Received: 20 March 2023 | Revised: 23 January 2024 | Accepted: 10 February 2024

DOI: 10.1002/ajp.23609

RESEARCH ARTICLE

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

# Dietary flexibility of the greater bamboo lemur (*Prolemur simus*), a specialized feeder, in eastern Madagascar

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## Abstract

The degree of dietary flexibility in primates is species specific; some incorporate a wider array of resources than others. Extreme interannual weather variability in Madagascar results in seasonal resource scarcity which has been linked to specialized behaviors in lemurs. *Prolemur simus*, for example, has been considered an obligate specialist on large culm bamboo with >60% of its diet composed of woody bamboos requiring morphological and physiological adaptations to process. Recent studies reported an ever-expanding list of dietary items, suggesting that this species may not be an obligate specialist. However, long-term quantitative feeding data are unavailable across this species' range. To explore the dietary flexibility of *P. simus*, we collected data at two northern sites, Ambalafary and Sahavola, and one southern site, Vatovavy, from September 2010 to January 2016 and May 2017 to September 2018, respectively. In total, we recorded 4022 h of behavioral data using instantaneous sampling of adult males and females from one group in Ambalafary, and two groups each in Sahavola and Vatovavy. We recorded 45 plant species eaten by *P. simus* over 7 years. We also observed significant differences in seasonal dietary composition between study sites. In Ambalafary, bamboo was the most frequently observed resource consumed (92.2%); however, non-bamboo resources comprised nearly one-third of the diet of *P. simus* in Sahavola and over 60% in Vatovavy. Consumption of all bamboo resources increased during the dry season at Ambalafary and during the wet season at Vatovavy, but never exceeded non-bamboo feeding at

**Abbreviations:** *B. vulgaris*, *Bambusa vulgaris*; CABI, Center for Agriculture and Biosciences International; CI, confidence interval; CIRAD, Center de Coopération Internationale en Recherche Agronomique pour le Développement; C. madagascariensis, Cathariostachys madagascariensis; *E. rufifrons*, *Eulemur rufifrons*; *H. aureus*, *Hapalemur aureus*; IDAO, Identification Des plantes Assistée par Ordinateur; INBAR, International Bamboo and Rattan Organization; IUCN, International Union for Conservation of Nature; NGO, non-governmental organization; POWO, plants of the world online; *P. simus*, *Prolemur simus*; RNP, Ranomafana National Park; *V. diffusa*, *Valiha diffusa*.

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**Funding information**
Re:wild; Margot Marsh Biodiversity Foundation; Omaha's Henry Doorly Zoo & Aquarium; Conservation International; Aspinall Foundation

the latter. Culm pith feeding was only observed at Ambalafary, where it was more common during the dry season. We identify *P. simus* as a bamboo facultative specialist capable of adjusting its feeding behavior to its environment, indicating greater dietary flexibility than previously documented, which may enable the species to survive in increasingly degraded habitats.

**KEYWORDS**
anthropogenic disturbance, conservation, dietary specialist, primates

## 1 | INTRODUCTION

As an order, primates are predominantly omnivorous and typically exploit a variety of resources (Chapman & Chapman, 1990; Garber, 1987; Sussman, 1987), demonstrating remarkable dietary flexibility, i.e., alterations in feeding behavior due to ecological changes (Nowak & Lee, 2013; Piersma & Drent, 2003). This has been shown to be a hallmark of all types of primates, both strepsirrhines (lemurs: Atsalis, 1999; Beeby & Baden, 2021; Curtis, 2004; Hemingway, 1998; Overdorff, 1993; Overdorff et al., 1997; Sato et al., 2016; Sefczek et al., 2020; lorises: Cabana et al., 2017; Swapna et al., 2010; galagos: Harcourt, 1986; Masters et al., 1988), and haplorrhines (tarsiers: Gursky, 2000; monkeys: Chaves & Bicca-Marques, 2013; Galetti & Pedroni, 1994; Garber, 1993; Harris & Chapman, 2007; Porfirio et al., 2017; apes: Doran, 1997; Doran-Sheehy et al., 2009; Head et al., 2011; Russon et al., 2009; van Schaik, 2009; Wrangham et al., 1998). Much of this dietary flexibility has been identified in the last 50 years as primates contend with seasonal fluctuations in resources (Baranga, 1982; Chapman, 1987; Clutton-Brock & Harvey, 1977; Garber, 1993; Harcourt, 1986; Hladik & Hladik, 1969; Nagy-Reis & Setz, 2017; Stone, 2007; Stoner, 1996; Watts et al., 2011) and/or anthropogenically modified habitats (Albert et al., 2014; Chaves & Bicca-Marques, 2016; Dunham, 2017; Ménard et al., 2014; Riley, 2007; Tesfaye et al., 2013). It is important to note that such dietary flexibility for a species can only be assessed because of the accumulation of ethological data over appropriate time scales and at multiple levels: individual, group, and population (Chapman & Rothman, 2009).

Dietary flexibility for lemurs, the endemic primates of Madagascar, is thought to be evolutionarily advantageous when dealing with the dramatic seasonal shifts that are common on the island (Dewar & Richard, 2007; Jury, 2003; Wright, 1999). Species from all the lemur families demonstrated an ability to alter their diets: Lemuridae (Beeby & Baden, 2021; Cameron & Gould, 2013; Donati et al., 2007a; Overdorff et al., 1997), Indriidae (Irwin, 2008; Norscia et al., 2006; Powzyk & Mowry, 2003; Sato et al., 2016; Thalmann, 2001), Daubentoniidae (Ancrenaz et al., 1994; Randimbiharinirina et al., 2018; Sefczek et al., 2020; Sterling, 1994), Cheirogaleidae (Atsalis, 1999; Hladik, 1979; Hladik et al., 1980), and Lepilemuridae (Rasoamazava et al., 2022; Thalmann, 2001). This dietary flexibility is proving particularly beneficial because of the dramatic declines in habitat availability across the island (Baden et al., 2019; Green & Sussman, 1990; Harper et al., 2007; Morelli et al., 2020; Sussman et al., 1994). And across a geological time scale, dietary flexibility was associated with species persisting through dramatic ecological shifts where mass extinction events resulted more often in the loss of specialists (Clavel et al., 2011; Machado et al., 2023).

