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ARTICLE
Animal Ecology

A long-term study on food choices and nutritional goals of a leaf-eating primate

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Abstract

Efficient foraging plays a critical role in fitness, yet food choices and underlying nutritional goals vary among animals. To understand those choices and therefore the importance of different food resources, many studies estimate food preferences by applying electivity indices that account for resource availabilities. However, the general applicability of electivity indices in biologically relevant foraging scenarios is unclear. Our major aims were to find effective methods to estimate animals' food choices and to investigate long-term food choices and underlying nutritional goals of the red colobus monkey (*Piliocolobus tephrosceles*) in Kibale National Park, Uganda, an endangered folivore. We used simulations of different foraging conditions to evaluate the applicability of electivity indices in biologically relevant scenarios to help interpret our results. Then, we used long-term data collected between 2006 and 2016 on the feeding behavior and ecology of red colobus to determine the consumption frequencies of different foods and their food preferences. Based on these results and nutritional concentrations of young leaves of frequently consumed tree species, we investigated the importance of the protein-to-fiber ratio in their diet. Our simulations highlight limitations of electivity indices in biologically relevant foraging scenarios. Further, red colobus clearly chose young leaves over other plant parts, and, considering species and plant part,

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red colobus fed on many different items, but few dominated their diet. The availability and spatial distribution varied across the most consumed foods, but red colobus preferences remained mostly stable over time. Protein-to-fiber ratio had no association with preference but with consumption frequencies of different young leaves. The limitations of electivity indices in different foraging conditions underline the importance of comparing food preferences with consumption frequencies to assess the importance of different food resources. Our results provide a robust understanding of the food choices and nutritional goals of a leaf-eating animal that can ultimately be used for implementing more effective conservation measures by directing habitat protection or restoration efforts toward these resources.

KEYWORDS
diet, electivity indices, endangered species, folivore, food availability, foraging frameworks, Kibale, red colobus, resource distribution

INTRODUCTION

A central tenet of evolutionary biology is that individuals aim to maximize their biological fitness, which requires access to sufficient food resources and foraging efficiently from these resources. How different organisms meet their food requirements is therefore one of the major questions in behavioral ecology (Davies et al., 2021).

Which resources animals include in their diet depends on their ecological niche and even closely related species may choose significantly different food resources (Garber, 1987). Leaves, consumed by folivorous animals, have been assumed to be a relatively homogeneous resource in terms of their spatial and temporal distribution compared with foods eaten by animals following different dietary strategies, such as frugivores (Hanya et al., 2011; Isbell, 1991; Lambert & Rothman, 2015). Additionally, many folivorous species live in forests, where leaves are abundant (Gates, 1996), which has led to the assumption that folivores are not particularly constrained in their dietary choices. However, different tree species may not be equally distributed in a habitat (Snaith & Chapman, 2008) and leaves can fundamentally vary in their nutrient composition and concentration of secondary components (e.g., toxins; Chapman et al., 2003; Rothman, Dierenfeld, et al., 2006). This variation does occur not only between different plant species but also within a plant species depending on the plant part and its developmental stage (e.g., young leaves vs. mature leaves) (Lambert & Rothman, 2015; Milton, 1979). Thus, folivorous animals may face unevenly distributed food resources and be selective in their dietary choices.

To better understand whether animals are selective in their diet, it is essential to investigate their food choices, but the most consumed resources are not necessarily the most preferred. Thus, many studies across a wide range of taxa estimate the importance of, or preference for, different potential food resources considering both their consumption and availability (Ganas et al., 2008; Ivlev, 1961; Kline & Wood, 1996; Mureb et al., 2023). For example, a highly available but less preferred resource may be consumed more than a more preferred but scarce resource. Calculating so-called electivity is a commonly used method to investigate food preferences that account for both the consumption and availability of different food resources (Lechowicz, 1982; Manly et al., 2007). The terms selectivity and preference have often been used interchangeably in the past, in many cases without prior definition (Hall et al., 1997). In this paper, we use the term preference and assume an item to be preferred when it is consumed more frequently than expected by its availability.

One potential shortcoming of electivity indices is that they have been developed assuming preferences scale proportionally to consumption rates of items and their availability in the environment. This likely oversimplifies the complex decision-making processes involved in foraging behavior, and alternative theoretical approaches include the optimal foraging theory (MacArthur & Pianka, 1966) and geometric framework models (Simpson & Raubenheimer, 2011). Optimal foraging theory assumes that animals forage to maximize a single currency (commonly energy) and adjust their dietary breadth accordingly (MacArthur & Pianka, 1966). In contrast, geometric framework models assume that animals aim to balance different nutrients to maintain a target ratio (Simpson & Raubenheimer, 2011), which can likely not be maintained by only consuming a single food resource. Instead, animals need to balance the consumption of different food items and contained nutrients (Lambert & Rothman, 2015).

The leaf-eating Ugandan red colobus (*Piliocolobus tephrosceles*) have been proposed to select for proteins while avoiding fibrous foods (Evans et al., 2021; Wasserman & Chapman, 2003). This balancing of different food components might be best reflected by theoretical assumptions of geometric framework models. Assuming animals' foraging behavior more closely resembles frameworks other than the simplified assumptions under which electivity indices have been developed, it remains unclear how well these indices reflect animals' true food preferences.

Another major limitation for drawing conclusions about the importance of different foods is the limited scope of empirical data sets. Many studies have been conducted over relatively short time periods (Arseneau-Robar et al., 2021; Chaiyarat et al., 2021; Chapman & Chapman, 2002; Dasilva, 1994; Wasserman & Chapman, 2003), and they only captured snapshots of individuals' life histories and foraging behaviors. Thus, to get a more robust picture of food choices and underlying nutritional goals, careful analyses of long-term data are required. This long-term picture would help to shed light on the ongoing debate regarding the importance of the protein-to fiber ratio (*P:F*) in folivorous primate diets (Chapman & Chapman, 2002; Dasilva, 1992; Milton, 1979; Oftedal, 1991; Ryan et al., 2013).

