

RESEARCH ARTICLE

Seasonal variability in the diet and feeding ecology of black-and-white ruffed lemurs (*Varecia variegata*) in Ranomafana National Park, southeastern Madagascar

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Abstract

Objectives: We characterized the diet and foraging ecology of the black-and-white ruffed lemur (*Varecia variegata*), a specialized frugivore, and investigated behavioral strategies exhibited in response to seasonal changes in resource availability.

Materials and Methods: Behavioral data were collected from the same two adjacent communities across 29 months during two observation periods (2007–2008; 2017–2018) in Mangevo, a primary rainforest habitat in southeastern Madagascar. To analyze feeding in the context of energy maximization versus time minimization strategies, we used nonparametric tests to compare plant part constituents, dietary diversity, activity budgets, and canopy strata use between fruit-abundant versus fruit-lean seasons.

Results: Individuals dedicated ~30% of their time to feeding year-round, mostly in the middle canopy (11–20 m). Animals fed primarily on fruits (74% of diet), but frugivory decreased and folivory increased markedly during fruit-lean seasons. Abundant season dietary diversity (98 taxa, $H' = 0.71\text{--}1.37$) was greater than lean season diversity (70 taxa, $H' = 0.56\text{--}1.06$), which coincided with less traveling, more resting, and higher canopy use—though interannual variation was observed.

Conclusions: Herein, we describe behavioral and dietary patterns that are concordant with a time minimizing behavioral strategy. Black-and-white ruffed lemur diets comprised lower taxonomic diversity, fewer fruits, and more leaves during fruit-lean months. Further, shifts toward less travel, more resting, and greater use of higher canopy levels during this time were most likely for thermoregulatory benefits.

KEYWORDS

activity budget, energy, foraging ecology, frugivore, primate

1 | INTRODUCTION

Dietary selectivity and variability are usually considered in terms of forest composition and resource availability and distribution (e.g., Gautier-Hion, Gautier, & Maisels, 1993), key factors determining primate social organization and behavior (Sterck, Watts, & van Schaik, 1997; van Schaik, 1983, 1989; Wrangham, 1980). Climatic seasonality drives the temporal availability of food resources through plant

phenology (van Schaik & Brockman, 2005), whereas the distribution and depletion of these food resources, in part as a result of within and between-group feeding competition, drives their spatial availability (Leighton & Leighton, 1982; White & Wrangham, 1988; Strier, 1989; Stevenson, Quinones, & Ahumada, 1998; Vogel, 2005). Primates are known to alter their foraging strategies in response to spatio-temporal changes in resource availability and distribution (e.g., Gautier-Hion, 1980). When favored foods become depleted in one area, animals can

travel more or into different habitat areas in search of favored foods, conserve energy (i.e., rest more) to reduce their nutritional requirements, and/or switch dietary constituents (van Schaik & Brockman, 2005). Seasonal diet switching may occur by feeding upon different (either more or less diverse) plant species or plant parts (Hemingway & Bynum, 2005) or resorting to fallback food items when preferred foods are unavailable (Marshall & Wrangham, 2007; Marshall, Boyko, Feilen, Boyko, & Leighton, 2009; Lambert & Rothman, 2015).

Optimal Foraging Theory (MacArthur & Pianka, 1966; Stephens & Krebs, 1986; Krebs & Davies, 1997) has been used to explain changes to individual activity budgets in response to varying resource availability. To maximize fitness, an animal is expected to adopt a foraging strategy that provides the greatest benefit (energy) at the lowest cost within the constraints of its environment. Based on this, two different foraging strategies have been proposed to explain the relationship between resource availability and activity budgets, “energy maximizing” and “time minimizing” (Hixon, 1982; Schoener, 1971). When high-quality food resources are unavailable, energy maximizers are expected to spend more time feeding and traveling (and less time resting) in search of food from a diverse range of resources. Conversely, time minimizers are expected to switch to nearby fallback foods, and subsequently spend less time feeding and/or traveling and more time resting, thereby minimizing energy expenditure (Cuthill & Houston, 1997). By adopting a strategy of decreased travel during lean seasons (Boinski, 1987; Hemingway & Bynum, 2005), time minimizers spend less time in active states, thereby minimizing their nutritional requirements for maintaining energetic homeostasis (Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; Tecot, 2008).

Most frugivores are expected to be energy maximizers, at least during fruit-abundant periods (Hixon, 1982; Schoener, 1971). However, Madagascar's lemurs have been broadly characterized as energetically frugal, likely as an adaptive response to the island's unpredictable environment (Wright, 1999). Compared to other tropical regions, Madagascar's climate is often considered to be especially harsh, suffering droughts, frosts and cyclones (Gould & Sussman, 1999; Wright, 1999; Dewar & Wallis, 1999; Dewar & Richard, 2007; Lewis & Bannar-Martin, 2012; but see Federman et al., 2017). Moreover, its forests are characterized by smaller, slower growing trees compared to other tropical forests, and are suggested to have lower fruit abundance and quality, lower soil fertility, and more substantial interannual variation in fruiting periodicity than other tropical forest regions (Dewar & Richard, 2007; Donati et al., 2017). In fact, compared to other rainforest sites, Madagascar's rainforests can have especially long periods without fruit, up to six months of the year (Dewar & Richard, 2007; Dunham, Razafindratsima, Rakotonirina, & Wright, 2018; Wright, Razafindratsita, Pochron, & Jernvall, 2005), in part because they have fewer staple species, such as figs (*Ficus* spp.) (Goodman & Ganzhorn, 1997). Ranomafana National Park, in southeastern Madagascar, comprises montane rainforest characterized by distinct seasonality in rainfall and temperature (e.g., Dunham et al., 2018; Hemingway, 1996; Tecot, 2008; Wright, 2006). Peak fruiting is typically during April, but this region is characterized by significant variability in fruiting periods linked to variation in rainfall (Dunham et al., 2018; Razafindratsima & Dunham, 2016). Ripe fruit availability can have