Despite the apparent adaptive advantage of dietary flexibility, globally as well as within Madagascar, greater bamboo lemurs (*Prolemur simus*) are perceived as obligate dietary specialists (Ballhorn et al., 2016; Itoigawa et al., 2021). Obligate specialists have a narrow, inflexible diet primarily consisting of difficult resources that necessitate specialized morphology, physiology or behaviors to process (Ballhorn et al., 2016; Shipley et al., 2009). Greater bamboo lemurs have been identified as obligate specialists on large-culm bamboo (Ballhorn et al., 2016; Itoigawa et al., 2021). A study by Tan (1999), to date the seminal study on *P. simus* diet, illustrated that 95% of the diet of one group of greater bamboo lemurs in Ranomafana National Park (RNP) was composed of a single species of endemic giant bamboo, *Cathariostachys madagascariensis*. From this plant, greater bamboo lemurs consumed leaves, pseudopetioles, new shoots, and the mechanically challenging pith of mature culms; this last resource, in particular, was identified as critical during the dry season with peak consumption (89%) in October (Tan, 1999).

This degree of dietary specialization on one resource species is extreme. Generally, when an herbivorous species possesses physiological or morphological adaptations that help it to consume a difficult resource, a threshold of approximately 60% of a diet composed of a single genus or family is accepted as the lower limit of specialization, especially when said resource is not used to a similar extent by sympatric herbivores (Shipley et al., 2009). On the other end of the specialization spectrum from obligate is facultative. Like obligate specialists, facultative specialists have narrow dietary niches and may have adaptations to process difficult foods. Where they differ is that facultative specialists can expand their diet to include less difficult foods when conditions allow, resulting in a broader fundamental niche (Shipley et al., 2009; Szumski et al., 2023). The fundamental niche is defined by a species' physiology associated with, for example, tolerances to plant secondary metabolites or nutritional requirements (Hutchinson, 1965; Roughgarden, 1974). The realized niche may be narrower than the fundamental niche due to extrinsic factors such as availability, preferences, or competition (Hutchinson, 1965; Roughgarden, 1974).

Since Tan's (1999) initial study, reports of *P. simus* at other locations have increased the known dietary repertoire of greater bamboo lemurs to include between 33 and 41 species (numerous taxa identified only to genus) from 18 families (Table S1; Andrianandrasana et al., 2013; Eppley et al., 2017; Eronen et al., 2017; Glander et al., 1989; Lantovololona et al., 2012; McGuire et al., 2009; Meier & Rumpler, 1987; Mihaminekena et al., 2012; Rakotoarinivo et al., 2017; Randriahaingo et al., 2014; Randrianarimanana et al., 2012, 2014; Ravaloharimanitra et al., 2011, 2013; Tan, 1999, 2007; Yamashita et al., 2009; Wright et al., 1987). This expansion of consumed dietary resources suggests that *P. simus* could, instead, be considered a facultative specialist. However, most of these feeding observations were recorded opportunistically and do not quantify the proportions of resources consumed, confounding the estimation of *P. simus*' fundamental niche.

*Prolemur simus* is listed as Critically Endangered on the IUCN Red List (Ravaloharimanitra et al., 2020), and has long been considered one of the most threatened of all lemur species (Wright et al., 2008). Conservation planning and evolutionary understanding is undermined by a lack of comprehensive information on key ecological traits, especially dietary breadth (Game, Kareiva, & Possingham, 2012; Hendry et al., 2010; Sinclair & Byrom, 2006). Therefore, it is critical to assess data from across the distribution of *P. simus* to adequately gauge its degree of specialization and develop a more accurate understanding of the species' fundamental niche. As some species can shift from being an obligate to a facultative specialist depending on resource availability (Apostolico et al., 2016; Szumski et al., 2023), long-term data on *P. simus* should be used to create a species-specific spectrum of specialization upon which populations can be assessed. Doing so would open doors to explore the drivers of dietary specialization and their implications on species viability in changing environments.

The main objective of this study was to investigate the diversity within the diet of greater bamboo lemurs across three sites (Ambalafary, Sahavola, and Vatovavy) and use the results from RNP (Eronen et al., 2017; Tan, 1999) as a baseline for comparative analyses. By exploring the dietary breadth of *P. simus* across its distribution and comparing our findings to previous publications on resource consumption by greater bamboo lemurs, we tested the hypothesis that greater bamboo lemurs are obligate bamboo specialists, i.e., at least 60% of feeding observations would be on woody bamboos (Bambusoideae) at every site (Shipley et al., 2009). Additionally, given that most lemurs demonstrate seasonal dietary changes, including *P. simus* at RNP (Eronen et al., 2017; Tan, 1999, 2000), we hypothesized that there will be seasonal differences on bamboo and non-bamboo consumption and seasonal differences in consumption of the parts (leaves, culm pith, shoots, etc.) of the large-culmed bamboo eaten by *P. simus*. Specifically, consistent with the results of Tan (1999) at RNP and the known phenology of bamboos in Madagascar (King et al., 2013; Randriahaingo et al., 2014), we predicted that shoots will be more frequently consumed during the wet season, while culm pith will be more frequently consumed during the dry season. As the sites in this study are nearly 300 kilometers apart, site is also hypothesized to influence both the frequency of consumption of bamboo and non-bamboo resources, as well as bamboo part.

## 2 | METHODS

### 2.1 | Study sites

This study was conducted in Madagascar at two sites in the northern part of the *P. simus* range in the Brickaville District, Ambalafary and Sahavola, and at one site in the southern reaches of its range, Vatovavy Forest (Figure 1). The first two sites are part of the mosaic of secondary vegetation habitats in the largely deforested landscape surrounding the Andriantantely lowland evergreen moist forest, while Vatovavy, also a lowland forest, has varying levels of degradation (Emberton, 1996; Gautier et al., 2018). All sites have two seasons: a hot/wet season (November to April) and a cold/dry season (May to October; Copernicus Climate Change Service, Climate Data Store, 2021). See below how temperature and precipitation were included in the data analyses.

