Ecological Flexibility of *Propithecus edwardsi* in Two Forest Habitats with Different Logging Histories in Ranomafana National Park, Madagascar

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Abstract
In the face of global change, where anthropogenic practices, such as logging, alter the structure and composition of forest habitats and impact primates' diets and activity budgets, it is essential to examine the ability of vulnerable species to persist. We studied the feeding ecology of the Endangered *Propithecus edwardsi* in two forest sites: one with a history of logging, and the other never logged, in Ranomafana National Park, Madagascar. During the dry season, from July-September 2016, we collected behavioral data on the taxonomic composition of the sifaka' diet, the plant parts they consumed, and the time they allocated to different activities in the two forest sites (a total of 431.5 hours). We found that the diversity of the diet of sifakas at each site was similar and that they only shared a small number of plant genera in their diet. Moreover, while the consumption of leaves, fruits, and seeds did not differ significantly between sites, we found differences in the time allocated to resting and feeding between sites. Our results suggest that habitat differences affect the feeding ecology of this species. Modifying their diet and behavior appears to enable sifakas to persist in anthropogenic habitats, providing support for ecological flexibility in primates with anatomical specializations for folivory.

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Introduction

Ecological flexibility describes an organism's ability to adjust its diet and behavior to different environments, allowing it to persist through disturbance events and avoid local extinctions (Isaac & Cowlishaw, 2004; Nowak & Lee, 2013). This is important in the maintenance of vulnerable species in changing landscapes, and therefore, has been the focus of many recent studies (Chaves & César Bicca-Marques, 2013; Dunham, 2017; Eppley *et al.,* 2017; Milich *et al.,* 2014; Sato *et al.,* 2016). This flexibility is particularly relevant in the context of primate conservation, as approximately 60% of primate species are threatened with extinction, and many species are highly dependent on forest habitats reduced by anthropogenic practices (de Almeida-Rocha *et al.,* 2017; Estrada *et al.,* 2017; Irwin *et al.,* 2010; Isabirye-Basuta & Lwanga, 2008; Lewis *et al.,* 2015).

Logging is one of the main causes of forest degradation through the removal of high-quality trees with both ecological and economic value (de Almeida-Rocha *et al.,* 2017; Johns, 1988; Saiful & Latiff, 2014). Harvesting trees is detrimental to the structure and composition of forests with implications for the ecological functioning of these habitats and the persistence of primate species (Brown & Gurevitch, 2004; Galat-Luong & Galat, 2005; Riley, 2007). This practice decreases mean tree diameter (Balko & Underwood, 2005; Cannon *et al.,* 1998; Teichroeb *et al.,* 2019), tree basal area (Cannon *et al.,* 1994; Skorupa, 1986; Teichroeb *et al.,* 2019), and tree height (Arrigo-Nelson, 2006; Balko & Underwood, 2005). It also promotes changes in canopy structure that result in the loss of canopy cover (Cannon *et al.,* 1994; Skorupa, 1986; Teichroeb *et al.,* 2019) and crown volume (Balko & Underwood, 2005; Milodowski *et al.,* 2021). Logging also can change plant species dominance and richness in forests by decreasing plant diversity (Balko & Underwood, 2005; Cannon *et al.,* 1998; Saiful & Latiff, 2014; Skorupa, 1986) and promoting the establishment of nonnative species that replace local endemics in these areas (Brown & Gurevitch, 2004; Johns, 1988, 1992; Saiful & Latiff, 2014).

Many studies focus on how vegetation changes resulting from logging affect primate populations (Berry *et al.,* 2010; Isabirye-Basuta & Lwanga, 2008; Sawyer *et al.,* 2017). Primate responses include changes in population density and group size (Chapman *et al.,* 2000; Galat-Luong & Galat, 2005; Herrera *et al.,* 2011; Johns, 1992), diet composition (Arrigo-Nelson, 2006; Irwin *et al.,* 2010; Johns, 1986; Johns & Skorupa, 1987; Milich *et al.,* 2014; Teichroeb *et al.,* 2019), home range size (Gerber *et al.,* 2012; Gonzalez-Monge & Behie, 2019; Irwin *et al.,* 2010; Johns, 1986), body mass (Irwin *et al.,* 2010; Johns & Skorupa, 1987), and activity budgets (Arrigo-Nelson, 2006; Johns, 1986; Li & Rogers, 2004; Milich *et al.,* 2014; Teichroeb *et al.,* 2019). Logging can create canopy gaps that increase sun light exposure and change the patterns of fruits and leaf production of the remaining trees (Ganzhorn, 1995). There is an increased availability of fruits and young leaves, which may benefit both folivorous and frugivorous species in the short-term (Balko & Underwood, 2005; Chaves & César Bicca-Marques, 2013; Isabirye-Basuta & Lwanga, 2008; Johns, 1988, 1992; Johns &

Skorupa, 1987; Rangel-Negrín *et al.,* 2018; Riley, 2007; Skorupa, 1986). However, in the long-term, the removal of larger trees, which are usually associated with high production of fruits, reduces the availability of these foods in the habitat even though the production of leaves can reach prelogging levels (Burivalova *et al.,* 2014; Cannon *et al.,* 1994, 1998; Chapman *et al.,* 2000; Johns, 1992; Riley, 2007; Sawyer *et al.,* 2017).