a pronounced effect on the home range sizes, day ranges, and activity patterns of arboreal frugivores (Clutton-Brock & Harvey, 1977; Lambert, 2007). However, the “energy maximization versus time minimization” framework has previously only been explored in a select few species of lemur (*Avahi meridionalis*: Norscia, Ramanamanjato, & Ganzhorn, 2012; *Propithecus verreauxi*: Norscia, Carrai, & Borgognini-Tarli, 2006; *Propithecus diadema*: Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015; *Eulemur rubriventer*: Tecot, 2008; *E. collaris*: Campera et al., 2014; *E. fulvus*: Sato, Ichino, & Hanya, 2014; *E. rufifrons*: Erhart & Overdorff, 2008; Overdorff, 1993). For instance, *E. rubriventer* are energy maximizers during fruit abundant seasons, maximizing their time spent feeding on preferred fruit resources, but switch to a more time minimizing strategy during lean seasons by decreasing their feeding time relative to resting (Tecot, 2008). *Propithecus diadema*—an anatomical folivore that preferentially consumes fruits when available – also minimizes time during lean seasons by feeding less when preferred foods are unavailable (Irwin et al., 2015). Similarly, *Eulemur collaris* minimize time during lean seasons by decreasing their travel, particularly in disturbed habitats (Campera et al., 2014). By contrast, *E. fulvus* increase their travel time during lean seasons, maximizing energy to maintain feeding time and meet their nutritional needs (Overdorff, 1993; Erhart & Overdorff, 2008). These previous studies have focused on three generalist-folivores (Irwin et al., 2014, 2015; Norscia et al., 2006, 2012) and four members of the genus *Eulemur*—known to exhibit variable levels of frugivory (e.g., Donati et al., 2011; Donati, Bollen, Borgognini-Tarli, & Ganzhorn, 2007; Overdorff, 1993; Tattersall & Sussman, 1998; Vasey, 2002). Most of these studies did not outright test energy maximization versus time minimization but do show seasonality of strategies and a trend toward overall time minimization in lemurs of both dietary guilds. Here, we apply this framework to what is arguably the most frugivorous, and one of the most ecologically sensitive lemur species, *Varecia variegata* (Balko, 1998; Britt, 2000; Ratsimbazafy, 1999; Ratsimbazafy, 2002; White, Overdorff, Balko, & Wright, 1995), to test the hypothesis that Madagascar's frugivores employ time minimizing strategies as part of the broader “lemur syndrome” which evolved under the ecological constraints of Madagascar's unpredictable environment (sensu: Wright, 1999).

Ruffed lemurs (genus: *Varecia*) are considered ripe-fruit specialists, exploiting the fruits of large, hardwood tree species (Dew & Wright, 1998; Martinez & Razafindratsima, 2014; Razafindratsima, Jones, & Dunham, 2014; Vasey, 2006; Wright et al., 2011). They have evolved a relatively simple digestive tract (Campbell, Eisemann, Williams, & Glenn, 2000), and have short gut transit and retention times relative to other more folivorous lemurs (Edwards, 1995; Moses & Semple, 2011; Razafindratsima et al., 2014). Resultingly, ruffed lemurs are likely unable to utilize microbial fermentation to any significant degree, thereby limiting their capacity to derive significant energy from plant cell wall constituents, such as those contained in more fibrous leaves (Edwards & Ulrey, 1999). Previous studies investigating the diets of black-and-white ruffed lemurs (*V. variegata*), in particular, have revealed that fruits form between 78 and 92% of the overall diet, though their degree of frugivory varies seasonally (Balko, 1998;

Britt, 2000; Balko & Underwood, 2005; Ratsimbazafy, 2002, Ratsimbazafy, 2006). The vast majority of leaves ruffed lemurs consume are during times of fruit shortage (Balko, 1998; Britt, 2000; Balko & Underwood, 2005; Holmes, Gordon, Louis Jr., & Johnson, 2016; Ratsimbazafy, 2002, Ratsimbazafy, 2006). Moreover, individuals show a high degree of preference for a low number of tree species (between 4 and 6), though this, too, varies seasonally (Balko, 1998). Previous studies have also shown that ruffed lemurs may spend more time higher in the canopy with more direct sunlight exposure (Britt, Welch, & Katz, 2001; Vasey, 2006). Such behavior has been linked to increased access to young leaves (Lambert & Rothman, 2015; van Schaik, Terborgh, & Wright, 1993) and may confer thermoregulatory benefits during colder months (Morland, 1993; Vasey, 2004, 2005).

Based on their high levels of frugivory, simplified gut morphology, short gut retention time, and marked periods of fruit-scarcity during lean season months, we suggest that ruffed lemurs may be physiologically constrained during fruit-limited, “lean” seasons. We therefore test the hypothesis that ruffed lemurs adopt a time minimizing feeding strategy during lean seasons, thereby reducing energy expenditure when fruit is scarce. To do this, we explore the relationships between climatic seasonality, plant parts consumed, plant taxon diversity (hereafter: dietary diversity), activity budgets, and canopy use in two groups (hereafter “communities”) of black-and-white ruffed lemurs. Further, comparing the foraging strategies of the same ruffed lemur communities across two temporally distinct datasets lends itself to identifying ecological flexibility of ruffed lemurs and their behavioral strategies through time, within the same habitat. Given previous findings, we expect to find (a) both greater levels of frugivory and greater dietary diversity during the abundant seasons and lesser frugivory and dietary diversity during lean seasons, when many tree species are not fruiting (e.g., Pochron, Tucker, & Wright, 2004). When diet shifts toward a greater reliance on leaves, we predict there to be (b) a shift toward greater proportions of time spent in the upper canopy where branches can reach more light to grow new leaves—especially if animals spend more time resting in close proximity to food resources. We also expect that (c) when diets consist of more leaf matter, animals will spend less time traveling between and feeding on highly clumped fruit patches (Marshall et al., 2009). Finally, we predict that (d) activity budgets will shift toward time- (and energy-) conservation during lean season months, with animals spending less time traveling and more time resting.

2 | METHODS

2.1 | Ethics statement

This research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates. Research complied with the laws and guidelines set forth by ANGAP/Madagascar National Parks, Stony Brook University's IACUC (#2005–20,081,449), and Hunter College IACUC (#AB-lemurs 5/20-01).

2.2 | Study site and subjects

Data were collected from two adjacent black-and-white ruffed lemur communities (*sensu* Baden, Webster, & Kamilar, 2016) at Mangevo bushcamp in Ranomafana National Park (RNP), Madagascar (Figure 1). Mangevo (21°22'60" S, 47°28'0" E) is a mid-elevation (660–1200 m) primary rainforest site in the southeast of RNP, a park comprising 435 km² of continuous montane rainforest located in the southeastern escarpment of Madagascar's central high plateau (21°02'–21°25' S and 47°18'–47°37' E; Wright et al., 2012).