Our aims were to evaluate methods to disentangle animals' food choices and to investigate the long-term food choices and nutritional goals of folivorous red colobus monkeys in Kibale National Park, Uganda, considering food availability and distribution. First, we evaluated the applicability of electivity indices in different foraging conditions using computer simulations. Then, we applied Vanderploeg and Scavia's electivity index to investigate red colobus' food preferences. To gain a robust picture of food choices, we compared the preferences with their consumption frequencies. Then, we tested whether the *P:F* of different foods can explain red colobus dietary choices by using the preference, as well as the consumption frequency of different items in relation to their nutritional content. We expected that items having a higher *P:F* would be both more preferred and more frequently consumed in accordance with previous short-term studies (Wasserman & Chapman, 2003). Furthermore, we investigated whether the most frequently consumed young leaves are evenly distributed. With our study, we aspire to improve theoretical ideas about the ecology and evolution of animal foraging behavior and to contribute to the improvement of conservation measures of red colobus and other folivorous animals.

METHODS

Study population and study area

The Ugandan red colobus (*P. tephrosceles*) is an endangered primate, native to Uganda and Tanzania (IUCN, 2019). They are folivorous, group-living, and mostly arboreal monkeys (Struhsaker, 2010). Ugandan red colobus populations are decreasing, and one major reason for this trend is logging and wood harvesting (IUCN, 2019). The largest viable population lives in Kibale National Park (795 km^2, hereafter Kibale), which is a moist, evergreen forest located in western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E) with two rainy and two dry seasons (Chapman et al., 2021; Chapman & Lambert, 2000). In Kibale, populations of red colobus and other diurnal monkeys seem to be increasing (Chapman et al., 2021, 2023).

For our study, we analyzed observational data recorded between 2006 and 2016 from one well-habituated group of red colobus ranging around the Makerere University Biological Field Station (MUBFS) at the edge of Kibale in combination with ecological data on the abundance, distribution, and phenology of different tree species in the group's home range.

Evaluation of electivity indices

Electivity indices are used to assess the food preferences for different resources by considering relative consumption and availability (Lechowicz, 1982). Electivity is a relative measure as each food resource is considered preferred (or avoided) compared with the other resources in the sample if they are consumed more (or less) often than expected by their availability. Thus, electivity scores from different studies can only be compared if the same (or at least similar) sets of resources were included. Nevertheless, it provides insights about which foods in a specific environment are the most (or least) preferred.

Before applying the electivity indices to our empirical data, we evaluated their applicability in simulated scenarios of animals following different foraging assumptions. A comprehensive description of the compared electivity indices, the simulated foraging conditions, and the results of the simulations can be found in Appendix S1. In summary, Vanderploeg and Scavia's electivity index (Vanderploeg & Scavia, 1979) provided the most reliable results for scenarios where individuals selected food items proportionally to their preferences and availability (Appendix S1: Figure S2). However, electivity indices generally have limited informative value if the preference does not scale proportionally with the diet and availability. For animals following the optimal foraging theory, this limitation arises because of a discrete threshold condition that determines the dietary breadth of individuals (Appendix S1: Figure S3). In geometric framework models, an animal's preference for a particular food resource is not stable but strongly influenced by its current nutritional state and nutrient limitations. Thus, the electivity scores for the same items are disproportionally influenced by resource availabilities (Appendix S1: Figures S4 and S5).

Given the limitations of electivity indices in these biologically relevant foraging conditions, we compared the estimated preferences with the overall consumption frequency of different food items to make more robust statements about the importance of different food resources for red colobus, and, more generally, to get a better understanding of how conclusions about food choices may vary depending on how observational data are evaluated.

Diet based on behavioral observations

To assess the consumption frequency of different food resources, we analyzed behavioral scan data collected from red colobus from 2006 until 2016. The data included observations from 166 individuals that were part of the study group during this period. For each scan, five adult individuals were randomly selected, and their behavior documented. When an individual was feeding, the plant species *s* and plant part *p* (hereafter food item *s*,*p*) was recorded. The scans were collected every 15 min (every 30 min if other data were collected at the same time) with the aim of collecting data between 8:00 a.m. and 4:00 p.m.

In total, we considered 38,768 feeding events, recorded on average on 8.3 observation days per month between July 7, 2006, and December 17, 2016. For each month *m* and food item *s*,*p*, we summarized the number of times this item was observed to be consumed ($D_{s,p,m}$). First, we investigated the overall diet by summarizing the consumption per item over the entire study ($D_{s,p} \quad \sum_m D_{s,p,m}$). Then, we investigated the variation of the diet over time by considering the number of times an item was included in the diet per month as proportion of the total number of observed feeding events in that month.

Availability of food items based on plant abundance and phenology

To estimate the monthly availability of different food resources within the red colobus home range, we used the Food Availability Index (FAI), a well-established method for estimating plant food availability (e.g., Arseneau-Robar et al., 2021). We calculated the monthly FAI for each plant item *s*,*p* in the following way:

$$\mathrm{FAI}_{s,p,m} \quad \mathrm{basalarea}_s \times \mathrm{phenologyscore}_{s,p,m} \tag{1}$$

Here, the basal area of each tree species in the red colobus home range ($\mathrm{basalarea}_s$) indicates how much area in the forest is covered by a specific tree species. This was based on 57 tree plots within the home range of the study group (Appendix S1: Figure S6; home range obtained from Kalbitzer et al., 2023), and for each of these 50 m × 50 m tree plots, all trees of a diameter at breast height (dbh; 1.2–1.3 m above the ground surface) larger than 10 cm were recorded. The tree plots, which were recorded between 2012 and 2014, included 3710 trees, belonging to 87 species. We considered this basal area per species as representative for the entire home range and the entire study period (2006–2016), because major changes in forest composition are not expected to occur over short time frames and major disturbances to the forest have not been reported (Chapman et al., 2021).