Ambalafary (S18.8008° E48.8092°) is located in the Rural Commune of Fanasana Gare, on the north bank of the Ivohitra River, west of the Mangabe fokontany (Mihaminekena et al., 2012; Ravaloharimanitra et al., 2013). Covering 130 ha from 60 to 125 m elevation, Ambalafary is comprised of zones rich in bamboos, including dense clumps of both green and yellow varieties of *Bambusa vulgaris* along the river edge, stands of *Valiha diffusa*, and areas of *Phyllostachys* sp. Other zones of secondary vegetation are dominated by *Ravenala* sp. or by overgrown plantations of bananas, lychees, coffee, and jackfruits (King et al., 2013).

Sahavola (S18.6899° E48.9768°) is located 21 km northeast of Ambalafary, in the Rural Commune of Anivorano Est, to the west of the Rianala River (Mihaminekena et al., 2012). Covering approximately 30 ha from 25 to 150 m elevation, Sahavola is private property comprising secondary vegetation dominated by *Ravenala* sp. and mature stands of the bamboo *Valiha diffusa*, with areas of plantations of jackfruits, lychees, cinnamon, and pineapples.

Vatovavy forest (S21.3981° E47.9428°) is a culturally protected area on Vatovavy Mountain that straddles the Rural Communes of Antsenavolo and Kianjavato. It covers 640 ha with an elevation ranging from 90 to 530 m (Holmes, 2012). This forest has areas of *V. diffusa* throughout and sparse stands of the green variety of *B. vulgaris* at the base of the mountain on the banks of the Fotobohitra River near the fokontany of Ambolotara. There are pockets of slash and burn agricultural activity within the forest (Manjaribe et al., 2013).

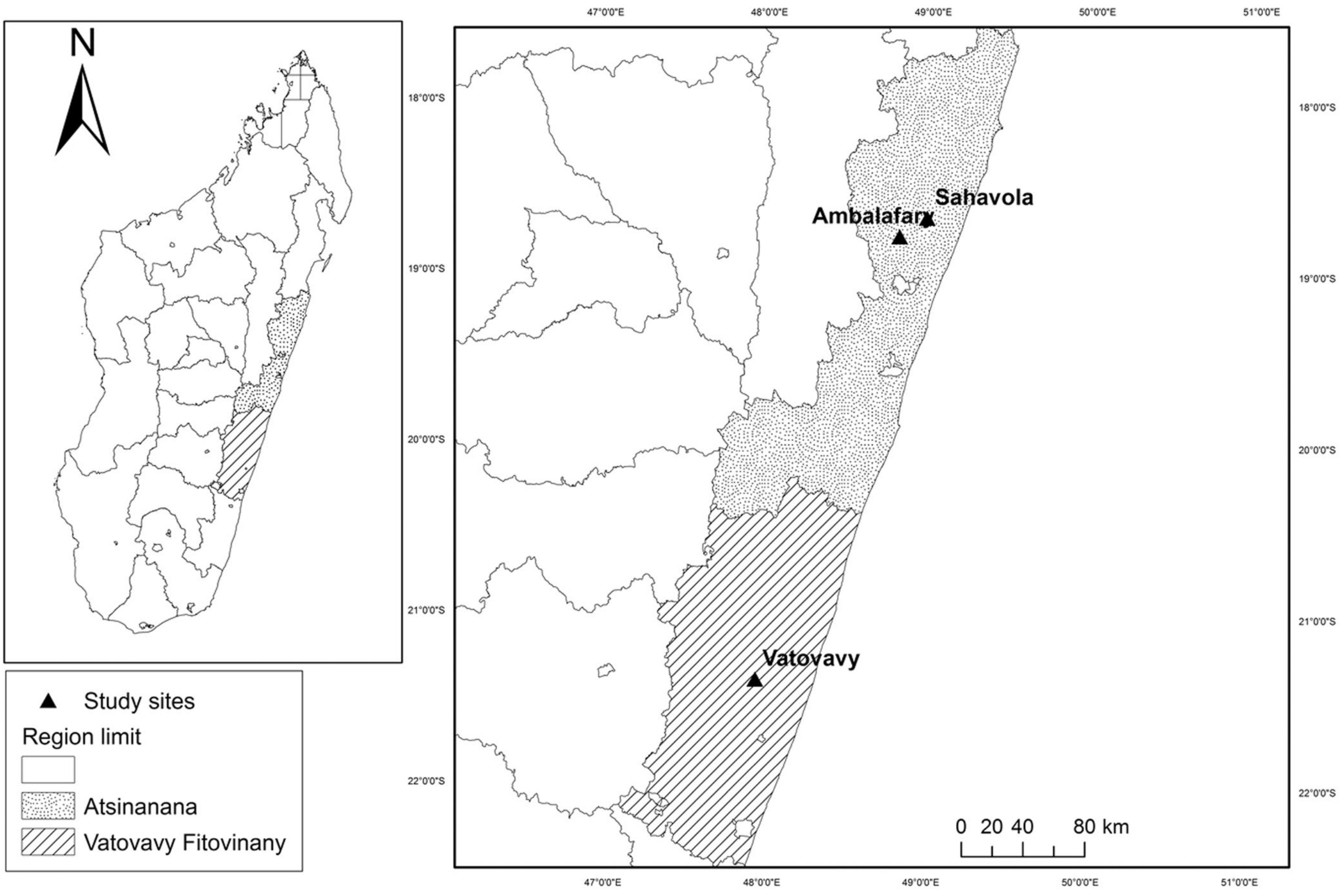



**FIGURE 1** Location of study sites in Madagascar.

## 2.2 | Behavioral data collection

We recorded behavioral observations using instantaneous recording methods at 5-min intervals (Altmann, 1974) between 05 and 19 h, depending on when the study group was first located by the observers each day. On average, individuals were followed for 5 h per day at Ambalafary and Sahavola, and 6 h per day at Vatovavy. Information on behavioral data collection per site, group, total number of individuals, and the total hours of data per individual are presented in Table S2. Furthermore, all individuals monitored for this study were free-ranging adult males and females, though immature individuals were also present.