During the 2007–2008 study, all subjects were adults and included 5 females and 3 males with radio-collars and 16 individuals with collar-tags but no radio-collars (3 females, 13 males) (as described in Baden et al., 2016). During the 2017–2018 season, all study subjects were adult and included 10 females and 5 males with radio-collars and 2 individuals with collar-tags but no radio-collars (1 female, 1 male). Focal individuals present in the study population differed across sampling periods due to the 10-year time gap between study periods. However, focal individuals were all from the same two adjacent communities at Mangevo and utilized broadly the same communal territories across data collection periods (Baden, unpublished data). The two datasets 2007–2008 and 2017–2018 will be referred to as D1 and D2, respectively.

2.3 | Ecological monitoring

Average temperature and total rainfall readings from the previous 24-hr period were taken once daily between 7 am and 9 am, to describe the climate of the research site. To identify climatic seasonality across sampling periods we analyzed mean daily temperature (°C) and monthly rainfall (mm) for both periods of observation. Temperature data were supplemented with data from Centre ValBio research station in RNP (approximately 30 km north of the study site) for the 4 months of September to December 2017 when data were unavailable from our study site, due to a broken temperature gauge.

Using previously published phenology from D1, we correlated monthly percentage fruit availability as estimated from 585 trees and lianas found within 12 botanical plots (each 50m²) established evenly throughout the communities' home ranges with total monthly rainfall and average monthly temperature to define “abundant” and “lean” seasons (for full details of phenological data collection see Baden, 2011; Baden et al., 2016). Note that temperature and rainfall data were collected during both D1 and D2 and showed similar trends (Figure S2). *T*-tests showed no significant differences between datasets (temperature: $t = -0.77$, $df = 14$, $p = 0.45$; rainfall: $t = -0.82$, $df = 22$, $p = 0.42$). Phenological data were only available for D1, thus were extrapolated to D2 for abundant and lean season categorizations—this relationship is assumed here, a caveat of this study, but future studies should incorporate simultaneous phenology and behavioral data for all periods.

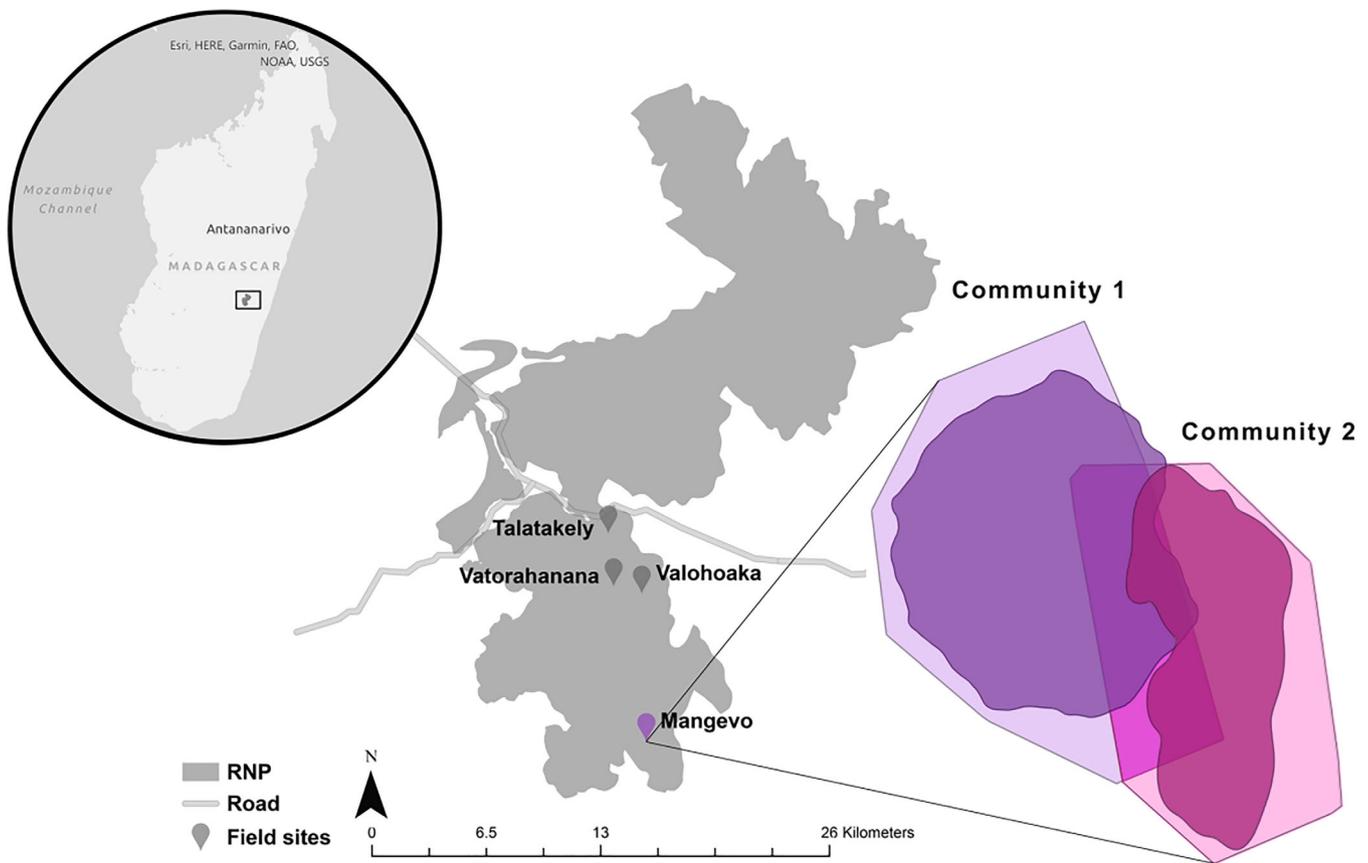


FIGURE 1 Map showing four established research sites in Ranomafana National Park (RNP), located in southeastern Madagascar. Mangevo (in purple) is located in the southern portion of RNP. The inset map illustrates the home ranges of our two study communities at Mangevo. Outer polygons represent 95% MCP home range estimates and inner polygons represent 95% KDE range estimates (see Baden, Oliveras, & Gerber, In Press for details)

2.4 | Observational data

Two teams of four observers each ($n = 8$) conducted dawn-to-dusk follows on focal individuals (i.e., two animals were followed daily). Data were collected from the same two communities across 29 months during two separate field seasons separated by 10 years; August 2007–December 2008, and September 2017–August 2018. To ensure comparability of data, field technicians were consistent between the two sampling periods. Checks were also made throughout observation periods to ensure consistency across observers. Every month, we targeted between 15 and 17 collared individuals for daily full-day follows. Observation periods lasted from 8 to 10 hr per day, between 07:00 and 17:00. Strict timings were adhered to, to avoid behavioral bias, that is, observation time was not extended if the subject was still feeding at the end of the day. New focal individuals were selected daily, based on a randomized list of individuals, balanced across core subgroups.