This value was multiplied with monthly phenology scores of the respective plant parts of that species $\mathrm{phenologyscore}_{s,p,m}$ (e.g., young leaves of species *s* in July 2010, see below), which indicate the temporal change in availability of different plant parts per species. To do so, the long-term field assistants of the project scored the availability of the different plant parts—unripe fruit (from 0 to 4 with 0 indicating no fruit and 4 maximum availability), ripe fruit (from 0 to 4), mature leaves (0 or 1, where 0 indicated a defoliated tree), young leaves (0–5), and flowers (0 or 1). During the study, an average of 8.9 trees per species and month (range 3–26) for 53 species in total were included for these estimates. To make the scores more comparable across plant parts, we rescaled all scores from 0 to 1 by dividing each score by its maximum attainable value. Additionally, we added bark as a plant part, and set the availability to 1, assuming that all trees included in the analysis had bark abundantly available. We added scores for the plant part leaf buds using the phenology score of young leaves in the month afterward, assuming the majority of leaf buds to develop into young leaves in the following month. Moreover, for any item that lacked a phenology score in a particular month but had sufficient phenology data in other years for that same month, we extrapolated the missing value by using the average monthly phenology score over all years from that item. Furthermore, we assigned a phenology score for commonly consumed young leaves whose species were represented in the basal area data but not in the phenology data to ensure that all important species are represented in the preference estimation. To do this, we calculated the mean phenology score for young leaves across all species per month for the following species: *Acacia brevispica*, *Albizia gummifera*, *Alangium chinense*, *Antiaris toxicaria*, *Bridelia* sp., *Ehretia cymose*, *Ficus brachylepsis*, *Ficus natalensis*, *Ficus sur*, *Newtonia buchananii*, *Pancovia turbinata*, *Persea americana*, *Pseudospondias microcarpa*, *Shirakiopsis elliptica*, and *Trema orientalis*.

To verify that the mean monthly phenology scores of young leaves across plant species can be used as a proxy for species without young leaf phenology information, we compared the mean monthly phenology of six randomly chosen tree species with complete young leaf phenology to the mean young leaf phenology across species (see Appendix S1: Phenology validation). Differences between estimated scores based on average values and actual phenology scores for these six species ranged from 0.061 to 0.123. This indicated that our assigned phenology scores for missing species should be close enough to the real values for the purpose of our study.

Distribution of commonly eaten tree species

To assess the spatial distribution of red colobus leaf food resources, we calculated the coefficient of variation (CV) of the basal area of the 17 most commonly consumed tree species across the 57 tree plots (see above and Appendix S1: Figure S6). The CV is a measure of relative variability that is calculated by dividing the standard deviation (SD) by the mean, here by using the SD and mean of the basal area of different tree species across the 57 tree plots. Low values indicate a homogeneous distribution of tree species, and high values suggest a clustered distribution.

Food preferences

To estimate monthly food preferences, we combined the relative diet ($rD_{s,p,m} = D_{s,p,m}/(\sum_s \sum_p D_{s,p,m})$) with the relative availability ($r\mathrm{FAI}_{s,p,m} = \mathrm{FAI}_{s,p,m}/(\sum_s \sum_p \mathrm{FAI}_{s,p,m})$) of different food items and applied Vanderploeg and Scavia's electivity index $E^*_{s,p,m}$:

$$W_{s,p,m} = \frac{rD_{s,p,m}/r\mathrm{FAI}_{s,p,m}}{\sum_s \sum_p rD_{s,p,m}/r\mathrm{FAI}_{s,p,m}}$$
$$E^*_{s,p,m} = \frac{W_{s,p,m}-(1/n)}{W_{s,p,m}+(1/n)} \tag{2}$$

We calculated the preference values for the 20 most consumed food items s,p separately in addition to values for the seven different plant parts p (young leaves, mature leaves, etc.) in general. Finally, we also calculated the electivity over the entire period from 2006 to 2016 by summarizing values for $rD_{s,p,m}$ and $r\mathrm{FAI}_{s,p,m}$ over the entire period of study.

Nutritional goals

To investigate red colobus' nutritional goals, we used information about their preferences and consumption frequencies, and the nutritional compositions of different food items. Because young leaves present the majority of consumed food items, we limited our analysis to young leaves and focused on the 15 most consumed species, which made up ~75% of the total consumed young leaves and ~58% of the total diet. We acknowledge that prior consumption of complementary nutrients might influence subsequent consumption patterns. Specifically, we wanted to test whether the *P:F* explains which young leaves the red colobus monkeys choose. We calculated the *P:F* for each item by dividing its crude protein content with its neutral detergent fiber content and then fitted linear models to investigate the association between this ratio to the calculated food preferences and consumption frequencies. All young leaves were sampled in the home range of the group multiple times to account for the possibility of seasonal and spatial intraspecific variation (Ryan et al., 2013; J. M. Rothman & C. A. Chapman, unpublished data). Protein and neutral detergent fiber analyses followed standard AOAC methods (Rothman et al., 2012).

Data analysis

We used R version 4.2.2 (R Core Team, 2022) and RStudio version 2022.12.0.353 (Posit team., 2022) to run all simulations and data analysis. For data wrangling and visualizations, we used the tidyverse package collection version 1.3.2 (Wickham et al., 2019). For the processing of geographic data, we used the sf package version 1.0-9 (Pebesma, 2018). For calculating linear models, we used the rethinking package (McElreath, 2020).

For the nutritional goals, we fitted two different multilevel Bayesian models with month as a grouping variable including varying intercepts and varying slopes (McElreath, 2020). First, we used the *P:F* as a predictor variable for the preference for young leaves of different species ($E^*_{s,p,m} = y_i$) as the outcome variable (monthly values: n_{month} 117, for young leaves of 15 different species). We scaled the preference from 0.001 to 0.999 and calculated a model with a beta distribution for this outcome variable:

$$
\begin{aligned}
y_i &\sim \text{Beta}(p,\theta)\\
\text{logit}(p) &\quad \alpha_{\text{Month}[i]} + \beta_{\text{Month}[i]} \times P:F\\
\begin{bmatrix}\alpha_{\text{Month}}\\ \beta_{\text{Month}}\end{bmatrix} &\sim \text{MVNormal}\left(\begin{bmatrix}\alpha\\ \beta\end{bmatrix}, S\right)\\
S &\quad \begin{pmatrix}\sigma_\alpha & 0\\ 0 & \sigma_\beta\end{pmatrix} R \begin{pmatrix}\sigma_\alpha & 0\\ 0 & \sigma_\beta\end{pmatrix}\\
\alpha &\sim \text{Normal}(0,1)\\
\beta &\sim \text{Normal}(0,1)\\
\sigma_\alpha &\sim \text{Exponential}(1)\\
\sigma_\beta &\sim \text{Exponential}(1)\\
R &\sim \text{LKJcorr}(2)\\
\theta &\sim \text{Exponential}(1)
\end{aligned}
\tag{3}
$$