We collected data over 112 days at Ambalafary (dry season: 63, wet season: 49) and 133 days from Sahavola (dry season: 66, wet season: 67) between September 2010 and January 2016. During follows, we changed focal individuals within the group every 2 h. In Vatovavy forest, between May 2017 and September 2018, we collected behavioral data on eight adults across two groups. Data were collected Monday through Friday, switching groups and following a different focal individual each day, for a total of 193 days of data (dry season: 128, wet season: 65). It is important to note that focal animals in Vatovavy forest were radio-collared to aid with individual identification in this monomorphic species (Frasier et al., 2015). These adult individuals were sedated, using 10 mg/kg Telazol® (Zoetis) delivered by dart from a $CO_2$-powered injection rifle, and fitted with a radio collar (Advanced Telemetry Systems M1545). The collaring procedure was detailed in Rakotonanahary et al. (2021). Vatovavy individuals were captured under the supervision of a veterinarian with over 20 years of experience and a qualified team.

During feeding observations, we recorded the plant species and part consumed. We classified various food items, including young or mature leaves, shoots, culm pith, and flowers, and ripe or unripe fruit. We combined the branch shoots and ground shoots under a single term "shoots." Large-culmed bamboo species were identified following King et al. (2013) with updated taxonomy based on the work of Dransfield (2016) and Zhang et al. (2017). Other plant species were identified using the Catalogue of the Plants of Madagascar (MBG, 2021), the Invasive Species Compendium (CABI, 2016), IDAO (CIRAD, 2016), Plants of the World Online (POWO, 2022), and through consultation with botanists at the Herbier d'Antananarivo. *Ravenala madagascariensis* was considered one species at the time of this study, but five new species were subsequently described (Haevermans et al., 2021). Species identification of ravenala plants at our study sites has not yet been completed and they are therefore referred to as *Ravenala* sp. in this study.

### 2.3 | Data analysis

We performed all statistical analyses using R (v3.6.1; R Core Team, 2019), and all tests were set at the same significance level ($\alpha = 0.05$). We used descriptive statistics to determine the percentage of feeding observations on different plant species and items consumed by *P. simus* during the observation period. We used the Shapiro–Wilk test of normality for daily occurrences of: (1) bamboo shoot consumption (Ambalafary: $W = 0.690$, $df = 111$, $p < 0.001$; Sahavola: $W = 0.345$, $df = 132$, $p < 0.001$; Vatovavy: $W = 0.561$, $df = 192$, $p < 0.001$); (2) bamboo leaf consumption (Ambalafary: $W = 0.734$, $df = 111$, $p < 0.001$; Sahavola: $W = 0.621$, $df = 132$, $p < 0.001$; Vatovavy: $W = 0.634$, $df = 192$, $p < 0.001$); (3) bamboo culm consumption (Ambalafary: $W = 0.722$, $df = 111$, $p < 0.001$); (4) all bamboo consumption (Ambalafary: $W = 0.926$, $df = 111$, $p < 0.001$; Sahavola: $W = 0.642$, $df = 132$, $p < 0.001$; Vatovavy: $W = 0.734$, $df = 192$, $p < 0.001$); and (5) all non-bamboo consumption (Ambalafary: 0.370, $df = 111$, $p < 0.001$; Sahavola: $W = 0.807$, $df = 132$, $p < 0.001$; Vatovavy: $W = 0.874$, $df = 192$; $p < 0.001$). All data were not normally distributed and there were not an even number of collection days in the wet and dry seasons across the three sites; therefore, we used the Wilcoxon signed rank test to compare seasonal differences in daily consumption of all bamboo parts, all non-bamboo resources, bamboo leaves, and bamboo shoots at all three sites, and of bamboo culm at Ambalafary.

Because the Wilcoxon signed rank test could not account for interannual variation, we used Bayesian models to investigate whether the diet of *P. simus* was influenced by changes in precipitation and temperature throughout our study period. Bayesian regression allows for a variety of response variable distributions and does not assume that model residuals are normally distributed as similar frequentist methods do (Bürkner, 2017, 2018). We downloaded monthly averages of daily temperature and precipitation data for the entire study period from the Copernicus Climate Change Service at 0.05° resolution (Copernicus Climate Change Service, Climate Data Store, 2021), and extracted values for each month in which data were collected at each study site. We used those weather data to model two different sets of outcome variables.

The first model included the percentage of *P. simus*' diet that was bamboo as the dependent variable. Temperature, precipitation, and study site were included as fixed, independent variables. The second model focused on observations of *P. simus* eating bamboo. There, we used the percent of those observations that were shoots, culm pith, and leaves as the multivariate dependent variables. We used the same independent variables as the first model.

We implemented these models in the brms package in R (Bürkner, 2017, 2018). We used uniform priors and assumed model convergence, indicating adequate iterations and burn-in, if for all Monte Carlo Markov chains $\hat{R} < 1.1$ (Gelman & Rubin, 1992). For the model where the dependent variable was "percentage of the diet that was bamboo," we used the beta response distribution, which is suitable for one continuous percentage. For the model where the dependent variable was "percentage of the diet that was bamboo," we used the Dirichlet response distribution, which is suitable for multivariate responses with categorical percentages. In both cases, we scaled the dependent variables to be within the open interval (0.1; Smithson & Verkuilen, 2006). We considered an independent variable as having a significant relationship with the dependent variable when its 95% credible interval (CI) was either positive or negative (i.e., the 95% CI does not include zero).

## 3 | RESULTS

### 3.1 | Resources consumed

Overall, there were 16 species of plants consumed by *P. simus* across the three sites (Table 1); the use of three of these species was not previously published (Table S1). Of the consumed resources, two were varieties of large-culmed bamboo, *B. vulgaris* and *V. diffusa*, the former being the most frequently consumed resource at Ambalafary and the latter being the most frequently consumed food at Sahavola and Vatovavy.

Large and medium-culmed bamboo were the most frequently observed resources consumed in Ambalafary, with non-bamboo species comprising only 7.8% of the feeding observations (Table 1). Non-bamboo resources comprised nearly one-third of the observed diet of *P. simus* in Sahavola and over 60% of the observed diet in Vatovavy. At Sahavola and Vatovavy, *Ravenala* sp. was the most frequently observed non-bamboo species eaten at 14.8% and 23.0%, respectively (Table 1).