Although most responses to disturbance are species-specific (Galán-Acedo *et al.,* 2019), folivorous primates tend to fare better in face of disturbance than frugivorous primates that are usually more vulnerable to changes in their habitat (Balko & Underwood, 2005; Chapman *et al.,* 2000; de Almeida-Rocha *et al.,* 2017; Irwin *et al.,* 2010; Isabirye-Basuta & Lwanga, 2008). In Kibale National Park, Uganda, not all primate species had recovered their prelogging population densities 28 years after logging ceased (Chapman *et al.,* 2000). In a heavily logged forest, where at least 50% of all trees were destroyed, the group density of frugivorous *Cercopithecus mitis* and *C. ascanius* continued declining even after almost three decades since the end of logging in the area. The recovery of folivorous primates was affected by the amount of logging and varied between species. The density of folivorous *Procolobus tephrosceles* recovered more slowly in a heavily logged forest compared to a more lightly logged forest, where only 25% of all trees were damaged or destroyed, whereas the density of the folivorous and ecologically flexible *Colobus guereza* was higher than any other primate species in all logged forests independent of disturbance levels (Chapman *et al.,* 2000).

Driven by alterations in the structure and composition of the forest, the quality, abundance, and spatiotemporal distribution of food resources also is expected to change with implications for the time primates allocate to different behaviors due to the tradeoff between the energy received and spent to obtain different resources (Arseneau-Robar *et al.,* 2021; Gerber *et al.,* 2012; Milich *et al.,* 2014; Riley, 2007; Teichroeb *et al.,* 2019). Although leaves are distributed homogeneously throughout the forest, their high fiber content and presence of secondary compounds lead folivorous primates to spend more time resting and less time traveling than frugivorous species (Korstjens *et al.,* 2010; Rangel-Negrín *et al.,* 2018). However, primate responses to disturbance vary widely, even across folivorous species. Immediately following logging, *Colobus angolensis ruwenzorii* included more young leaves and fewer fruits in their diet compared with the prelogging period, with an increase in the time spent resting and socializing, and a decrease in the time spent feeding and traveling (Teichroeb *et al.,* 2019). In contrast, decades after logging, *Piliocolobus tephrosceles* females spent more time feeding and less time resting and traveling, and ate fewer leaves and more fruits, than their counterparts in old-growth forests (Milich *et al.,* 2014).

In Madagascar, the selective removal of high-value trees with hand saws is an ongoing practice by artisanal loggers that leads to some of the same trends found in other logged forests worldwide (Brown & Gurevitch, 2004; de Almeida-Rocha *et al.,* 2017; Irwin *et al.,* 2010). Here too, folivores seem better able to cope with disturbance than frugivorous species, as their presence increased or did not change after anthropogenic activities in the rainforest (Herrera *et al.,* 2011; Irwin *et al.,* 2010). The genus *Propithecus* show adaptations to a folivorous diet and the ability to use

different resources, allowing them to modify their behavior and adjust to new conditions (Campbell *et al.,* 1999; Guevara *et al.,* 2021; Irwin, 2006; Sato *et al.,* 2016). Logging and fragmentation have a negative impact on the diet of *Propithecus,* reducing its taxonomic diversity and reducing the consumption of preferred and energy-rich plant parts, such as fruits and seeds (Arrigo-Nelson, 2006; Irwin, 2008). These dietary changes were associated with alterations in behavior, as *Propithecus* in undisturbed areas spent more time traveling and less time resting (Arrigo-Nelson, 2006). Seasonality is another important predictor of the diet of these lemurs, as the presence of different plant parts is highly dependent on environmental conditions (Hemingway, 1998). During the dry season, more nutritious foods are less available and *Propithecus* rely more on leaves to fulfill their nutritional requirements (Arrigo-Nelson, 2006; Hemingway, 1998; Irwin, 2008).

Like other species within the genus, the Endangered *Propithecus edwardsi* is a large-bodied folivore (average mass of 5.0-6.5 kg) with a diet based on a combination of leaves, whole fruits, and seeds, and the occasional consumption of soil and insect larvae (Hemingway, 1996, 1998; Wright *et al.,* 2011). The group size of this diurnal lemur ranges from 2 to 9 individuals and its home range size varies between 30 and 55 hectares (Gerber *et al.,* 2012; Wright, 1995). Most populations of this species are found in Ranomafana National Park (RNP), which was established in 1991 and has areas with different histories of human use, including those where local communities have practiced timber extraction before the creation of this protected area (Wright *et al.,* 2002, 2011). These forest areas still show differences in structure and composition, even decades after the termination of the practice (Arrigo-Nelson, 2006; Balko & Underwood, 2005; de Winter *et al.,* 2018; King *et al.,* 2012).