For the second model, we used *P:F* as a predictor variable for the consumption frequencies ($D_{s,p,m}$ y_i) as the outcome variable (monthly values n_{month} 117, for young leaves of 15 different species). We modeled this outcome variable using a Poisson distribution and, because months differed regarding the total number of observed feeding events, we included the monthly feeding events as a log-transformed offset variable ($\log \tau_{s,p,m}$):

$$
\begin{aligned}
y_i &\sim \text{Poisson}(\lambda_i)\\
\log(\lambda_i) &\quad \alpha_{\text{Month}[i]} + \beta_{\text{Month}[i]} \times P:F + \log \tau_i\\
\begin{bmatrix}\alpha_{\text{Month}}\\ \beta_{\text{Month}}\end{bmatrix} &\sim \text{MVNormal}\left(\begin{bmatrix}\alpha\\ \beta\end{bmatrix}, S\right)\\
S &\quad \begin{pmatrix}\sigma_\alpha & 0\\ 0 & \sigma_\beta\end{pmatrix} R \begin{pmatrix}\sigma_\alpha & 0\\ 0 & \sigma_\beta\end{pmatrix}\\
\alpha &\sim \text{Normal}(0,1)\\
\beta &\sim \text{Normal}(0.5,0.5)\\
\sigma_\alpha &\sim \text{Exponential}(1)\\
\sigma_\beta &\sim \text{Exponential}(1)\\
R &\sim \text{LKJcorr}(2)
\end{aligned}
\tag{4}
$$

RESULTS

Consumption, availability, and distribution of different food items

Between 2006 and 2016, the red colobus group fed on 441 different food items (*s*,*p*) from 123 different plant species (*s*). The top 20 most consumed items made up 69.4% of the diet (Table 1). Young leaves were the most consumed plant part, making up 77.5% of the diet, and the young leaves of *Prunus africana* were the most consumed food item, making up 9.1% of the diet (Table 1, Figure 1a). Red colobus also fed on other plant parts, such as bark, mature leaves, flowers, and even sometimes fruits from various species (Table 1, Figure 1a). The consumption of the most consumed items mostly remained relatively stable over time (Figure 2a).

We calculated the FAI for 272 different food items. *P. africana* was the most available species, and bark and mature leaves were the most available parts (Figure 1b). There were considerable differences in availability between the most consumed items, but within these items, the availability remained relatively stable over time (Figure 2b).

The distribution of 17 commonly consumed tree species within the group's home range varied (CV range: 2.12–7.34), with *P. africana* (CV 2.12) and *Celtis durandii* (CV 2.37) being the most homogeneously distributed and *N. buchananii* (CV 7.34) and *Eucalyptus* sp. (CV 7.13) the most clustered resources (Table 1; Appendix S1: Table S1).

Food preferences

Red colobus showed a clear and temporally stable preference for young leaves (Figure 3a). There were also mostly stable differences in preferences for specific food items with *N. buchananii* young leaves being the most preferred item most of the time (Figure 3b).

Comparison of preferences and consumption frequencies

Comparing preferences with consumption frequencies for different plant parts (Figures 1 and 3, Table 1), young leaves were the most preferred as well as the most consumed plant part. On the food item level, preferences and consumption frequencies were less consistent. For example, *P. africana* young leaves were the most consumed item, but because of its high availability, they were only

TABLE 1 Overview of the 20 most consumed items between 2006 and 2016 with information about availability, distribution, preference, and protein-to-fiber ratio of these items.

Item	Consumption (*n*)	Diet composition (%)	Average availability (FAI)	Tree distribution (CV)	Average preference	Preference rank	Protein-to-fiber ratio
Prunus africana YL	3530	9.11	229.65	2.12	−0.8812	13	0.84
Trilepisium madagascariense YL	3220	8.31	19.75	3.96	−0.1659	6	0.40
Celtis africana YL	2604	6.72	103.42	2.43	−0.8194	11	0.80
Prunus africana BA	1989	5.13	605.73	2.12	−0.9724	19	…
Newtonia buchananii YL	**1799**	**4.64**	**0.64**	**7.34**	**0.8470**	**1**	**0.45**
Celtis durandii YL	1460	3.77	145.50	2.37	−0.9209	16	0.78
Albizia grandibracteata YL	1453	3.75	54.63	3.15	−0.8126	10	0.68
Macaranga sp. YL	1272	3.28	146.52	3.43	−0.9328	17	0.51
Millettia dura YL	**1168**	**3.01**	**1.61**	**5.24**	**0.4894**	**2**	**0.75**
Trema orientalis YL	**1063**	**2.74**	**6.29**	**6.63**	**−0.1137**	**5**	**0.53**
Dombeya kirkii YL	1047	2.70	32.76	5.20	−0.7915	9	0.60
Eucalyptus sp. BA	**1013**	**2.61**	**3.61**	**7.13**	**0.0874**	**3**	…
Funtumia africana YL	942	2.43	70.11	2.49	−0.8959	14	0.46
Bridelia sp. YL	876	2.26	72.27	4.31	−0.9010	15	0.35
Parinari excelsa YL	815	2.10	6.39	6.51	−0.3735	7	0.25
Strombosia scheffleri YL	667	1.72	6.85	4.4	−0.4726	8	0.57
Persea americana BA	544	1.40	27.21	3.78	−0.8431	12	…
Celtis africana LB	500	1.29	103.68	2.43	−0.9618	18	…
Vepris nobilis YL	**475**	**1.23**	**2.20**	**6.38**	**−0.1082**	**4**	**0.65**
Prunus africana ML	466	1.20	605.46	2.12	−0.9936	20	…
Other consumed items (*n* = 421)	11,865	30.61	…	…	…	…	…

Note: The five top-preferred items appear in boldface. High CV values indicate a clustered distribution of resources within a certain habitat.
Abbreviations: BA, bark; LB, leaf buds; FAI, Food Availability Index; ML, mature leaves; YL, young leaves.