The Bayesian model that examined influences on the amount of bamboo eaten by *P. simus* achieved convergence (all $\hat{R} = 1.00$). In this model, which included study site, temperature, and precipitation as predictors, only study site was significant. Temperature (95% CI: −0.03 to 0.19) and precipitation (95% CI: 0.00–0.00) did not significantly affect the proportion of bamboo to non-bamboo plants eaten. However, *P. simus* at Ambalafary ate significantly more bamboo than lemurs at Sahavola (95% CI: 0.85–2.04), and Vatovavy lemurs ate significantly less bamboo than at Sahavola (95% CI: −1.94 to −0.80).

### 3.2 | Seasonal dietary composition

At Ambalafary, there was a significant difference in daily consumption of all bamboo resources in the wet season in comparison to the dry season ($Z = 1968$; $df = 111$, $p = 0.013$; Figure 2). This coincided with a significant difference in non-bamboo resources consumed during the same time ($Z = 1175$, $df = 111$, $p = 0.001$). At Sahavola, we did not find any significant differences in consumption of bamboo resources ($Z = 2477.5$, $df = 132$, $p = 0.226$) and non-bamboo resources ($Z = 2358.5$, $df = 132$, $p = 0.495$) between seasons. At Vatovavy, there was a significant difference in consumption of bamboo resources in the wet season compared to the dry season ($Z = 1855$, $df = 192$,

**TABLE 1** Percentage of feeding observations on resources consumed by *Prolemur simus* between September 2010 and January 2016 at Ambalafary and Sahavola, and between May 2017 and September 2018 at Vatovavy forests, Madagascar.

| Family | Scientific name | Part(s) | Ambalafary | Sahavola | Vatovavy |
|---|---|---|---|---|---|
| Bamboos | | | | | |
| Poaceae | *Bambusa vulgaris* (green form) | Shoots | 14.5 | – | – |
| | | Leaves | 16.5 | – | – |
| | | Culm pith | 38.2 | – | – |
| | *Bambusa vulgaris* (yellow form) | Shoots | 5.4 | – | – |
| | | Leaves | 3.1 | – | – |
| | | Culm pith | 1.4 | – | – |
| | *Phyllostachys* sp. | Shoots | 3.6 | – | – |
| | *Valiha diffusa* | Shoots | 7.6 | 5.4 | 15.7 |
| | | Leaves | 1.7 | 66.2 | 21.0 |
| Other monocots | | | | | |
| Arecaceae | *Dypsis nodifera* | Ripe fruit | – | – | 2.1 |
| | | Leaves | – | – | 7.3 |
| Flagellariaceae | *Flagellaria indica* | Leaves | – | 5.4 | 15.7 |
| | | Stem pith | – | – | <0.1 |
| Musaceae | *Musa* sp. | Ripe fruit | <0.1 | – | – |
| Poaceae | *Olyra latifolia* | Leaves | – | – | 4.4 |
| | | Stem pith | – | – | 0.4 |
| | *Oryza* sp. | Stem pith | – | <0.1 | – |
| Strelitziaceae | *Ravenala* sp. | Flower | 0.4 | 14.2 | 17.0 |
| | | Petiole | 1.1 | 0.6 | 6.0 |
| Zingiberaceae | *Afromomum angustifolium* | Ripe fruit | <0.1 | – | – |
| | | Pith | – | 1.9 | – |
| Unidentified | Unidentified | Stem pith | – | – | 0.3 |
| Unidentified | Unidentified | Leaves | – | – | <0.1 |
| Dicots | | | | | |
| Anacardiaceae | *Mangifera indica* | Ripe fruit | – | – | 0.1 |
| Melastomataceae | *Clidemia hirta* | Ripe fruit | <0.1 | 1.1 | 3.3 |
| Moraceae | *Artocarpus heterophyllus* | Ripe fruit | 6.0 | 1.2 | 0.3 |
| Moraceae | *Streblus mauritianus* | Ripe fruit | – | – | 0.3 |
| Rosaceae | *Rubus alceifolius* | Culm | – | 0.1 | – |
| | | Shoots | – | 0.5 | – |
| | | Ripe fruit | – | 2.6 | – |
| Sapindaceae | *Litchi chinensis* | Ripe fruit | 0.3 | 0.4 | – |

$p < 0.001$), though there was no significant difference in consumption of non-bamboo resources between seasons ($Z = 3790$, $df = 192$, $p = 0.313$). While frequency of bamboo feeding was greater than non-bamboo feeding at both Ambalafary and Sahavola for both wet and dry seasons, non-bamboo feeding was higher at Vatovavy throughout the year.

## 3.3 | Seasonal bamboo part consumption

Pith of large-culm bamboo was only eaten at Ambalafary (Figure 3). Specifically, culm pith of *B. vulgaris* was the most frequently observed plant part consumed (38.2%), followed by leaves and shoots (Table 1). Indeed, at Ambalafary, the daily consumption of large-bamboo culm

FIGURE 2 Percentage of observations during which *Prolemur simus* consumed bamboo and non-bamboo resources between season at the study sites.