Data on feeding tree visits were collected during instantaneous scans of the focal individual at five-minute intervals during full day follows (Altmann, 1974). If the interval between samples is short relative to the average duration of the behavior, this method provides a reasonable estimate of the time spent eating particular food items

(Martin & Bateson, 1986). The total number of 5-min instantaneous scans over the two field seasons was 50,732 (D1: 30,430; D2: 20,302), equating to 4228 observation hours. Individuals were sampled as evenly as possible during each study period, usually comprising one follow per radio-collared individual per month, plus opportunistic follows on collar-tagged individuals if located prior to 10 h00.

Four broad behavioral states were used to calculate activity budget: feeding, socializing, traveling, and resting. The tree taxon and plant part eaten were recorded for all feeding tree visits. For this study, we consider feeding to be all time spent actively searching for and consuming food items (sometimes categorized as foraging and feeding, respectively). Plant parts consumed included fruits (FR), leaves (LE), flowers (FL), buds (BU), petioles (PE), and bark (BA), as well as occasional fungi (FU) and soil (SO). If multiple plant parts of the same tree were eaten during a feeding bout, the part being eaten at the time of the scan was recorded. Each plant species visited was identified by at least two technicians to ensure correct identification. The focal animal's height (in meters) in the forest canopy was also estimated and recorded during scans. Canopy heights were subsequently split into three categories; <10, 11–20, and 21+ m, based on the upper limit of canopy height being approximately 30–35 meters (Beeby and Baden, unpublished data).

2.5 | Data analysis

We calculated descriptive statistics to characterize behavioral correlates of resource seasonality. We used focal follows of all individuals observed during both seasons for analysis (D1: $N = 9$ and D2: $N = 15$). We used instantaneous scan data to quantify activity budget, dietary composition (including plant taxon and part), and use of different canopy heights. Analyses were conducted on each dataset (D1 and D2) individually. All analyses were run in R, version 1.1.456 (R Studio, 2018). Shapiro–Wilk tests were used to identify normal distribution of datasets and values were log-transformed when the data did not meet the assumptions of parametric testing. Due to the small sample size and non-normal distributions of much of the data we used Wilcoxon signed-rank tests to make pairwise comparisons within each individual, across seasons. Finally, we used post-hoc full and partial Spearman's Rank correlations to investigate the relationships among ambient temperature, canopy height use, and dietary plant parts (fruits and leaves) consumed. Significance was set at $\alpha = 0.05$ for all tests, with Bonferroni corrections applied.

To analyze dietary diversity, we calculated the Shannon's Diversity Index for all plant taxa exploited by *V. variegata* during each month of the periods of observation. Indices were calculated using a vector of frequencies (counts of scans feeding on each taxa) using the following formula:

$$H' = -\sum (p_i)(\ln p_i)$$

Index scores usually vary from one to four, with a higher score indicating a greater diversity of plant taxa being fed on in a particular sample. The number of taxa present and/or evenness of taxa, can influence diversity scores. Higher values for either variable result in a greater diversity score (Shannon & Weaver, 1949). The frequency of a taxon is the number of points at which the species is recorded at least once, expressed as a proportion of the total number of points in the sample. In this case, frequency is the number of scans during which focal individuals were feeding on each taxon, as a proportion of the total number of feeding scans during each month.

3 | RESULTS

3.1 | Climate

The mean monthly temperature across our observation periods was 18.2°C, with a minimum of 7°C and a maximum of 38°C. Average monthly rainfall was 260 mm. The “abundant” season includes months that were hot and wet (>18°C and > 300 mm) with greater than ~8% fruit availability, and the “lean” season includes months that were cool and dry (<18°C and <300 mm), with below ~8% fruit availability (mean across 12 months = 8.3%). These combined data show a generalized pattern of the abundant season occurred from November to April and the lean season from May to October, with April and October being somewhat transitional as the last month of

each season. July 2018 was an outlier to the general rainfall trend, with >300 mm rainfall, but was considered as lean based on fruit availability (Figure S1).

3.2 | Dietary diversity

Subjects fed on a total of 111 plant taxa across the two observation periods. Of these, 87% were consumed for their fruits. Subjects consumed fruits from 97 different plant taxa; leaves from 15 taxa; flowers from 9 taxa; and flower buds from 7 taxa. In many cases, multiple different plant parts were eaten from the same taxon, sometimes during the same feeding tree visit and other times during different months. The number of plant species consumed differed temporally; only 48 of 111 species were shared between the two periods (43% of total plant taxa).

The top 15 most frequently visited plant taxa from each dataset are illustrated in Table S1. These taxa are those each constituting over 1% of the diet. Interestingly, the top five taxa from each dataset account for almost 50% of their annual diet, each individually making up over 5% of the diet. The most frequently consumed plant taxa during D1 and D2 show some striking variation, with only one taxon appearing in the top 5 of both datasets.

Our Shannon's Diversity indices showed that focal individuals generally fed on a lower diversity of plant taxa during lean season months, from May to October, compared to abundant season months (see Table S2). During D1, the month with the lowest diversity index was August ($H' = 0.56$) and the month with the highest index was December ($H' = 1.28$), followed by April ($H' = 1.20$)—the first and penultimate months of the abundant season. D2 showed a lesser degree of variation over the course of the year. April had the lowest diversity ($H' = 0.58$); a month during which this species traveled very little and fed mostly on *lanary* fruits (*Plagioxyphus louvelii*). February had the highest diversity ($H' = 1.10$), followed by December ($H' = 1.07$); both months were in the abundant season.