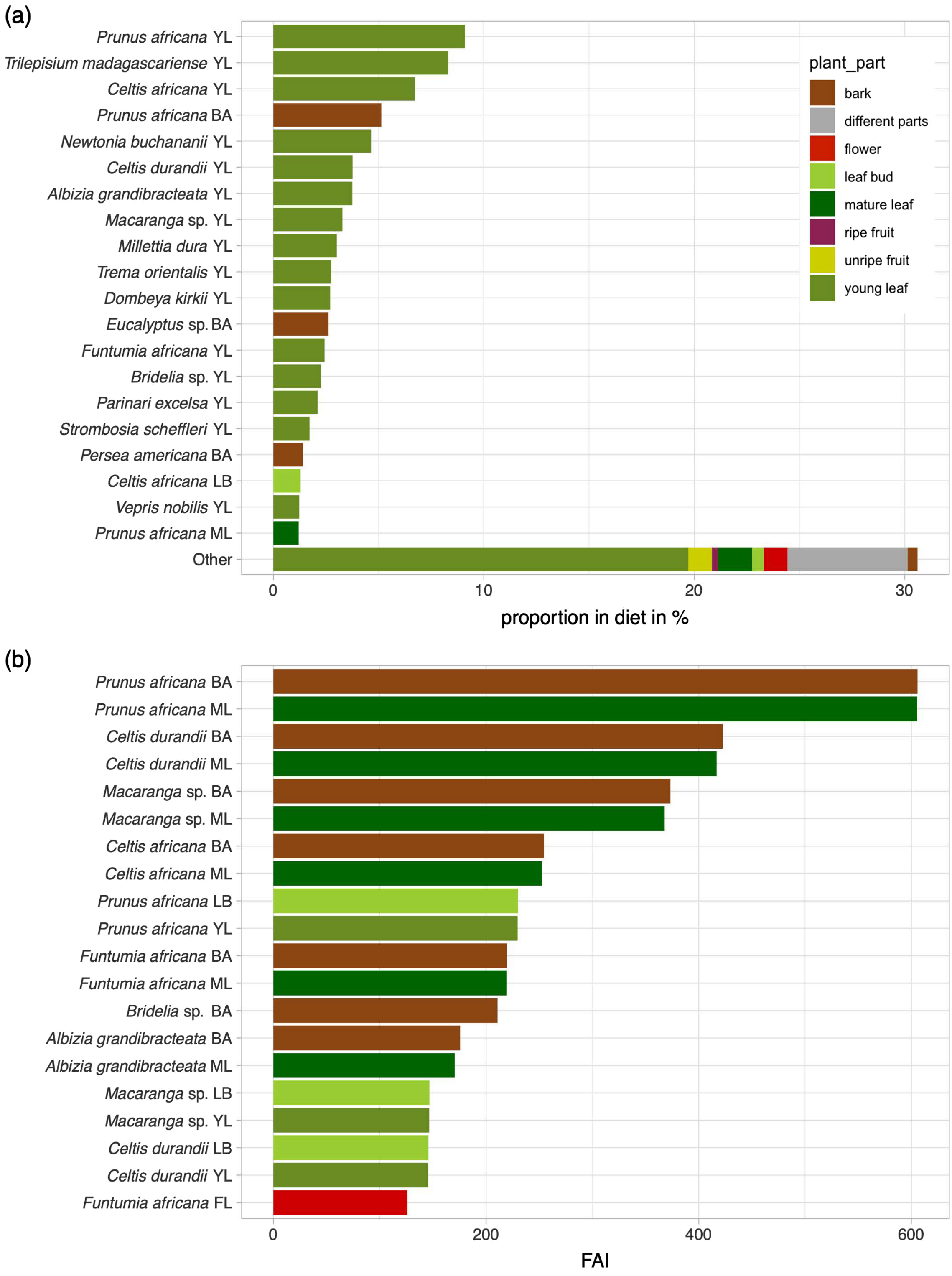

FIGURE 1 (a) Top 20 most consumed items; (b) top 20 most available items within the study group's home range between 2006 and 2016. BA, bark; FAI, Food Availability Index; FL, flower; LB, leaf buds; ML, mature leaves; YL, young leaves.

the 13th preferred item (Figure 2, Table 1). These group-level patterns of differing consumption frequency and preferences are similar in both male and female individuals (Appendix S1: Figure S8).

Red colobus nutritional goals

There was no clear association between the *P:F* and preferences for young leaves of different species