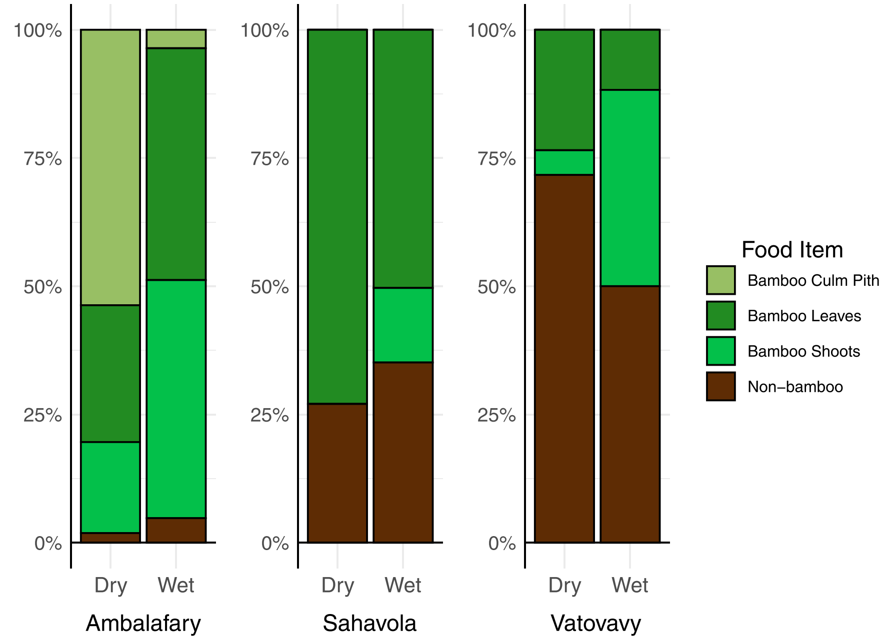
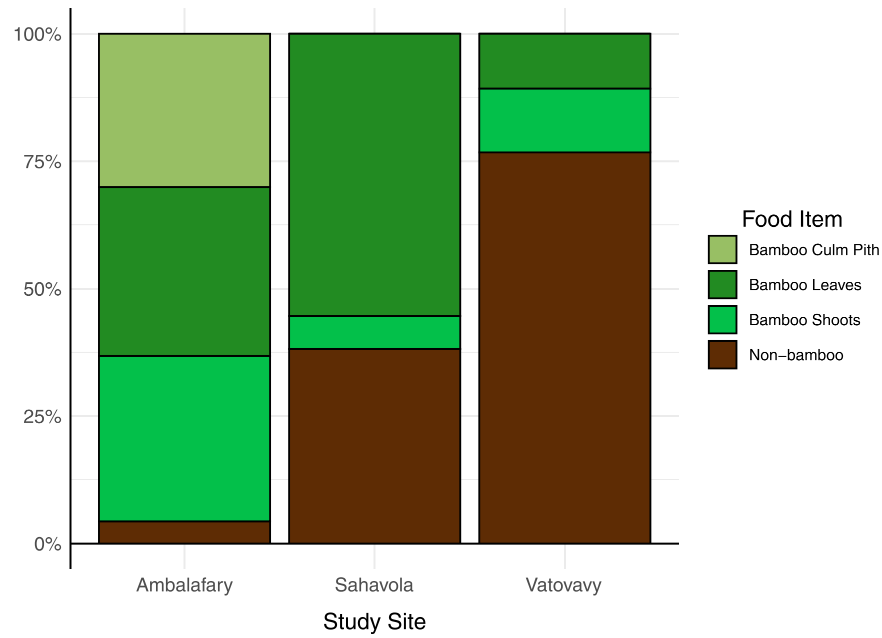



FIGURE 3 Percentage of observations during which *Prolemur simus* consumed bamboo culms, shoots, and leaves at the study sites.




pith was significantly greater during the dry season than the wet season ($Z = 2690$, $df = 111$, $p < 0.001$). In Sahavola and Vatovavy, we never observed feeding of culm pith from *V. diffusa*. Instead, leaves of this large-culmed bamboo were the most frequently observed plant part eaten at both sites (66.2% and 21.0%, respectively). Bamboo leaf consumption was not significantly different between seasons at Ambalafary ($Z = 1764$, $df = 111$, $p = 0.181$); however, there was a significant decrease in the wet season compared to the dry season at Sahavola ($Z = 2779$, $df = 132$, $p = 0.009$) and Vatovavy ($Z = 3239.5$, $df = 192$, $p = 0.005$). Bamboo shoots were consumed by *P. simus* considerably more frequently during the wet season than the dry season at all three sites (Ambalafary: $Z = 805$, $df = 111$, $p < 0.001$; Sahavola: $Z = 1560$; $df = 132$, $p < 0.001$; Vatovavy: $Z = 1586$, $df = 192$, $p < 0.001$).

For the Bayesian model examining influences on the part of the bamboo plant that was eaten, study site was again significant, as was temperature. Lemurs ate a significantly greater proportion of culm pith at Ambalafary relative to Sahavola (95% CI: 0.81–2.33). They also ate more shoots at Ambalafary (95% CI: 1.05–2.58) and at Vatovavy (95% CI: 0.69–2.19) in comparison to Sahavola. Across sites, *P. simus* ate a greater proportion of bamboo shoots in warmer temperatures (95% CI: 0.19–0.49). This model also achieved convergence (all $\hat{R} = 1.00$). For full model parameters for both models, see Tables S3 and S4.

## 4 | DISCUSSION

The fundamental niche, a key concept underlying dietary specialization, of *P. simus* was tangentially addressed in previous studies (Table S1), but never critically assessed with quantifiable data across multiple sites until now. Through observing populations spanning the species' geographical distribution, we documented broader dietary plasticity than predicted. Therefore, we reject the hypothesis that *P. simus* is an obligate specialist. *Prolemur simus* populations at Ambalafary, Sahavola, and Vatovavy demonstrated dietary diversity in terms of both species richness and resource type. The observed individuals had variable diets, consuming a combination of structurally and nutritionally diverse items (fruits, flowers, nectar, leaves, shoots, and culm pith) from 45 species of plants, including three that were previously not identified in the species' dietary repertoire—*Olyra latifolia*, *Phyllostachys* sp., and *Streblus mauritianus* (Table S1). We are now aware that the diet at RNP represents an extreme specialized feeding behavior for *P. simus*, where annual consumption of one bamboo species comprised more than 95% of the diet (Tan, 1999). Annual bamboo consumption was similar at Ambalafary with 92%, declined to 71.6% at Sahavola, and was lowest at Vatovavy with 36.7%, well below the 60% traditionally associated with obligate feeding (Figure 3; Shipley et al., 2009). Though the low bamboo consumption at Vatovavy is enough to suggest a divergence from the obligate specialist definition for *P. simus*, long-term data from multiple sites is still necessary to define the limitations of the species' fundamental niche and to identify extrinsic factors that shift feeding behavior from being confined to a narrow band of the species' fundamental niche to using a broader range of its spectrum.

The characterization of *P. simus* as an obligate bamboo specialist does not accurately convey the species' ability to vary its diet across time and space. The designation of facultative specialist is more appropriate as *P. simus* has numerous adaptations that allow it to process the most difficult of bamboo resources including morphological (Eronen et al., 2017; Lauterbur, 2019; Ravosa, 1992; Vinyard et al., 2008), genetic (Itoigawa et al., 2021), and physiological (Hemingway et al., 2020), but is not confined to dependence on a severely restricted range of food types. The characterization of specialization also depends on the level of taxonomic hierarchy of a species' vital resources. The vast majority of *P. simus* feeding observations (86.3%–93.7% annually; Table 1) occurred on plants from six families and three orders (Arecales, Poales, Zingiberales) within the commelinid monocots; (Angiosperm Phylogeny Group, 2016). Though *P. simus* appears to specialize on a single lineage, this clade is taxonomically diverse and widely distributed within Madagascar and globally (Barrett et al., 2013; Givnish et al., 2010).