3.3 | Plant parts consumed

Fruits made up 25–99% of this populations' diet on a monthly basis throughout the year, and leaves formed 0–56% (Figure 2). Together, fruits and leaves formed between 69% and 100% of the population's diet during all months (with the exception of August 2008). During D1, the population showed significantly greater levels of frugivory during the abundant season than the lean season (abundant = 88%; lean = 52%; $W = 30$, $p = 0.004$; see Figure 3). Pairwise comparisons of individuals observed during each season showed statistical significance ($W = 30$, $p = 0.004$). Leaves and flowers both made up a greater portion of diets during the lean season, though not significantly after Bonferroni corrections (leaves: $W = 1$, $p = 0.031$; flowers: $W = 0$, $p = 0.031$). Individuals in D2 did show significant seasonal differences in the proportion of feeding on fruit (abundant = 96%, lean = 63%; $W = 118$, $p = 0.001$), but not for any other plant part with Bonferroni

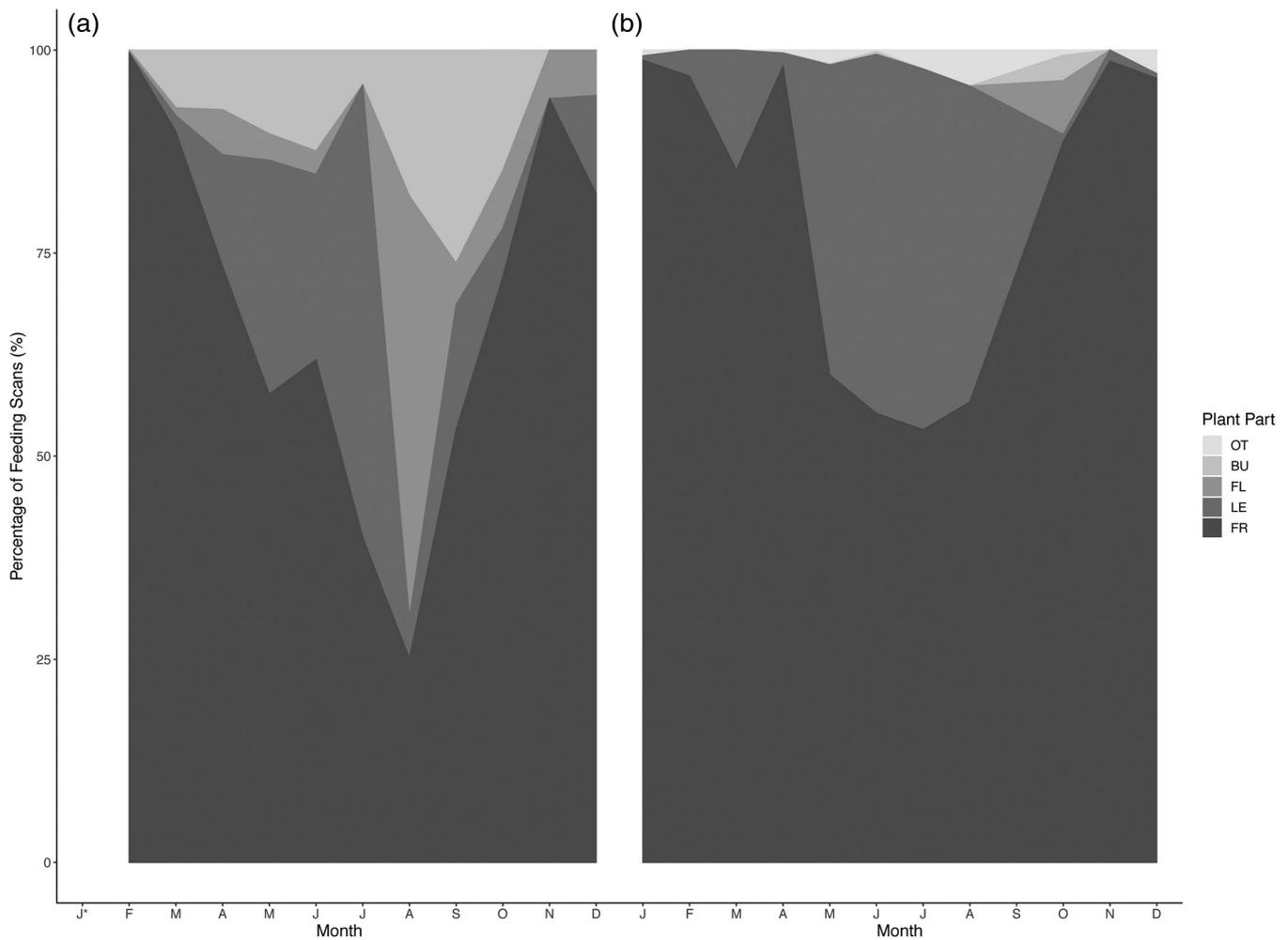


FIGURE 2 Monthly variation in dietary profile (quantified as % feeding time) of *V. variegata* during (a) D1 and (b) D2. FR = fruit, LE = leaves, FL = flowers, BU = buds, OT = other. *No data points for January 2008 or September 2017 due to no plant part data collected during these months. The category “other” refers to uncommon food items such as bark, fungi, and soil

corrections (leaves: $W = 4$, $p = 0.05$; flowers: $W = 12$, $p = 0.3$; also see Figure 3).

3.4 | Activity budget

Individuals spent an average of 29.5% of their daily activity budget feeding, 55.3% resting, 9.0% traveling, 4.0% socializing, and 2.2% other (e.g., self-grooming, alarm calling). Individuals did not differ significantly in their socializing ($W = 25.5$, $p = 0.061$), feeding ($W = 2$, $p = 0.017$) or resting ($W = 7$, $p = 0.1775$) time between seasons during D1 (Figure 3). However, they did spend a significantly lower proportion of time traveling during the lean season (travel: $W = 45$, $p = 0.004$). During D2, individual traveling and resting time differed significantly between seasons (Figure 3). Animals rested more ($W = 2$, $p = 0.001$) and traveled less ($W = 119$, $p = 0.001$) during the lean season. Feeding and socializing did not differ significantly between seasons (feeding: $W = 25$, $p = 0.3$; socializing: $W = 20$, $p = 0.81$).

3.5 | Use of canopy strata

Individuals spent 68–81% of their total time in the middle canopy (11–20 m), with no significant seasonal variation (D1: $W = 18$, $p = 0.66$; D2: $W = 21$, $p = 0.69$). During both periods, however, individuals spent significantly less time feeding in the lower canopy during lean versus abundant seasons (D1: $W = 35$, $p = 0.016$; D2: $W = 115$, $p = 0.001$). During these lean seasons, animals also spent more time in the upper canopy (D1: lean = 28%, abundant = 22%; D2: lean = 16%, abundant = 5.5%), though individual pairwise comparisons show no statistical significance with Bonferroni corrections (D1: $W = 5$, $p = 0.08$; D2: $W = 2$, $p = 0.01$). Height profiles for each activity state (feeding, resting, socializing, and traveling) show that seasonal shifts in canopy level use are relatively consistent across activities (Figure 4).