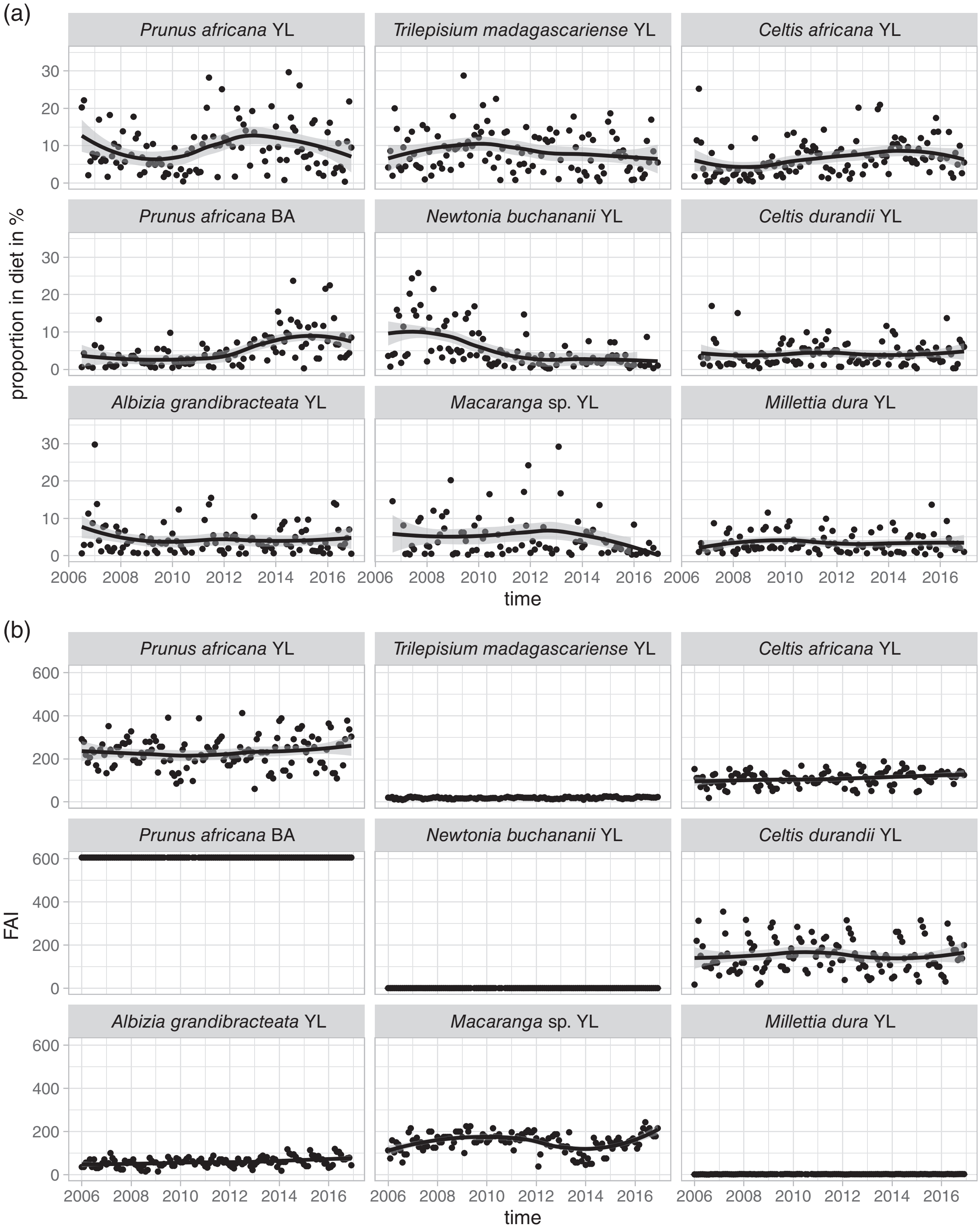

FIGURE 2 (a) Top 9 most consumed items over time with (b) respective availability of the top 9 most consumed items within the study group's home range between 2006 and 2016. The black lines represent the trend based on locally weighted scatterplot smoothing. BA, bark; YL, young leaves.

(Figure 4a, Table 2). However, there was an association between the *P:F* and how often young leaves of different species were consumed (Figure 4b, Table 2).

DISCUSSION

We aimed to find effective ways to estimate animals' food choices and to investigate the long-term food choices and

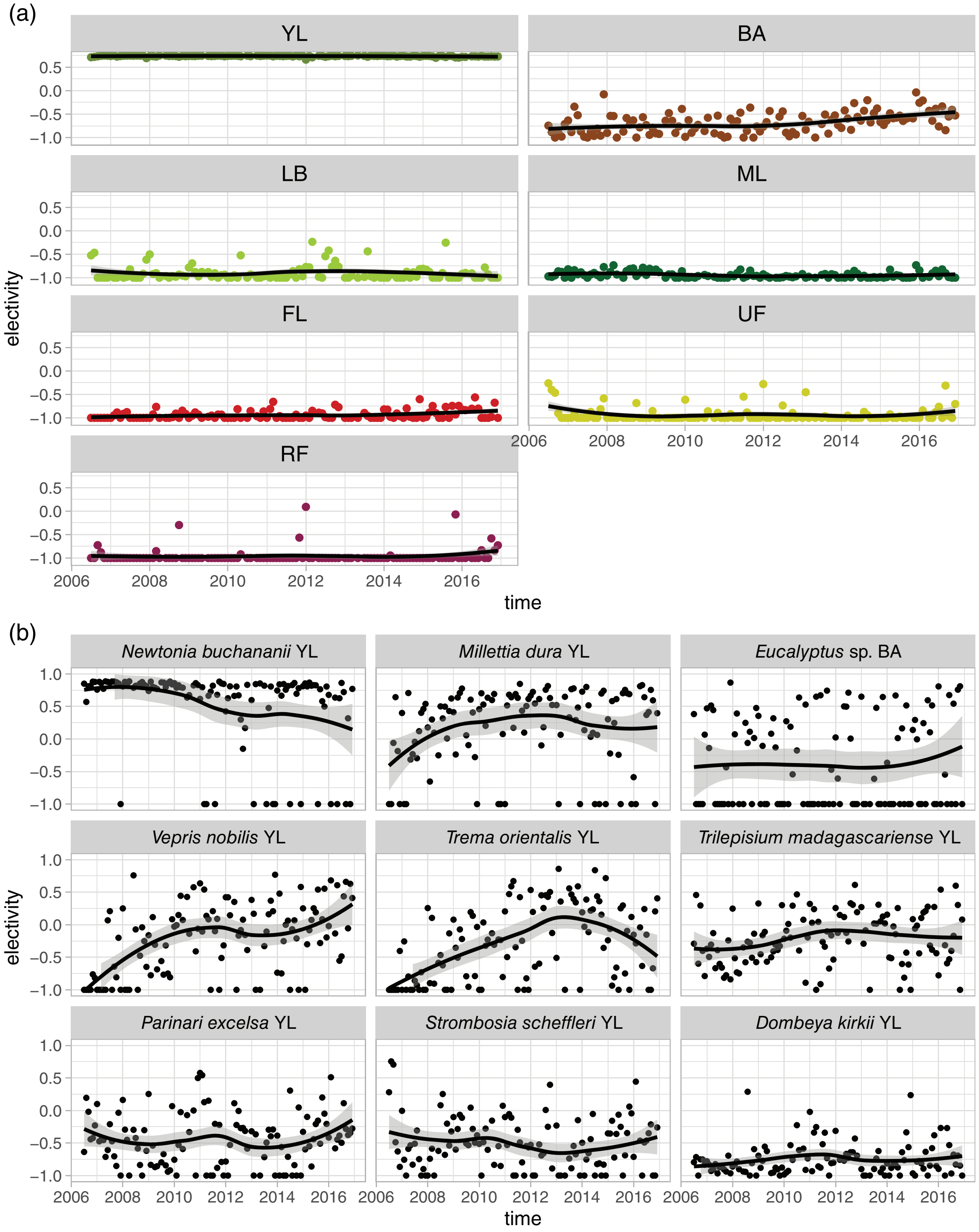

FIGURE 3 (a) Red colobus preference for different plant parts and (b) top 9 most preferred items over time. The dots represent the monthly electivity scores, and the black lines show the trend based on locally weighted scatterplot smoothing. BA, bark; FL, flower; LB, leaf buds; ML, mature leaves; RF, ripe fruit; UF, unripe fruit; YL, young leaves.

nutritional goals of a folivorous primate, the Ugandan red colobus.

