Feeding adaptation of François' langurs (Trachypithecus francoisi) to the fragmented limestone habitats in Southwest China

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Running Title: Feeding adaptation of Francois' langurs to the fragmented limestone habitats

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Abstract: Limestone forests are an unusual habitat for primates, especially fragmented limestone habitats. However, limited research has been conducted on Francois' langurs (*Trachypithecus francois*) in these habitats, and there is a need to understand their behavioral adaptations to the fragmented limestone habitat. We collected data on the diet of Francois' langurs in a fragmented limestone habitat in Encheng National Nature Reserve, southwestern Guangxi, China, and their feeding adaptations to the fragmented forest were examined. The results indicated that a total of 101 species of plants were consumed by the langurs. The langurs ate a higher number of food species throughout the year when compared with other species, maintained a high level of food diversity, and ate more vines. Moreover, they were highly selective in their use of vegetation in their home range, and fewer plants provided a high-quality food source. During the season when food resources were scarce, similar to monkey populations in other geographic populations, the consumption of fruits and young leaves decreased as their availability decreased. This led to the use of other species, such as mature leaves and seeds. Overall, Francois' langurs in Encheng National Nature Reserve are generally considered to employ energy minimization strategies. The findings support that Francois' langurs adjust their feeding behavior to cope with seasonal and micro-variations in their dietary requirements and to adapt to their particular environment.

Key words: Francois' langurs, Feeding adaptation, Limestone habitat, Fragmentation

1 Introduction

Habitat loss and fragmentation are two of the biggest threats to the survival of non-human primates (Crooks et al., 2017). High forest dependence makes primates vulnerable to deforestation and habitat fragmentation, and these threats increasingly force them to inhabit isolated small forest patches that are surrounded by anthropogenic activities. Consequently, populations have declined dramatically, with non-human primates being one of the most vulnerable groups threatened with extinction (Arroyo-Rodriguez and Dias, 2010; Estrada et al., 2017). Although the effects and modalities of these impacts differ for different species, habitat fragmentation poses a significant threat to their survival (Dirzo et al., 2014; Fahrig, 2003). Habitat fragmentation leads to reduced available habitats (Marsh, 2003), increased marginal effects (Laurance et al., 2002), the disruption of gene flow (Ricardo et al., 2021), lack of resources (Arroyo-Rodriguez et al., 2007), disease transmission (Gabriel et al., 2018), and changes in sensitivity to climate change and human disturbance (Onderdonk & Chapman, 2000). In addition, habitat fragmentation even affects the behavior of primates by altering their activity time allocation, roaming distance, and foraging (Campera et al., 2014; Chaves & Cesar Bica-Marques, 2013; Chaves et al., 2012; Irwin, 2008).

Foraging activity is one of the most important behavioral activities for animals to complete (Rayner et al., 2010). Non-human primates mostly inhabit forest habitats, and, thus, they have developed characteristics that are suitable for forest survival, such as highly flexible eating habits and seasonal use of food and resources (Estrada & Coates-Estrada, 1996). However, several of these characteristics may influence their ability to live in fragmented forests (Onderdonk & Chapman, 2000). For example, spatiotemporal variations in the availability of food resources may limit the proliferation of certain specialized fruit primates (Estrada & Coates-Estrada, 1996; Irwin, 2008). Additionally, when the size of the fragments decreases, the forest plant diversity decreases and the vegetation structure degrades (Arroyo Rodriguez et al., 2007), which may lead to a decrease in the food supply of the species that inhabit the fragments (Zanette et al., 2000; Fahrig, 2003). Therefore, habitat fragmentation may affect the foraging ecology of species by affecting the habitat quality, such as the presence, abundance, or phenology of food plant resources. The longer habitat fragmentation persists, the greater the differences in the flora composition, vegetation structure, and plant phenological cycles between the forest patches (Arroyo-Rodriguez & Mandujano, 2006; Hill & Curran, 2003). For example, the abundance of large trees varies between forest fragments (Arroyo-Rodriguez & Mandujano, 2006; Arroyo-Rodriguez & Mandujano, 2006; Onderdonk & Chapman, 2000).

However, species do not always passively face changes in habitat and often respond through ecological, behavioral, and genetic adaptations that consist of appropriate adjustments to their survival patterns (Begon et al., 1996). Different species often adopt different foraging and dietary strategies to cope with forest fragmentation and seasonal changes in food distribution and availability. For example, some primates become more flexible in their diet, and some specialized foragers show flexibility in responding to temporal changes in food availability and habitat disturbances (Fahrig, 2003; Hou et al., 2018; Kifle & Bekele, 2021). Furthermore, Johns (1991) found that there were clear differences in the feeding time, food composition, feeding routes, and group patterns between the species in fragmented and non-fragmented habitats. In addition, the diets of some species differ between intact forests and forest fragments, suggesting that primates exhibit some foraging flexibility (Chaves et al., 2012; Chaves & Cesar Bica-Marques, 2013). This flexible response of primates may include increasing or decreasing dietary diversity, where they consume locally abundant tree species and exotic and secondary successive species, such as vines or climbing plants, or increase their leaf consumption (de Luna et al., 2017; Dias et al., 2014; Irwin, 2008; Onderdonk & Chapman, 2000).