Our results partially supported our other hypotheses: (1) there are seasonal and site differences on bamboo and non-bamboo consumption and (2) there are seasonal and site differences in consumption of different parts (leaves, culm pith, shoots) of the large-culm bamboo eaten by *P. simus*. The proportion of bamboo to non-bamboo feeding was significantly different across sites. This is likely related to availability of resources. Though not quantified, we did observe when and where certain resources were available. At Ambalafary, both *B. vulgaris* and *V. diffusa* were available and both were consumed, though in different proportions (Table 1). At Sahavola, *V. diffusa* was the only bamboo resource available, and at Vatovavy, both bamboo species were also present, but feeding was only observed on *V. diffusa*. We are uncertain why *B. vulgaris* was not consumed at Vatovavy when it was at Ambalafary, as there were no physical barriers preventing access to this resource. It is possible a microhabitat difference was imposing limitations on *P. simus*, though this is beyond the scope of our study.

Alternatively, the presence of other, non-bamboo resources could have influenced the feeding preference of *P. simus*. For example, culm pith was only consumed at Ambalafary and only from *B. vulgaris* (Figure 3). We never observed culm consumption at Sahavola or Vatovavy; instead, *P. simus* had higher frequencies of *Ravenala* sp. and non-bamboo leaf consumption. This could indicate a preference for *B. vulgaris* culm pith, especially as other food plants used at Sahavola and Vatovavy were also present at Ambalafary. Alternatively, culm pith of *B. vulgaris* may be a fallback food, a resource that is consumed when preferred resources are scarce (Lambert, 2007; Marshall & Wrangham, 2007), like the culm pith of *C. madagascariensis*, which was suggested to be a fallback food for *P. simus* at RNP (Eronen et al., 2017). Future research should explore if there are differences in resource availability and abundance estimates that may influence frequency of feeding on bamboo resources by *P. simus*.

The effects of season on feeding behaviors are not as clear (Figure 2, Table S3). Bamboo feeding did not change significantly at Sahavola between seasons, yet significant seasonal differences were revealed at Ambalafary and Vatovavy, with proportions of bamboo feeding decreasing in the former while increasing in the latter during the wet season (Figure 2). Unlike overall bamboo consumption, we identified a significant interaction between temperature and bamboo shoot consumption with more shoots consumed during the wet season at every site (Table S4), which is when bamboo shoot production peaks (King et al., 2013; Randriahaingo et al., 2014). Also, as predicted, culm consumption, where it was observed, increased in the dry season (Figure 2), when bamboo shoot availability is lower.

Though bamboo consumption is more variable across *P. simus*' range than expected, it is still an important component of its feeding repertoire. Similar to previous findings on *P. simus* at RNP (Eronen et al., 2017; Tan, 1999, 2000), we found that, overall, the most frequently consumed plants were large-culmed bamboos, though instead of *C. madagascariensis*, these lemurs consumed either *B. vulgaris* or *V. diffusa* (Table 1). Different resources have been generalized to fulfill certain key nutritional categories, for example, fruits are often associated with sugar, leaves with protein, and wood with fiber (Machado et al., 2023). Though it is beyond the scope of this study, it is possible that large-culmed bamboos serve to fulfill an essential nutritional requirement for *P. simus*. Habitat disturbance may also be important in assessing *P. simus* behaviors. As discussed by Olson et al. (2013), *P. simus* are most often found in habitats with low to moderate disturbance and high bamboo density, perhaps because species of bamboo, such as *C. madagascariensis* and *V. diffusa* exploit open canopies (Dransfield, 1998; Frasier et al., 2015; Gagnon & Platt, 2008; King et al., 2013; Olson et al., 2013). Indeed, all observations on *P. simus* were recorded in habitats that have various levels of disturbance (Bonaventure et al., 2012; Dolch et al., 2008; Frasier et al., 2015; King et al., 2013; Lantovololona et al., 2012; Meier & Rumpler, 1987; Mihaminekena et al., 2012; Olson et al., 2013; Petter et al., 1977; Rakotoarinivo et al., 2017; Rakotonirina et al., 2011; Randriahaingo et al., 2014; Wright et al., 2008), including Tan's (1999) at Talatakely, a site that was commercially logged through the 1980s.

### 4.1 | Relevance of findings to bamboo-feeding lemurs

On an island where lemurs evolved to fill a variety of ecological niches, it seems that the bamboo lemurs, both *Hapalemur* (Eppley et al., 2017) and *Prolemur*, may have filled that of disturbed or edge habitats. This may explain the decline in *P. simus* density at RNP as the establishment of the protected area in 1991 resulted in the cessation of logging at Talatakely, allowing the forests to regenerate and attain a closed canopy similar to that of undisturbed sites in the park like Vatoharanana (de Winter et al., 2018). Since 2008, *P. simus* has rarely been encountered in RNP and, if so, only in secondary forest (de Winter et al., 2018; Herrera et al., 2011). Future research should not only continue to explore the effects of disturbance regimes on *P. simus* distribution within its range but also focus on the behavioral adaptations exhibited by groups at sites of variable states of degradation to ascertain the optimal association between anthropogenic and faunal use of forest resources. This will be especially valuable knowledge for species associated with bamboo, a resource whose commercial utilization in Madagascar is being encouraged (International Bamboo and Rattan Organisation INBAR, 2018).