Post-hoc Spearman's Rank Correlations revealed significant relationships between lower canopy use and both temperature ($R = 0.86$, $p = 0.0013$) and fruit consumption ($R = 0.92$, $p < 2.2 \times 10^{-16}$) in D1, and upper canopy use and temperature ($R = -0.81$, $p = 0.0025$) in D2,

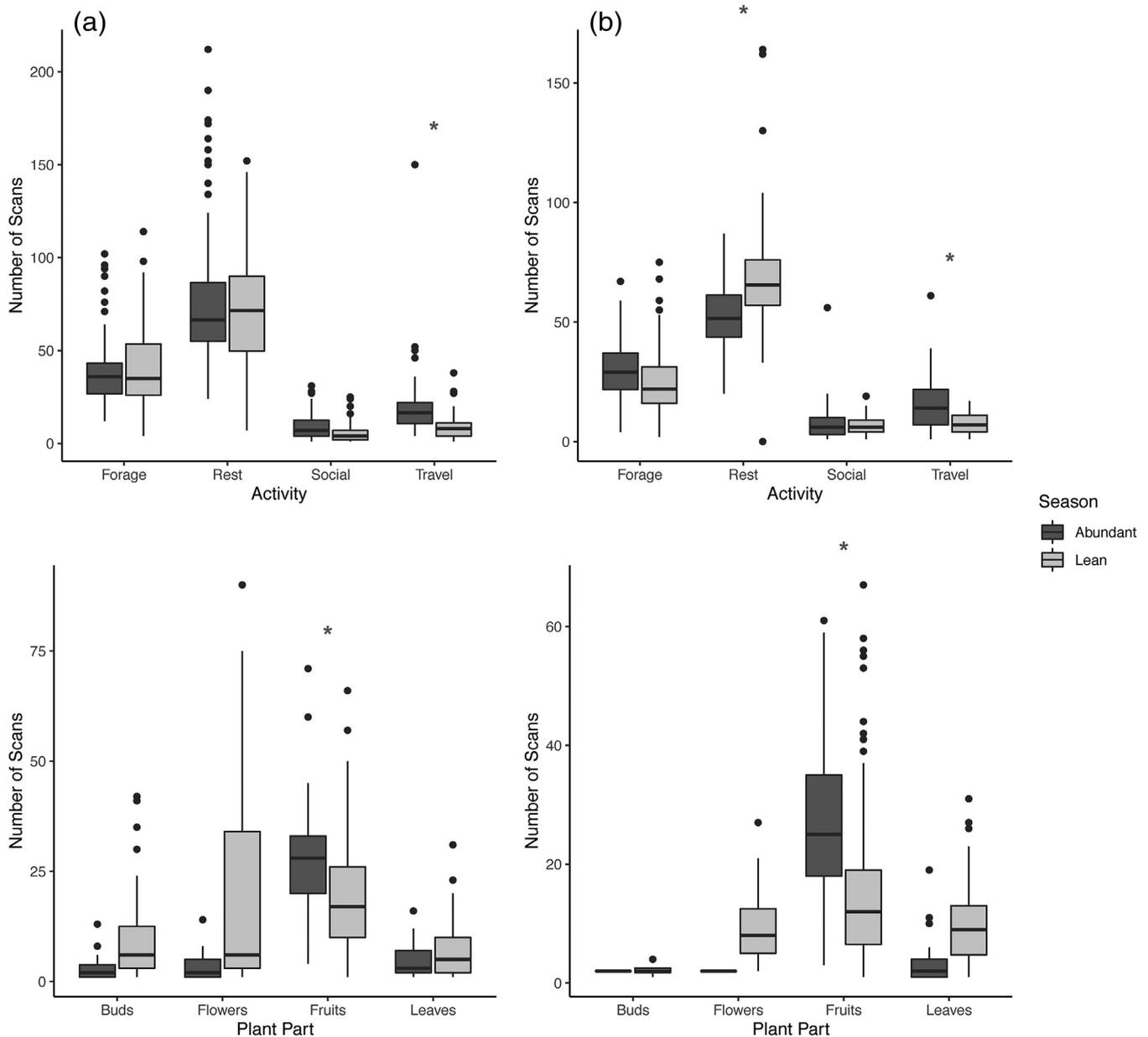


FIGURE 3 Box plots showing activity budgets (top) and percentage of feeding scans for each plant part consumed (bottom) by *V. variegata* in periods D1 (a: Left) and D2 (b: Right). The box represents the interquartile range including all values between the first and third quartiles, the whiskers represent minimum and maximum values excluding outliers, and the line represents the range of values with the middle of the box representing the median. *asterisks represent statistically significant differences across seasons (after Bonferroni corrections applied)

after Bonferroni corrections ($p < 0.008$); there were no significant relationships between canopy use and leaf consumption (D1 lower: $R = -0.72$, $p = 0.012$; D1 upper: $R = 0.71$, $p = 0.014$; D2 lower: $R = -0.58$, $p = 0.066$; D2 upper: $R = 0.71$, $p = 0.014$). However, partial correlations reveal no significant patterns after controlling for the other related variables.

4 | DISCUSSION

The primary goal of this study was to characterize the annual and seasonal foraging patterns of the highly frugivorous, ecologically sensitive

black-and-white ruffed lemur, and test the hypothesis that ruffed lemurs use a time minimizing strategy in response to temporal changes in climate and resource availability. We observed differences in diet choice, canopy height use, and activity budget between abundant and lean seasons, lending support for time minimization in this species.

Our study found seasonal differences in levels of frugivory, being high during fruit-abundant seasons and unexpectedly low during lean seasons. Leaf consumption during some lean season months (see Figure 2) was much higher than previously documented in this species (e.g., Balko, 1998; Britt, 2000; Ratsimbazafy, 2002). Moreover, the top taxa consumed by ruffed lemurs differed strikingly between our two