The red colobus clearly chose young leaves over other plant parts, which is consistent with previous studies (Chapman & Chapman, 2002; Struhsaker, 2010; Wasserman & Chapman, 2003). This pattern can likely be explained by the higher *P*:*F* of young leaves than of mature leaves (Lambert & Rothman, 2015). Nevertheless,

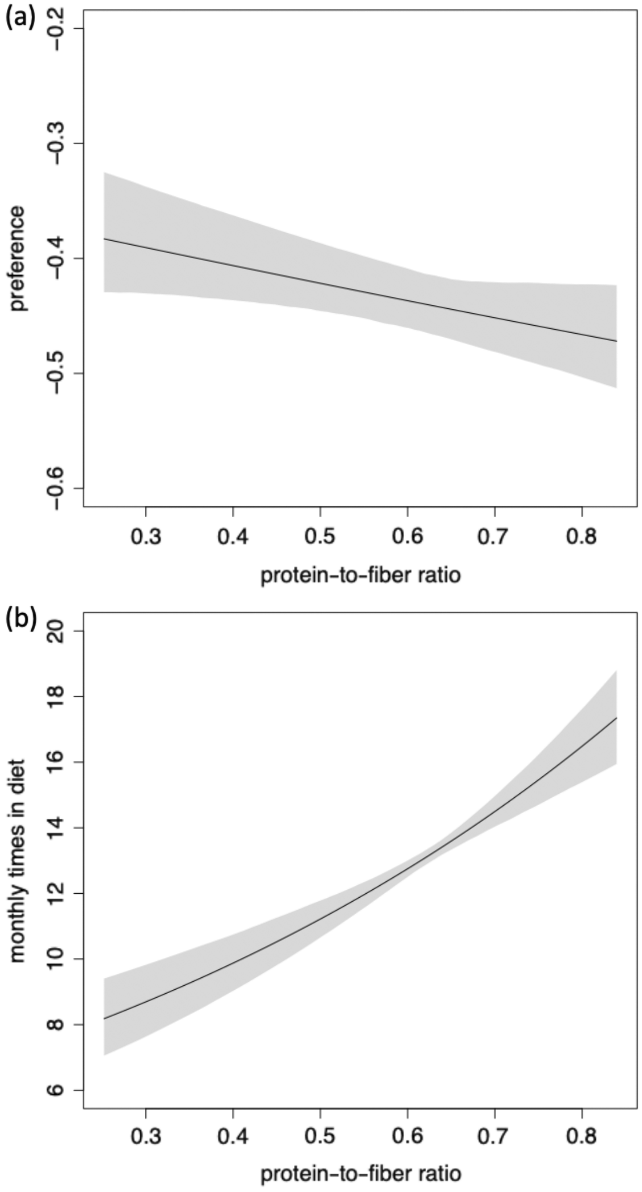

FIGURE 4 (a) Protein-to-fiber ratio predicting preferences and (b) consumption frequencies of the different species of the most consumed young leaves. The black line represents the mean estimated slope, and the gray shaded area represents the 95% posterior credible interval. The monthly times in diet is shown assuming a total monthly observation of 200 feeding events. The protein-to-fiber ratio ranged between 0.25 and 0.84.

TABLE 2 Model output for protein-to-fiber-ratio predicting preference of different young leaves and for protein-to-fiber ratio predicting the times different young leaves were included in the diet.

Model	Term	Mean	SD	CI 2.5%	CI 97.5%
Preference (Beta)	Intercept	−0.84	0.03	−0.89	−0.79
	Slope	−0.06	0.03	−0.11	0.00
Diet (Poisson)	Intercept	−3.52	0.12	−3.77	−3.19
	Slope	1.28	0.19	0.91	1.67

the red colobus showed a high selectivity for a small range of items, as the top 20 most consumed items made up around 70% of their diet. An exact order of importance among those 20 items is difficult to interpret because the consumption frequency largely differed from estimated preferences. For example, young leaves of *P. africana* were the most consumed, but only the 13th most preferred item, which can be explained by the high density of *P. africana* trees in the group's home range. On the other hand, many preferred species are rare in the groups' home range; thus, the red colobus might deplete the respective trees (Snaith & Chapman, 2005), which would prevent them from being consumed more often.

In comparison with other studies on nearby groups, some results were consistent (Chapman & Chapman, 2002; Ryan et al., 2013; Struhsaker, 2010; Wasserman & Chapman, 2003), whereas others were substantially different. For example, the young leaves of *P. africana*, a light-dependent forest edge species, have been frequently consumed by our group and the groups reported in Chapman and Chapman (2002), but hardly ever in another neighboring group (Struhsaker, 2010). These dietary differences among neighboring groups suggest that red colobus monkeys might not be obliged to consume particular items but have alternative ways to fulfill their nutritional goals. Differences in the dietary patterns also expand to different folivorous primates in Kibale. For example, groups of black and white colobus monkeys located in areas close to our group have been reported to show large variation in the feeding intensity on *A. grandibracteata*, *C. durandii*, and *P. africana* (Harris & Chapman, 2007). The young leaves of these species were also among the most selected items by red colobus in our study. A major factor driving the differences in diet and preferences between the folivorous community in Kibale is likely a difference in food species densities in the core areas of different groups.

The most consumed tree species, *P. africana*, is widely available and homogeneously distributed within our groups home range but considered a rare, light-dependent edge species in broader areas of Kibale (Chapman & Chapman, 2002). This might explain why red colobus groups in other areas of the park substitute *P. africana* with alternative food species (Struhsaker, 2010). Nevertheless, for future research, it would be intriguing to investigate whether the distribution of different food species, specifically edge species such as *P. africana*, impacts red colobus distribution at larger scales within the forest.