We compared the diets of *Propithecus edwardsi* in two forest sites with distinct logging histories (one site that has been logged in the past, and another that has not), examining the plants consumed, the type of plant parts consumed, and the time spent feeding. We collected data during the dry season, because differences between sites may be more apparent during lean seasons when the availability of preferred food resources decreases (Beeby & Baden, 2021; Gerber *et al.,* 2012). Although both sexes modify their feeding ecology seasonally, the dry season is particularly important to females, because they lactate during this period, and their nutritional requirements increase (Koch *et al.,* 2017; Norscia *et al.,* 2006; Pochron *et al.,* 2003; Wright, 1995). Data for the dry season are thus particularly important to assess the potential dietary constraints on the reproductive success of this species and its long-term persistence in these forests (Meyers & Wright, 1993). We hypothesized that forest history will influence the sifakas' diet and behavior due to differences in forest composition, as in previous studies of this species (Arrigo-Nelson, 2006; Gerber *et al.,* 2012). Specifically, we predicted that *Propithecus* in the logged forest, which is likely to have reduced plant diversity based on other logged sites (Balko & Underwood, 2005; Cannon *et al.,* 1998; Saiful & Latiff, 2014; Skorupa, 1986), will feed on fewer plant genera than their counterparts in the unlogged forest. If sifakas eat plant parts according to their availability, then we predicted that flowers, fruits, and seeds will be more common in the diet of sifakas in the unlogged forest, where we assume that these plant parts are more available (Burivalova *et al.,* 2014; Cannon *et al.,* 1994, 1998; Chapman *et al.,* 2000; Johns, 1992; Riley, 2007; Sawyer *et*

al., 2017). We also predicted that differences in the plant parts consumed and their associated digestion time will influence *Propithecus* activity budgets. Specifically, we predicted that *Propithecus* inhabiting the logged forest will feed more on leaves and spend less time feeding and more time resting than those in the unlogged forest. In contrast, we predicted that *Propithecus* in the unlogged forest will include more flowers and fruits in their diet and spend more time feeding and less time resting than *Propithecus* in the logged forest because these foods are easier to process (Milich *et al.,* 2014).

Methods

Study Site

RNP is in a southeast montane rainforest of Madagascar, 21°16'S latitude and 47°20'E longitude, in the province of Fianarantsoa. This area contains moist evergreen forest and an elevation range between 500 and 1,500 m above sea level (de Winter *et al.,* 2018; King *et al.,* 2012; Wright, 1995; Wright *et al.,* 2011). Before the establishment of the park in 1991, sites were subject to variable degrees of logging intensity (Wright *et al.,* 2002, 2011). We conducted this study at two sites in RNP, with different logging histories (Fig. 1). Mangevo (565-1,065 m) is a primary forest site, located 20 km from the national highway RN25, and has been subject to minimal human disturbance. Vohiparara (1,075-1,275 m) is a secondary forest site near the national road that bisects the park (RN25). This site was logged for
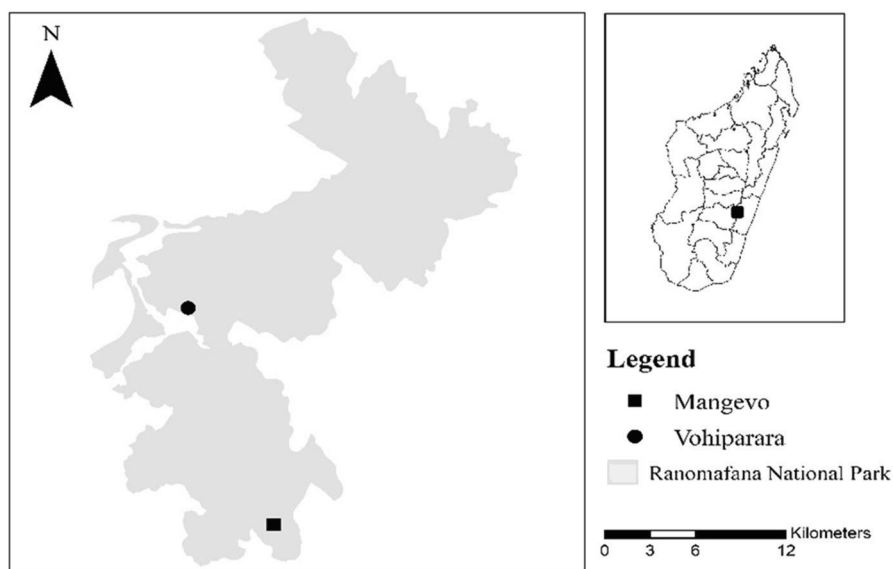

Fig. 1 Study sites in Ranomafana National Park, Madagascar. Mangevo has never been logged. Vohiparara has a history of logging that ceased approximately 30 years ago.

local use before the establishment of the park (Wright *et al.,* 2011), and as in other sites in RNP described in the literature (Arrigo-Nelson, 2006; Balko & Underwood, 2005; de Winter *et al.,* 2018), it still shows several structural characteristics that differ from those of Mangevo, including a decrease in several structural measurements, including mean DBH, basal area, tree height, and canopy cover and volume. These areas also include the presence of patches of small, understory invasive plants, *Psidium cattlynum* (Andriamaharavo *et al.,* 2010; Brown & Gurevitch, 2004; de Winter *et al.,* 2018). Our descriptions are only based on the literature on other sites in RNP with the same logging history, because we did not collect any botanical data about the structure and composition of the forest at any site.