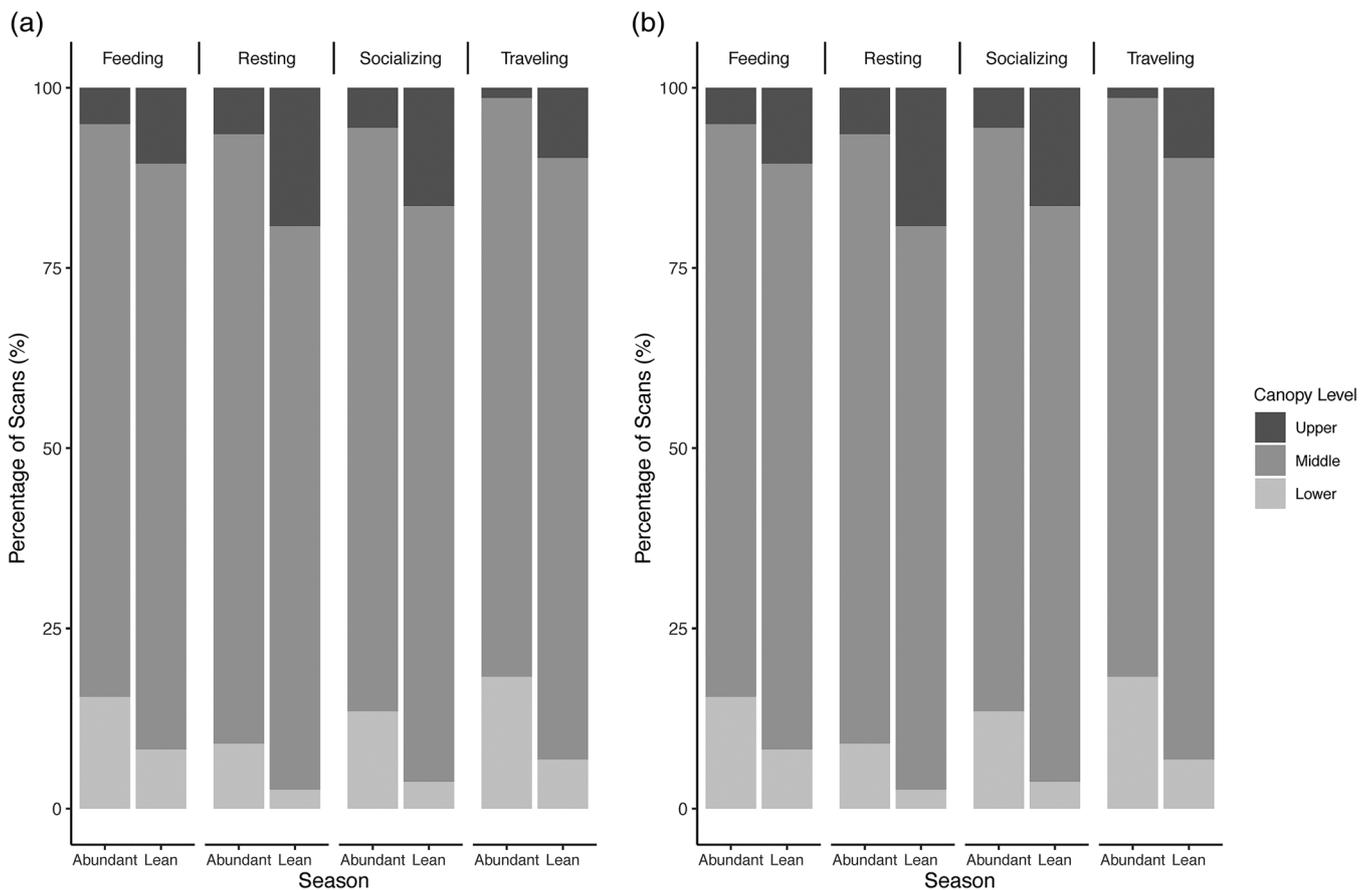


FIGURE 4 Seasonal height profiles by activity state (feeding, resting, socializing, and traveling) in periods (a) D1 and (b) D2. Stacked bars show the percentage of total scans per activity at each canopy level, separated into abundant and lean seasons

sampling periods (Table S1), as well as from those recorded from a variety of different forest areas (e.g. Balko and Underwood, 2005; Ratsimbazafy, 2006). Once believed to be ecologically inflexible (Vasey, 2002), increased sampling from across a broader geographic and temporal range reveals substantial variation in feeding ecology, even within the same population. The contrast between D1 and D2 dietary profiles presented in this study, as well as results from earlier studies, contribute to a growing literature describing the ecological flexibility of this species (e.g., Balko, 1998; Balko & Underwood, 2005; Britt, 2000; Holmes et al., 2016; Ratsimbazafy, 2002, Ratsimbazafy, 2006). Moreover, they further reinforce the value of longitudinal studies on primate behavioral ecology.

Members of a single social group (community) can exhibit drastically different patterns of individual range use and overlap (Baden et al., In Press). It is therefore possible that some of the variation captured by our study can be explained by individual patterns of range use and habitat quality. For instance, Ratsimbazafy (2002) found that animals living in degraded areas of littoral forest in Manombo exhibited less variation in levels of frugivory across seasons than more pristine areas of the same forest. Similarly, preferred fruit species consumed by animals in our study at Mangevo, an undisturbed montane rainforest study site, differed greatly from those reported by Balko and Underwood (2005) at Vatoharanana, a moderately degraded

montane rainforest site located only 9 km north of Mangevo. Thus, while beyond the scope of the current study, future work might investigate whether individuals with greater degrees of habitat similarity or those living in closer physical proximity exhibit more similar patterns of resource exploitation.

Plant diversity in the diet was generally higher during fruit-abundant versus lean season months (total diet $H' = 1.55$; abundant mean $H' = 1.17$; lean mean $H' = 1.01$). Of the 111 taxa consumed, fruits were eaten from 97 taxa, compared to 15 taxa for leaves, 9 taxa for flowers, and 7 taxa for buds (Table S1). Though we cannot say conclusively, moderately low species richness in the diet may be due to low species evenness, as many plant taxa were consumed only very occasionally. There were significant differences between D1 and D2, with only one top five most exploited plant taxon being the same in both periods. These data show moderate interannual variation is present in the diet of this population, most likely due to the significant interannual variability in fruiting periodicity of many trees in Ranomafana (Dunham et al., 2018; Razafindratsima & Dunham, 2016). Further, individual plants of the same species can also be asynchronous in phenology, meaning that relatively few fruit-producing trees may be fruiting at any given time (Balko & Underwood, 2005; Goodman & Ganzhorn, 1997). Previous studies show the climate of Madagascar's eastern rainforests to be characterized by high

unpredictability of rainfall, which results in variable, unpredictable, and often asynchronous availability of fruits (e.g., Overdorff, 1991; Hemingway, 1996; White et al., 1995; Balko, 1998; Balko & Underwood, 2005; but see Federman et al., 2017). During our study, fruit availability dropped to $\leq 5\%$ between April and June (Figure S1). Increased leaf consumption during periods of decreased fruit availability suggests that leaves may serve as fallback food items during periods of fruit scarcity. The combined effects of high leaf consumption and low dietary diversity may drive this species' need to conserve energy during nutrient-poor fruit-lean periods or, alternatively, may increase the need to rest more to digest fibrous leaf material (Campbell et al., 2000; Campbell, Williams, & Eisemann, 2004; Donati et al., 2007; Eppley, Watzek, Ganzhorn, & Donati, 2017). Forthcoming nutritional analyses will allow us to determine whether the observed seasonal dietary changes are associated with concordant changes in nutritional intake (Beeby and Baden, unpublished data).