Many studies on foraging behavior in folivorous primates report the *P:F* of resources to be an important determinant of dietary choices as well as primate biomass (Chapman et al., 2004; Chapman & Chapman, 2002; Milton, 1979; Ryan et al., 2013). The methodological aspects of this ratio, particularly when relying on crude protein measures, have faced criticism. One critique is that nitrogen is often bound in fibrous contents, which results in its presence in both the numerator and denominator of the protein-to-fiber-ratio (Wallis et al., 2012). In addition, relative to crude protein, available protein measures that account for nitrogen bound to fiber and the potential impact of tannins could improve estimates of protein digestibility by primates (Evans et al., 2021). We acknowledge this methodological caveat as a potential limit of inference of this study and previous studies using crude protein measurements. More generally, the importance of the *P:F* for primates has also been criticized. For example, Ganzhorn et al. (2017) questioned the general importance of protein in primate diets, unless environmental nitrogen is limited. Additionally, some empirical studies found no relation between the *P:F* and folivore's dietary choices (Dasilva, 1992). Many studies on folivore foraging behavior have been conducted over relatively short periods and only captured snapshots of individuals' life histories and foraging behaviors. For the 10 years of data that we analyzed, there was a positive association between the *P:F* and the consumption frequency of, but not the preferences for, different food resources.

Methodological differences (preference vs. consumption) among studies investigating nutrition is common and result in different inquiry levels (Felton et al., 2009). The consumption frequency has the advantage of functioning as a better proxy for the overall intake of nutrients, whereas preference has the advantage that it better reflects the effort used in acquiring the resources. Using electivity indices for preferences, however, come with inherent limitations. As explored in our simulations, for animals following the assumptions of optimal foraging theory or geometric framework models (see Appendix S1), electivity indices have limited informative value in these biologically relevant scenarios. Additionally, animals' perceptions of the world can differ from what we quantify; thus, the perceived availability of resources may differ from the estimated availability. For example, different food resources may have different cues like colors or aroma that influence how easily animals can locate them (Norbury & Sanson, 1992). Moreover, spatial memory influences how animals perceive their environment. This applies especially for cognitively developed animals like primates, which may use spatial memory to find important food items (e.g., wild capuchin monkeys [*Cebus apella*]; Janson, 1998). In our study, red colobus preferred *N. buchananii* young leaves the most, a rare and clustered, yet frequently consumed item. Like other primates, red colobus monkeys might remember where important resources are located and actively seek them out, which further expands the gap between perceived and estimated food availability. Given these limitations of electivity indices and that consumption frequency, in contrast to preferences reflects actual nutrient intake, consumption frequencies may be the better method to make statements about nutritional goals. In that regard, our study supports the importance of the *P:F* on folivorous dietary choices.

In addition to the importance of the balance between protein intake and fiber avoidance in young leaves, our study suggests that complementary nutrients are important for red colobus to achieve their nutritional goals, as seen by the frequent consumption of bark that has a higher sodium and higher sugar content than leaves (Lambert & Rothman, 2015; Rode et al., 2003). In many central African forests, sodium is limited and therefore animals go to great lengths to obtain it (Kaspari, 2020). This is also the case for Ugandan forest-dwelling primates (Fedurek et al., 2024; Rothman, Van Soest, & Pell, 2006; Venable et al., 2020). A noteworthy food item in this context is the bark of *Eucalyptus*, which was a very frequently consumed and highly preferred food item. *Eucalyptus* is a non-native tree that does not occur naturally in the park. Indeed, *Eucalyptus* trees within the park have been removed (Jacob et al., 2017), but are commonly planted at the border of the park. These plantations were mostly planted in the 1960s and were frequently visited by the red colobus. The bark of *Eucalyptus* is known to be a sodium source for some folivores (Au et al., 2017; Grueter et al., 2018; Rothman & Bryer, 2019), including colobus in Kibale (Harris & Chapman, 2007; Rode et al., 2003). The leaves of *Eucalyptus* contain high concentrations of plant secondary metabolites (PSMs) that deter most folivorous animals. However, several species of marsupials have coevolved and tolerate these elevated PSM levels (Jensen et al., 2014). Investigating whether the bark of *Eucalyptus* has similar concentrations of PSMs and if so, why red colobus frequently consume this food item would be a fruitful area for future research.

The reliance on non-native food sources has been observed in many primates (Rothman & Bryer, 2019). Our study expands this observation and reports the heavy reliance on a non-native, newly introduced food item for a folivorous primate species, which indicates a potential for rapid responses to new resources. This behavioral plasticity of red colobus has a great potential, as observed in their ability to alter their activity budget and adjust to completely new habitats like savanna woodlands (Kibaja et al., 2023) or riverine forests (Chapman et al., 2002). Their fast responses to new food resources and habitats may buffer them from the effects of habitat destruction and climate change. The mechanisms facilitating and limiting this behavioral flexibility are largely unclear and provide another important area for future research (e.g., testing of social learning strategies). Generally, studies are often conducted in human-modified landscapes and understanding the reliance of nonnatural food resources might help conservation efforts (Irwin et al., 2015; Takahashi et al., 2023).

In conclusion, despite being folivorous, red colobus monkeys were relatively selective in their diet. Our study, based on robust long-term data, supports the notion that the *P:F* is an important factor in determining the diet of folivorous primates. Additionally, it reveals the potential importance of a reliance of primates on non-native foods. Our study contributes valuable insights into the foraging behavior of leaf-eating animals which could serve as a foundation for more goal-oriented and effective conservation. By identifying the tree species that provide important food items, conservation efforts could be targeted toward protecting those vital resources from logging activities or using those species in restoration efforts. Furthermore, our study highlights limitations of electivity indices in biologically relevant foraging conditions and thus underlines the importance of comparing the estimated food preferences with the diet composition to make more robust statements about the importance of different food resources. Moving forward, we underline the importance of long-term data for a comprehensive understanding of food choices, encourage future research on animals' food choices, and highlight the urgency of continued efforts in the conservation of endangered primate species.

AUTHOR CONTRIBUTIONS

Patrick Lauer and Urs Kalbitzer conceived the ideas and designed the methodology. Colin A. Chapman, Patrick Omeja, Jessica M. Rothman, and Urs Kalbitzer designed and supervised the data collection. Patrick Lauer and Urs Kalbitzer analyzed the data. Patrick Lauer led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Lauer et al., 2024) are available from Edmond, the Max Planck Digital Library: https://doi.org/10.17617/3.XCUGKY.

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SUPPORTING INFORMATION

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

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