Behavioral Data Collection

We followed 15 adult and subadult individuals (>3 years old) of *Propithecus edwardsi* between July and September 2016 during the dry season, for 7 weeks. These individuals lived in five groups: two in the unlogged forest (groups 1 and 2 with three sifakas each), and three in the logged forest (group 3 with five sifakas; group 4 with four; and group 5 with three). We followed three males and three females in the unlogged forest, and five females and four males in the logged forest (Table I). We followed a different group each week (3-5 days), and each day (6-10 hours per day, from dawn to dusk) two members of the team simultaneously followed a male and a female from the same group to collect instantaneous and continuous data. To calculate activity budgets, we collected instantaneous samples at

Table I Group composition of *Propithecus edwardsi* at each site (Mangevo: unlogged forest; Vohiparara: logged forest) in Ranomafana National Park, Madagascar, during the dry season between July and September 2016				

Site	Group	Sex	Age (yr)	Age category
Mangevo	1	Female	>4	Adult
		Female	>4	Adult
		Male	>4	Adult
	2	Female	>4	Adult
		Male	>4	Adult
		Male	3–4	Sub-adult
Vohiparara	3	Female	>4	Adult
		Male	>4	Adult
		Female	3–4	Sub-adult
		Male	3–4	Sub-adult
		Female	1–2	Juvenile
	4	Female	>4	Adult
		Female	>4	Adult
		Male	>4	Adult
		Female	1-2	Juvenile
	5	Female	>4	Adult
		Male	>4	Adult
		Female	1–2	Juvenile

5-minute intervals (Altmann, 1974), which we categorized as feeding, resting, traveling, other individual behaviors (including self-grooming and scent-marking), and social behaviors (including social grooming and play). We recorded "out of sight" (OOS) when we could not see the focal animal at the time of the sample. When we observed the focal animal feeding, we recorded additional information on the specific food item consumed, including the plant part (flowers, fruits, and/or seeds or leaves), and its taxonomic information (Wright, 1995). Centre Valbio technicians trained by the Missouri Botanical Garden classified the plants eaten. We used continuous sampling to record the duration of each feeding bout performed by the focal animal (Altmann, 1974). We defined feeding bout length as the duration of uninterrupted feeding, from the moment an individual placed the food in its mouth until the moment it changed food source or activity, with breaks no longer than 10 s.

Statistical Analyses

To test for differences between sites in the consumption of plant parts, we constructed linear mixed-effects models that account for the nonindependence between each observation due to repeated sampling of the same individuals and groups. To select the model that best fit our data, we used the Akaike Information Criterion (AIC) and chose the models with the lowest AIC value. To test the validity of the model, we examined the distribution of its residuals and the random effect coefficients, which are independent and follow the same distribution. We then assessed the effect of study site on the consumption of each food using an analysis of deviance (ANOVA). We did all the analyses using R 4.1.1 software.

We used the instantaneous categorical data collected to test for differences in the frequency of the daily activities performed by sifakas inhabiting the two different sites. We made 5,178 focal observations, 2,992 of which were from the unlogged forest and 2,186 of which were from the logged forest. To compare the frequency of each activity between sites, we used chi-square tests due to the categorical nature of the data, although these fail to account for the dependence of repeated data for the same individuals and groups.

Ethical Note

Subjects were always in their natural habitat and were habituated to human presence before conducting this study. None of the subjects were provisioned with supplemental food items. No direct physical contact by the observers to subjects was made at any time, and we kept a distance of 3 m between observer and sifaka at all times. The research adhered to the legal requirements of the country in which the research was conducted, and IACUC approval was provided through Stony Brook University (IACUC number 1501887-1). The authors declare that they have no conflict of interest.

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Results

Diet Taxonomic Diversity

For this analysis, we used a total of 1,511 feeding bouts, 855 of which we recorded in the unlogged forest and 656 in the logged forest. The taxonomic composition of the sifakas' diet in the two forests showed similar numbers of plant families and genera consumed. In the unlogged forest, sifakas ate from 30 plant families and 48 plant genera, from which only 11 families and 12 genera represented ≥1% of their total feeding time. In this site, more than 50% of all food items consumed came from the plant genera *Syzygium* (26.1%; Myrtaceae), *Agelaeae* (20.3%; Connaraceae), and *Bakerella* (14.9%; Loranthaceae). In the logged forest, their diet consisted of 28 families and 38 genera, from which 13 families and 13 genera represented ≥1% of their total feeding time. Unlike in the unlogged forest, in this site, only genera *Bakerella* (36.2%; Loranthaceae) and *Syzygium* (17.6%; Myrtaceae) accounted for more than half of the time sifakas spent feeding. In both sites, plant genera that made ≥1% of total feeding time accounted for more than 90% of the total number of genera consumed by sifakas during the dry season (Table II).

We found low dietary overlap between the sifakas at the two sites (family = 51.4%; genus = 35.8%). When only accounting for those species that made up ≥1% of the total feeding time, the number of plant families and genera shared between sifakas at each site decreased to 38.9% overlap at the family level and 19% at the genus level.

Dietary Profile

The linear mixed-effects models that we built included the proportion of each individual's feeding time as the dependent variable, the study site as the independent variable, and individual identification as a random effect. Overall, all models seem to show a strong predictive effect, although there is some variability in their confidence intervals (Table III). In all models, the independent variable has a significant relationship with the dependent variable in the model ($P < 0.5$).