An additional avenue of future research should focus on competition. Ranomafana National Park has a diverse assemblage of lemurs, including multiple species that could be considered generalists, such as *Eulemur rubriventer* and *E. rufifrons*, which may monopolize “easy” foods with fewer secondary metabolites and less demanding mechanical properties (Overdorff, 1993). To avoid competition for non-tough resources, members of the genus *Hapalemur* and *Prolemur* may have increased their bamboo consumption. Unlike other localities with published data, RNP is the only site with three sympatric bamboo specialists, including *H. aureus* whose relative bite force overlaps with the lower end of *P. simus*' biting abilities (Vinyard et al., 2008; Yamashita et al., 2009). As Tan (1999) already hypothesized, this additional competition may have pushed *P. simus* to further specialize in the most mechanically challenging bamboo resource, the culm (Sato et al., 2016; Vinyard et al., 2008; Yamashita et al., 2009). It is not uncommon for primates to evolve specialized processing adaptations to exploit mechanically demanding resources to expand their diet during resource scarcity (Lambert, 2007; Makedonska et al., 2012; Marshall & Wrangham, 2007; Porter et al., 2009; Vogel et al., 2009; Yamashita et al., 2009). It is important, therefore, to determine the role of sympatric lemurs on *P. simus* feeding behavior. Additionally, simultaneous monitoring of *Hapalemur* species at each of these localities would provide valuable insight by revealing possible concomitant shifts in the feeding behavior of sympatric bamboo specialists.

## 5 | CONCLUSION

Proper understanding of the dietary profile of a species across its distribution can have profound impacts on targeted conservation initiatives (Chapman & Peres, 2001; Sutherland et al., 1998). The subtle difference in the dietary classification of *P. simus* we propose highlights the potential ecological flexibility of this species, which has traditionally been seen as having an extremely rigid diet. This change may confound downstream studies that rely on this premise. For example, Ballhorn et al. (2016) postulated that relaxing dietary specialization allowed *Hapalemur*, the sister genus to *P. simus*, to radiate into a broader spectrum of habitats. However, across its range, the dietary diversity of *P. simus* (Table S1) falls within the range of other bamboo lemurs (Eppley et al., 2016a; Tan, 1999). Similarly, Eronen et al. (2017) highlighted dependence on culm pith consumption during the dry season, up to 91% of the monthly diet in 2007 in RNP, as increasing the species' vulnerability to extinction. It was proposed that the species would experience increased tooth wear as it would be forced to persist on the challenging culm pith for longer periods of time as dry seasons were predicted to extend due to climate change. However, unlike at RNP, culm pith feeding was not observed at either Sahavola or Vatovavy. The risk of tooth wear associated with increased culm pith consumption should still be considered but may be more of a concern for localized extinctions. For *P. simus*, estimating the risk of extinction of the species as a whole may require evaluating the feeding behaviors of animals in populations as obligate or facultative, perhaps even assessing individual specialization (Bolnick et al., 2003). This also begets further research into what extrinsic factors narrow *P. simus*' realized diet to such extremes at RNP and Ambalafary.

A change in habitat has been shown to affect many aspects of the ecology and behavior of animals, including dietary composition and diversity (Schwitzer et al., 2011). Nowak and Lee (2013) noted that even specialist primates can be flexible in response to habitat alteration. Considering imminent deforestation threats, there is an immediate need to expand our understanding of ecological nuances of primates (Schwitzer et al., 2013) to maintain forest structures that are supportive of threatened populations (Razafindratsima et al., 2014). In the case of *P. simus*, being able to consume and metabolize a range of food items, both bamboo and non-bamboo, as we have shown here, allowed us to broaden our concept of this species' habitat requirements and may enable the species to survive within increasingly degraded habitats due to human disturbance and climate change (Machado et al., 2023).

## AUTHOR CONTRIBUTIONS

**T. Hasimija Mihaminekena**: conceptualization (equal); data curation (equal); formal analysis (equal); writing—original draft (equal). **Ando N. Rakotonanahary**: conceptualization (equal); data curation (equal); formal analysis (equal); writing—original draft (equal). **Cynthia L Frasier**: conceptualization (equal); formal analysis (equal); writing—review & editing (equal). **Hery N. T. Randriahaingo**: data curation (equal). **Timothy M. Sefczek**: conceptualization (equal); formal analysis (equal); writing—review & editing (equal). **Jen Tinsman**: formal analysis (equal); writing—review & editing (supporting). **H. L. Lucien Randrianarimanana**: data curation (equal). **Maholy Ravaloharimanitra**: project administration (equal). **Toky Hery Rakotoarinivo**: data curation (equal). **Jonah Ratsimbazafy**: project administration (equal). **Tony King**: supervision (equal); writing—review & editing (equal). **Edward E. Louis**: supervision (equal); writing—review & editing (equal).

## ACKNOWLEDGMENTS

We thank the Ministry of the Environment and Forests of the Government of Madagascar, particularly, the Direction of the Protected Areas System, for delivering the permits to undertake this study. This study benefited from the continuous support of The Aspinall Foundation, the Madagascar Biodiversity Partnership NGO, the Département de Biologie Animale et Ecologie and the Ecole Doctorale Génie du Vivant et Modélisation of the University of Mahajanga, the local authorities in the regions where we worked for their permission and participation, the community associations with whom we worked, and all the local assistants who helped with the field research. Thank you to Lauren Scott for improving the layout of our tables. This work was funded through The Aspinall Foundation, within the framework of their "Saving *Prolemur simus*" project, the Margot Marsh Biodiversity Foundation, Conservation International, Re:wild, and Omaha's Henry Doorly Zoo and Aquarium.

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data are available from the corresponding author upon reasonable request.

## ETHICS STATEMENT

Research was conducted in agreement with the authorization of the Ministère de l'Environnement et du Développement Durable (research authorizations: 141/18/MEEF/SG/DGF/DSAP/SCB.Re, 078/11/MEF/SG/DGF/DCB.SAP/SCB, and 039/12/MEF/SG/DGF/DCB.SAP/SCBSE), and of Omaha's Henry Doorly Zoo and Aquarium's Institutional Animal Care and Use Committee guidelines (97-001, 12-101). All procedures were carried out with permission of the Malagasy Government and complied with the Code of Best Practices for Field Primatology.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Mihaminekena, T. H., Rakotonanahary, A. N., Frasier, C. L., Randriahaingo, H. N. T., Sefczek, T. M., Tinsman, J., Randrianarimanana, H. L., Ravaloharimanitra, M., Rakotoarinivo, T. H., Ratsimbazafy, J., King, T., & Louis, E. E. (2024). Dietary flexibility of the greater bamboo lemur (*Prolemur simus*), a specialized feeder, in eastern Madagascar. *American Journal of Primatology*, e23609. https://doi.org/10.1002/ajp.23609