We observed shifts in activity budget that aligned with seasonal patterns in resource availability. Contrary to our expectation, however, time dedicated to feeding was relatively consistent year-round. Rather, unlike *Eulemur rubriventer*, which maximize time and energy during the abundant season by increasing feeding time (Tecot, 2008), animals in our study maintained consistent proportions of time feeding across seasons. Individuals increased their travel time during the abundant season, presumably moving between fruit patches to consume more easily digestible resources, higher in fats and sugars (reviewed in: Lambert & Rothman, 2015). Travel time decreased during the lean season (as observed in *Varecia rubra*; Vasey, 2005), possibly as a time minimizing strategy. This reduction in travel coincided with reduced dietary diversity, reduced frugivory, and lower fruit availability. Low availability of high-quality food patches (such as large fruiting trees) could have resulted in less time spent traveling in search of such resources. Conversely, during the fruit abundant season, individuals may be able to invest more time traveling to search for food items if there is a greater payoff when those resources are found (Milton, 1993). Here, the addition of ranging data would be of interest, to compare distance traveled to activity budget data and see if these animals also utilize an area-minimizing strategy (sensu Mitchell & Powell, 2004, 2012) during lean seasons, as observed in *Eulemur collaris* (Campera et al., 2014).

Most feeding occurred in the main crowns of large trees between 11 and 20 meters above ground (Figure 4), and as predicted, foraging shifted toward higher canopy levels during the lean season. The percentage of time feeding below 10 m (9.3%) was lower than that found at other sites (e.g. Britt, 2000: 18.5% at Betampona Reserve). During Britt's (2000) study, Betampona Reserve was considered around 70% relatively undisturbed, suggesting that the canopy height could have been lower and/or the understory denser than that of our pristine site, Mangevo. As previous studies have shown, feeding in the middle canopy is likely the result of trade-offs between access to food resources and predation pressures (Britt et al., 2001; Irwin, Raharison, & Wright, 2009; Vasey, 2006), most notably from raptors (Karpanty, 2006). Animals spent more time in the upper canopy during the lean season, a behavioral shift that coincided with increased

folivory (see Figures 2 and 3), reduced travel, and increased resting time during these coldest months of the year. Taken together, this suite of behaviors supports the notion of a time minimizing strategy. Like all lemurs, ruffed lemurs have a low basal metabolic rate, and often rest in the upper canopy and actively sunbathe to stay warm during austral winter months (Morland, 1993; Baden, personal observation). Sun exposure in the upper canopy also promotes the growth of young leaves, a significant dietary component for ruffed lemurs' when fruits are scarce. Post-hoc Spearman's Rank correlations suggest there is a combined effect of temperature and diet on canopy use in this population, though the effect of temperature was more pronounced. Individuals spent more time in the lower canopy as both temperature and fruit consumption increased. Conversely, they spent more time in the upper canopy at cooler temperatures. Animals may therefore spend more time higher in the canopy during the lean season to access sunlight for thermoregulation, despite the elevated risk of predation by raptors (Karpanty, 2006). As Morland (1993) showed in this species in northeastern Madagascar, access to sunlight in the upper canopy during cooler months is a key driver of seasonal changes in canopy use. Further, ruffed lemurs may also spend more time feeding in the lower canopy during the abundant season to avoid sun exposure during these warmer months (Vasey, 2004). As frugivores, with short digestive tracts, ruffed lemurs may also need to spend more time resting during the lean season to digest the proportionately higher levels of leaf matter consumed during this period (Campbell et al., 2000, 2004; Donati et al., 2007; Eppley et al., 2017). In this case it may be advantageous to spend less time traveling between limited fruit patches and more time remaining adjacent to young leaves and sunny spots (Balko & Underwood, 2005; Goodman & Ganzhorn, 1997).

In summary, our study found that black-and-white ruffed lemur feeding behaviors are impacted by seasonality, and that ruffed lemurs adopt a time minimizing strategy during lean season months. Diet is characterized by a shift from extreme frugivory during the abundant season to a significant reliance upon leaves during the lean season, as well as reduced dietary diversity. This parallels similarly pronounced shifts in frugivory observed in *Varecia rubra* (Martinez & Razafindratsima, 2014). Lean season activity budgets show significant reductions in traveling, and canopy use significantly shifts away from lower levels. Ecological conditions likely drive these seasonal behavioral shifts, enabling black-and-white ruffed lemurs to maximize time spent searching for high-quality fruit resources during abundant periods and minimize energy expenditure during periods of resource scarcity. These results coincide with studies on several other lemur species, including both frugivores (*Eulemur collaris*: Campera et al., 2014; *Eulemur fulvus fulvus*: Sato, 2013) and folivores (*Propithecus verreauxi*: Norscia et al., 2006; *Propithecus diadema*: Irwin et al., 2014) in providing further evidence that Madagascar's pronounced seasonality for a tropical forest region strongly influences lemur dietary strategies (Dewar & Richard, 2007; Dunham, Erhart, & Wright, 2011; Wright, 1999). Our results lend themselves to further characterizing the diet of this Critically Endangered fruit-specialist and emphasizes how flexible behavioral strategies enable species to cope with variable

ecological conditions and resource availability. This is increasingly important to understand in the face of ongoing deforestation and anthropogenic disturbance to Madagascar's forests (Harper, Steininger, Tucker, Juhn, & Hawkins, 2007; Morelli et al., 2020; Vieilledent et al., 2018; Wright et al., 2005), particularly given that frugivorous diets are commonly associated with high sensitivity to habitat modification (Boyle & Smith, 2010; Eppley, Santini, Tinsman, & Donati, 2020; Harcourt, 1998; Marsh, Johns, & Ayres, 1987; Richard & Sussman, 1987; Struhsaker, 1997).

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AUTHOR CONTRIBUTIONS

Andrea Baden: Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; writing-original draft; writing-review and editing.

CONFLICT OF INTEREST

The authors confirm there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available upon reasonable request from the authors.

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SUPPORTING INFORMATION

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

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