Leaves were the most consumed food item in both forests (unlogged forest = 67.5%; logged forest = 58.7%), with more taxonomic genera represented than any of the other plant parts consumed. In the unlogged forest, sifakas consumed leaves from 41 plant genera, corresponding to 26 families, although only 10 genera (and 9 families) represented more than ≥1% of the total time spent feeding on leaves. Of these, two genera accounted for approximately 50% of time spent feeding on leaves: *Agelaeae* (29.71%; Connaraceae) and *Bakerella* (21.96%; Loranthaceae) (Fig. 2). In the logged forest, sifakas ate leaves from 34 genera from 23 different families, although only 12 genera (and 12 families) represented more than ≥1% of the total time spent feeding on leaves. In this site, the leaves consumed came

Table II Consumption of different plant genera by *Propithecus edwardsi* at two sites (Mangevo: unlogged forest; Vohiparara: logged forest) in Ranomafana National Park, Madagascar, during the dry season between July and September 2016. We included only genera that accounted for more than 1% in at least one of the sites. N = the total number of feeding bouts recorded at each site

Plant		No. feeding bouts recorded		Mean ± SD duration of feeding bouts (min)		% Total time spent feeding	
Family	Genus	Mangevo	Vohiparara	Mangevo	Vohiparara	Mangevo	Vohiparara
Connaraceae	*Agelaeae*	139	0	5.91 ± 2.48	0.00 ± 0.00	20.30	0.00
Fabaceae	*Albizia*	39	4	4.40 ± 1.48	1.89 ± 3.78	3.66	1.21
Euphorbiaceae	*Antidesma*	17	0	9.41 ± 4.86	0.00 ± 0.00	2.92	0.00
Rubiaceae	*Antirhea*	3	42	1.67 ± 2.66	2.84 ± 1.52	<1.00	3.26
Loranthaceae	*Bakerella*	166	223	4.26 ± 0.71	7.74 ± 3.27	14.92	36.24
Lamiaceae	*Clerodendrum*	2	29	0.60 ± 0.89	3.27 ± 1.54	<1.00	3.60
Aquifoliaceae	*Ilex*	7	7	1.14 ± 1.58	4.83 ± 8.93	<1.00	2.52
Euphorbiaceae	*Macaranga*	0	16	0.00 ± 0.00	13.65 ± 11.59	0.00	5.94
Clusiaceae	*Mammea*	12	0	4.71 ± 5.64	0.00 ± 0.00	2.75	0.00
Apocynaceae	*Mascarenhasia*	25	4	2.65 ± 1.02	1.11 ± 2.53	1.64	<1.00
Primulaceae	*Oncostemum*	37	54	7.98 ± 4.86	6.65 ± 2.04	4.53	8.38
Pittosporaceae	*Pittosporum*	37	1	3.12 ± 1.61	0.38 ± 1.06	2.55	<1.00
Apocynaceae	*Plectaneia*	9	27	1.03 ± 1.73	5.42 ± 5.61	<1.00	5.82
Araliaceae	*Polyscias*	24	11	2.79 ± 1.00	1.59 ± 1.55	1.29	<1.00
Lauraceae	*Potameia*	61	0	6.21 ± 1.31	0.00 ± 0.00	8.68	0.00
Acanthaceae	*Ruellia*	0	8	0.00 ± 0.00	1.46 ± 2.52	0.00	1.28
Sapotaceae	*Sideroxylon*	0	17	0.00 ± 0.00	4.59 ± 6.84	0.00	4.48
Smilaceae	*Smilex*	9	6	0.84 ± 1.08	3.85 ± 8.43	<1.00	1.76
Fabaceae	*Strongylodon*	44	0	2.84 ± 2.35	0.00 ± 0.00	3.89	0.00
Clusiaceae	*Symphonia*	3	13	0.75 ± 1.41	5.65 ± 4.71	<1.00	2.59
Myrtaceae	*Syzygium*	116	136	10.75 ± 2.87	7.68 ± 5.25	26.08	17.61

Table III Summary of results for the linear mixed-effects models built to account for differences in the consumption of different food items by *Propithecus edwardsi* in Ranomafana National Park, Madagascar, during the dry season between July and September 2016

