. Despite these top-down regulatory approaches, deforestation continues. In addition, the declaration of protected areas does not necessarily provide a robust solution to deforestation with effectiveness being highly heterogeneous (Buřivalová et al., 2021). The aim of our wider project is to create a viable conservation action plan for the BAAPA habitat

in Paraguay, based on the ecological requirements of our flagship the hooded capuchin, that could have benefits for the wildlife and the local people.

One of the issues gaining the support for conservation initiatives is the lack of profitable alternatives for smaller landowners besides timber and charcoal production (Da Ponte et al., 2017a). One promising alternative is the Payments for Environmental Service (PES) Program in which landowners would receive compensation for maintaining forest on their land (Da Ponte et al., 2017a). A survey of 277 households across the BAAPA region showed that 95% of small scale (<20 ha) and 78% of medium scale (20-50 ha) farmers supported reforestation on their land and 48% of large scale (>50 ha) farmers, did if it did not affect their agricultural land (Da Ponte et al., 2017a).

Our results indicate that the diet of hooded capuchins in Paraguay's BAAPA is flexible in response to anthropogenic change, within the constraints of our two-site comparison. Hooded capuchins appear able to adapt their diet, an important part of long-term survival, in small fragments without having to engage in risky crop foraging behaviour, consistent with the behaviour of other members of their genus. We propose that this indicates that it may be worth directing more conservation efforts towards smaller fragments that currently have little protection. Throughout the Atlantic Forest range more than 70% of what remains of this forest type exists in fragments of less than 100 ha (WWF, 2017).

Landscape connectivity enhances population viability for many species (Beier and Noss, 1998) and combining these results and the proper implication of PES legislation may provide an opportunity to begin reconnecting fragments. The capuchins can exploit new food sources (e.g., pine seeds) that are safely available. Small-scale landowners could be incentivised to create corridors between forest fragments on their land using native trees, mixed with shade-grown yerba mate (*Ilex paraguariensis*) bordered by Slash Pine plantations. Though some pine species including the slash pine have been shown to have the potential to become invasive there is no evidence in the area around San Rafael that the pine trees have become invasive, and though common, they are always found in plantations, rather than in the remaining forest (Smith, pers. obs). Participants could receive compensation through a PES scheme, providing cost-share incentives to landowners investing in reforestation including 75% of site preparation costs, 75% of maintenance costs during the first three years (Gonzalez-Gimenez, 2002) and a 50% reduction in property tax for reforested land (Frey, 2007). Native saplings could be provided at a subsidised rate through organisations such as Instituto Forestal Nacional (INFONA). Landowners could collect a profit from the pine timber and yerba mate leaves and wildlife would benefit from the increased connectivity of the forest.

The main barriers to successful implementation of such projects in Paraguay have historically been lack of public understanding, support and widespread corruption (WWF, 2011). For a proposal such as this to be successful, the Paraguayan public would need to support it. The use of a charismatic species increases support for conservation initiatives over the concept of saving ecosystems (Dietz et al., 1994; Westervelt et al., 2007). The hooded capuchin is potentially a suitable flagship and umbrella species for BAAPA conservation (Smith, 2021) as it the most well-known primate in Paraguay by the public (PLT, unpubl. data). This combinatorial approach of ecological research informing educational outreach and a robust management plan with financial benefits to human stakeholders, has been extremely successfully implemented in the Brazilian Atlantic Forest with the Golden Lion Tamarin (Kleimann et al., 1986; Engels and Jacobsen, 2007). It has yet to be applied in Paraguay at a large scale in any habitat.

Understanding how the capuchins in Paraguay's BAAPA adapt their diets to habitat degradation could provide the first step towards a comprehensive conservation management plan, using the capuchins as an umbrella species for Paraguay's BAAPA.

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Statement of ethics

Our research was approved by the Ministerio de Ambiente y Desarollo Sostenible (MADES) and the Fundación Para La Tierra Scientific Council. The research complied with all local laws (ethics board approval is not required in Paraguay). All of our data was collected in a non-invasive manner and complied with the American Society of Primatologists Code of Best Practices 2014.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Author contributions

RL Smith: principal investigator, project design, data collection, writing, analysis; E Megaponas: data collection, writing; K Rebergen: data collection, writing; C Payne: data collection, writing; D Lusseau: analysis, writing.

Data availability

This dataset is available at https://github.com/dlusseau/capuchins

Supplementary material

Supplementary material is available online at: https://doi.org/10.6084/m9.figshare.19071518

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