Parameter	Beta	Lower-95% confidence limit	Upper-95% confidence limit	Random effect (SD)	*P* value
Leaves: AIC = −8322.82 (2096.3 difference to the next best-fit model)					
Intercept	161.17	139.32	183.01	103.17	<0.001
Study site	-75.95	-98.92	-52.98	58.19	<0.001
Fruits and seeds: AIC = −2128.75 (524.6 difference to the next best-fit model)					
Intercept	89.40	89.399	89.405	54.05	<0.001
Study site	−22.70	−22.71	−22.70	19.67	<0.001
Flowers: AIC = −844.96 (197.4 difference to the next best-fit model)					
Intercept	384.05	267.49	500.61	160.53	<0.001
Study site	-328.07	-444.99	211.16	143.92	<0.001
Soil: AIC = −273.41 (44.92 difference to the next best-fit model)					
Intercept	674.99	519.72	830.26	139.94	<0.001
Study site	−345.56	−538.18	−152.95	121.73	<0.001
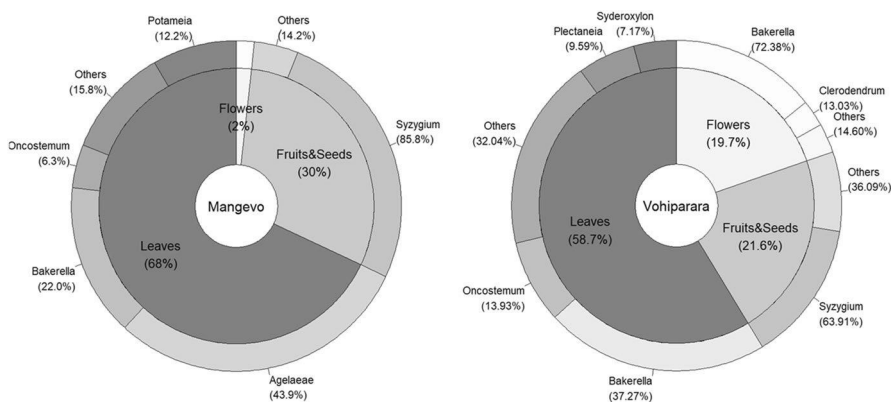
Fig. 2 Genera of plant parts consumed by Propithecus edwardsi in an unlogged forest (Mangevo) and a logged forest (Vohiparara) in Ranomafana National Park, Madagascar, during the dry season between July and September 2016.

mainly from *Bakerella* genus (Loranthaceae), accounting for 37.27% of the total consumption of leaves in this site (Fig. 2: Vohiparara). We found no statistically significant differences between sites in the consumption of leaves (Analysis of Deviance: $\chi^2 = 3.091$, df = 1, $P = 0.079$).

Fruits and seeds were the second most consumed item (unlogged forest = 30.3%; logged forest = 21.6%). For both sites, the most consumed genus was *Syzygium* from the Myrtaceae family, accounting for more than 60% of all fruits and seeds eaten during the study period (unlogged forest = 85.29%; logged forest = 63.93%). In the

logged forest, sifaka consumed fruit and seeds of ten genera (nine families), but only five genera and five families contributed ≥1% of fruits and seeds in the diet (Fig. 2). In the unlogged forest, sifaka also consumed fruit and seeds from ten genera (8 families), but only four genera and three families contributed ≥1% of the diet) (Fig. 2). We found no statistically significant differences between sites in the consumption of fruits and seeds (Analysis of Deviance: $\chi^2 = 1.035$, df = 1, $P = 0.309$).

Flowers were the least consumed plant parts in both sites (unlogged forest = 1.9%; logged forest = 19.6%). In the unlogged forest, sifakas included 2% of flowers (Table II), belonging to eight genera and seven families of plants in their diet, all of which accounted for less than 1% of the total feeding time. Two genera accounted for about 50% of the total time spent feeding on flowers: *Potameia* (26.07%; Lauraceae) and *Pittosporum* (23.68%; Pittosporaceae). In the logged forest, sifakas consumed flowers from six genera and five families, from which four genera (and 4 families) represented >1% of the total time spent feeding on flowers. At this site, the genus *Bakerella* (Loranthaceae) accounted for 72.38% of the time sifakas spent feeding on flowers (Fig. 2). Flowers were the only plant part consumed that showed significant differences between sites (Analysis of Deviance: $\chi^2 = 11.641$, df = 1, $P = 6.451 \times 10^{-4}$).

The remaining feeding time was spent eating soil and other ground products, including fungus (unlogged forest = 0.42%; logged forest = 0.37%). In both sites, sifakas come down to the ground sporadically to complement their diet with these food items. The consumption of soil varied significantly between sites (Analysis of Deviance: $\chi^2 = 5.273$, df = 1, $P = 0.022$).

Activity Budgets

While resting was the most frequent behavior in the unlogged forest (44.89%), the most frequent behavior in the logged forest was feeding (43.16%). In the unlogged forest, sifakas spent significantly more time resting than their counterparts in the logged forest ($\chi^2 = 57.003$, df = 1, $P < 0.001$). In the logged forest, sifakas spent significantly more time feeding than their counterparts in the unlogged forest ($\chi^2 = 67.479$, df = 1, $P < 0.001$). Although there also are differences in the frequency of other behaviors (Fig. 3), only feeding and resting differed significantly between sites (Traveling: $\chi^2 = 2.006$, df = 1, $P = 0.1566$; Self-Grooming: $\chi^2 = 1.656$, df = 1, $P = 0.1982$; Social grooming: $\chi^2 = 0.269$, df = 1, $P = 0.6039$; Scent marking: $\chi^2 = 0.123$, df = 1, $P = 0.7258$). We did not include "Play" due to its very low frequency of occurrence. Play was only displayed once by one of the adult males. OOS also showed significant differences between sites ($\chi^2 = 16.894$, df = 1, $P < 0.05$), being more frequent in the unlogged forest, but with low frequencies (unlogged forest = 0.39%; logged forest = 1.04%).

Discussion

We found low dietary taxonomic overlap and differences in the time spent feeding and resting between *Propithecus edwardsi* inhabiting two forest sites with different logging histories in RNP during the dry season. Sifakas at the two sites did not
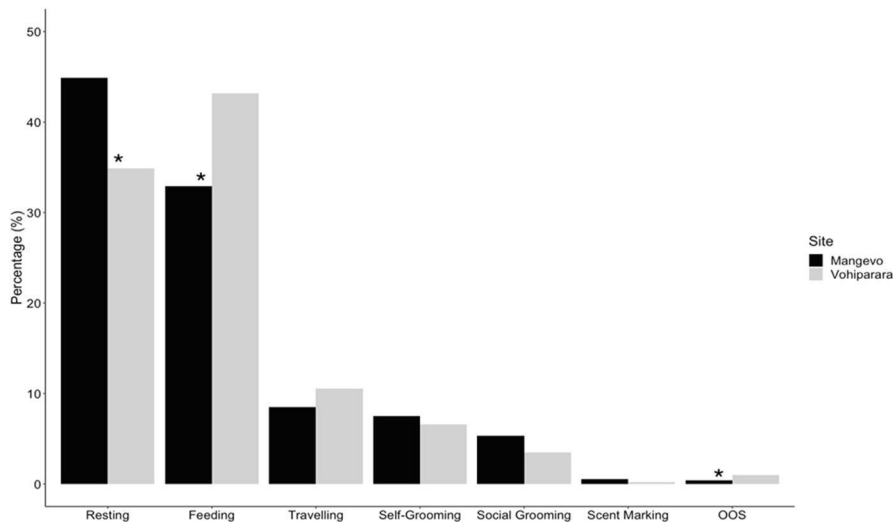
Fig. 3 Percentage time allocated to daily activities by *Propithecus edwardsi* in an unlogged forest (Mangevo) and a logged forest (Vohiparara), in Ranomafana National Park Madagascar, during the dry season between July and September 2016. OOS = "out of sight". *Significant χ^2 comparison between sites ($P < 0.05$).

differ significantly in the consumption of most plant parts (leaves, fruits, and seeds), but they varied in the consumption of flowers by approximately 18%. These differences may reflect the differing ecological characteristics of the two forests. Sifakas in the two forests also showed several similarities. They consumed similar numbers of plant families and genera, more than 90% of the total number of genera consumed was from plants that made up $\geq$1% of total feeding time, and leaves were the most consumed food item followed by fruits and seeds. We also found no significant differences in traveling, social grooming, and scent marking between the two sites.

In line with previous studies, we found differences in the taxonomic composition of sifaka diets between unlogged and logged forests, with sifakas in the unlogged forest showing a higher dietary diversity at the genus level (Arrigo-Nelson, 2006; Irwin, 2008). Although the number of both families and genera were similar when we only accounted for those plants that represented more than 1% of the diet, from these only 19% were shared between sites. This suggests that sifakas may show some selectivity in their dietary choices. In undisturbed forests, sifakas spent more time feeding on more abundant tree taxa, whereas their counterparts in a disturbed forest selected the remaining trees of preferred foods, consuming them more than expected from their availability (Arrigo-Nelson, 2006; Hemingway, 1998). The small diet overlap between the two sites accounts for less than half of the plant genera included in the diet of sifakas in the two sites, suggesting that sifakas may compensate for the lack of some taxa by consuming food items from others that are more readily available. This evidence supports the hypothesis that *P. edwardsi* adjusts its diet according to resource availability.

Sifakas showed a very diverse diet in terms of plant parts consumed, eating leaves, flowers, fruits, and seeds (Arrigo-Nelson, 2006; Hemingway, 1998). We predicted that sifakas in the logged site would consume greater proportions of leaves and lower proportions of other plant parts, such as flowers, fruits, and seeds, than in the unlogged forest; however, our results do not support this. In fact, the consumption of flowers was significantly higher at the logged site than at the unlogged site. Sifakas in the logged forest consumed flowers mostly from the *Bakerella* genus, whereas flowers of this plant accounted for less than 1% of feeding time spent on flowers in the unlogged forest. Species of this genus have been described as important fallback foods for *P. diadema* during the dry season in continuous forests and all year round in fragmented forests (Irwin, 2008). Because the consumption of this genus accounted for a large proportion of the total feeding time in both sites, we do not think that these differences are associated with differences in the availability of *Bakerella* species. Instead, this difference may be the result of the extended phenology of this vine that allows it to produce reproductive parts for almost the entire year, even during the dry season when other plants are not flowering and fruiting (Watson, 2001).

Altitude has also been associated with the characteristics of plant communities and their structure (Lehman, 2014; Matthews *et al.,* 2019). While lowland forests are biologically rich environments characterized by continuous forest canopy and high levels of rainfall, montane forests are characterized by lower levels of rainfall and a cooler environment, with less continuous canopy (Lehman, 2014). These differences in forest structure and rainfall patterns are likely to influence the patterns of production of leaves, fruits, and other plant resources, changing their availability throughout the forest, and therefore, their presence in primate diets (Hemingway, 1998; Matthews *et al.,* 2019). In addition to different logging histories, the study sites investigated here differ in altitude. The difference in altitude may confound our findings, as the characteristics of elevation match those left by past disturbance, leading to possible misinterpretation of the causes behind different vegetation patterns. Future research should investigate the factors behind forest structure and production patterns not only from an anthropogenic perspective but also based on forest topography.

Although usually described as folivorous (Arrigo-Nelson, 2006; Hemingway, 1998), sifakas have a very diverse diet compared with some other folivores. *Indri indri* relies more on young leaves and therefore has a higher fiber intake than sifakas, who eat higher levels of fat and water-soluble carbohydrates present in other plant parts, such as fruits, seeds, and flowers (Powzyk & Mowry, 2003). Although they select leaves less than stricter folivores, *Propithecus* species show the gastrointestinal adaptations necessary for the effective extraction of nutrients from different plant parts, including hard-to-digest leaves (Campbell *et al.,* 2000, 2004). This ability to feed on different resources and change their diet according to resource availability in the habitat confers ecological flexibility that allows *Propithecus* species to cope with changing environments (Herrera *et al.,* 2011; Irwin *et al.,* 2010). In relation to frugivorous species, such as *Eulemur* species, sifakas show a higher variation in the primary foods consumed over the year, consuming fruits and leaves equally (Sato *et al.,* 2016). This ability to use different resources and cope with disturbance is further supported by studies of the abundance of more specialized species, such as the highly frugivorous *Varecia variegata* (Wright *et al.,* 2011). Unlike *P. edwardsi,*

V. variegata declined following logging practices associated with the decrease in available food sources (Gerber *et al.,* 2012; Herrera *et al.,* 2011; White *et al.,* 1995). Although the effects of logging are still visible in RNP today, *V. variegata* is now returning to areas that have been recovering since 1991, suggesting that these forests are recovering their ecological functionality (de Winter *et al.,* 2018).

Differences in primate diet are often tied to behavioral strategies associated with the digestive requirements for the plant parts consumed. While fruits are higher in easily digestible energy, leaves have a higher fiber content and structural plant cell walls that increase digestion time and affect the time allocated to different activities (Campbell *et al.,* 2000, 2004). Several studies have found a positive correlation between the presence of leaves in the diet and the time individuals spend resting, whereas fruit consumption is negatively correlated with resting and positively correlated with active behaviors, such as feeding and traveling (Arrigo-Nelson, 2006; Beeby & Baden, 2021; Korstjens *et al.,* 2010; Milich *et al.,* 2014; Rangel-Negrín *et al.,* 2018; Teichroeb *et al.,* 2019). Our results are consistent with these patterns as we found that the site where sifakas spent more time resting and less time feeding was the same where sifakas included more leaves and fewer flowers in their diet. This suggests that sifakas can engage in different energetic strategies according to the resources available further supporting the ecological flexibility of this species. However, for *P. edwardsi*, the dry season is not only the time when preferred and higher energy food resources are less available, but also the females' lactating period, when they have higher energetic requirements (Meyers & Wright, 1993; Wright, 1995). To overcome the challenges of Madagascar's highly seasonal conditions, females have physiological and behavioral adaptations that allow gestation and lactation to occur during periods when more energetic food resources are less available (Pochron *et al.,* 2003; Wright, 1999). Increasing body mass through the consumption of certain plant parts in association with certain activity patterns also can be a favorable strategy for these species as it can be related to improved reproductive success (Dufour & Sauther, 2002). A previous study on this species found a relationship between the presence of fruits in sifaka's diet and the reduction of time spent traveling, which was associated with mass gain in females during the dry season (Arrigo-Nelson, 2006). In other lemur species, females increase their nutrient intake and body fat before and after the scarcity period, by increasing the time spent feeding (Atsalis, 1999; Tarnaud, 2006), whereas in other lemur species, females maintain a consistent intake of food year-round (Vasey, 2005). Interestingly, we did not find differences between the sites in the time spent traveling or engaged in social interactions, such as grooming, suggesting that sifakas in the logged forest may not be badly stressed by the limiting conditions of their habitat. However, future research should focus on the relationship between body mass and the reproductive success of sifakas, which is crucial for the species conservation.

Conclusions

This study advances our understanding of the ecological flexibility of *Propithecus edwardsi* during the dry season by showing their ability to use different resources in different habitats. We tested the effect of past disturbance on the diet and activity

budgets of sifakas by comparing study groups in two different sites in RNP. We found that sifakas at each site share a small number of plant families and genera in their diet and that the dietary diversity of sifakas in the unlogged forest was higher than in the logged forest. For plant parts consumed, we only found significant differences in the consumption of flowers between sites, which contrary to our predictions, was higher in the secondary forest site. Although the consumption of leaves did not differ significantly between the sites, we found differences we found in resting and feeding behaviors which follow the patterns previously described for folivorous primates, with the consumption of leaves being an important determinant in the time individuals allocate for resting, whereas the consumption of fruits, seeds, and flowers can have implications for the time individuals spend feeding. Differences in the frequency of these behaviors during the dry season, when females experience a lack of more nutritious foods, may have implications for their reproductive success due to its relationship with gain in body mass. Less active females may increase their mass and experience a less stressful lactating period. Although the logged forest we studied is recovering from past anthropogenic activities, these differences may still have implications for the long-term persistence of sifakas in RNP.

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