Francois' langur (*Trachypithecus francois* (de Pousargues, 1898)) is one of the most threatened non-human primates in the world and is listed as endangered by the International Union for Conservation of Nature (IUCN 2022). Currently, Francois' langurs are only distributed in a small area of the karst mountain forests from Vietnam to China, and their distribution is separated by roads, farmlands, and towns into more than 40 independent subpopulations, with a total population of less than 2000 individuals (Zhou et al., 2018). In China, the wild population size of this langur is 1589–1718 individuals (Yi et al., 2023). In recent years, habitat fragmentation has had a dramatic impact on the Francois' langur's population size and behavioral response (Li et al., 2007; Li et al., 2009; Huang et al., 2008). Although habitat fragmentation has had a dramatic hey can adapt to habitat fragmentation through shifts in their activity patterns and dietary choices (Huang et al., 2005; Zhou & Huang, 2021). Given the many differences between the species, rapid habitat changes, and increased human activity, it is critical to improve our understanding of how Francois' langur has adapted to this fragmented habitat. As previous studies have not focused on some of the highly representative geographical populations, we attempted to explore this aspect.

To better understand the feeding ecology and adaptation to extremely fragmented environments in Francois' langurs, the diet composition of wild Francois' langurs was investigated over 10 months in Encheng National Nature Reserve (ECNNR), which includes an extremely fragmented habitat in Southwest Guangxi, China. Firstly, the diets and their seasonal changes were determined. Secondly, the relationship between food composition and food availability was analyzed, and the feeding strategy of the Francois' langurs was determined. Finally, the flexibility of the foraging strategy of the langurs was examined. The hypotheses are as follows:

1) Fragments are often characterized by reduced food availability for primates due to changes in forest structure, including the reduction in the number of large trees and increases in the abundance of pioneer species, exotic species, and lianas (Zhu et al., 2004). We hypothesized that Francois' langurs eat fewer food species and more lianas in extremely fragmented habitats due to lower food diversity.

2) Primates prefer fruits and young leaves and are affected by seasonal fluctuations in food resources (Tsuji et al., 2013). Thus, we hypothesized that during the dry season, Francois' langurs consume fewer young leaves and more alternative type foods, e.g., insects, mature leaves, and flowers, and that the consumption of fruits and young leaves increases with their availability.

3) When preferred foods are scarce, primates usually consume fallback foods (Marshall & Wrangham, 2007). Primates in tropical monsoon forests rely mainly on mature leaves and seeds as fallback foods (Zhang et al., 2017, 2021). Therefore, we predict that the consumption of fallback foods, especially mature leaves, is inversely proportional to the availability of their preferred foods.

2 Method

2.1 Study site and subject

The research was conducted on Francois' langur at ECNNR, Guangxi Province, China (22deg36'32"–22deg49'53"N, 106deg58'12"–107deg15'45"E; Figure 1). The main study site was a 258.196 km² karst hill, which is located at an elevation of 300 to 700 m above sea level. From July 2019 to June 2020, the mean minimum and maximum temperatures were approximately 10.22 and 34.28 degC, respectively (n = 10, the annual average temperature is 22.37 degC). The total annual precipitation at the site during the study period was 1,462.9 mm, with 83.2% of the rain falling between April and September (Figure 2). There was a dry (October to March) and wet season (April to September) based on the precipitation distribution. One group of Francois' langur was monitored, which was composed of six individuals (two adult males and four adult females) at the beginning of the study period and increased to eight individuals due to the birth of two infants by the end of the study period.



FIGURE 1 Location of the study site, Enchang National Nature Reserve



FIGURE 2 Monthly average temperature (maximum [Tmax] and minimum [Tmin]) and rainfall at the main study site

2.2 Vegetation characterization and phenology

The forest in the ECNNR was divided into four habitat types: cliff face, slope, mountain peak, and valleyfloor flatland. These habitats were analyzed using stratified random sampling methods. We sampled 18 plots $(20 \times 20 \text{ m})$ within the main study site, including four plots that were located in the valley-floor flatland, nine on slopes, two on cliff faces, and three on mountain peaks. These plots were located in the core area of the langurs' home range, which included more than 4% of the langurs' annual home range (unpublished data). Within these plots, all the trees with a [?] 3 cm diameter at breast height (DBH) were tagged. In addition, to evaluate the dominance of each species within a plot, the re each lative density (RD), relative frequency (RF), and relative coverage (RC) were calculated for species as follows (Burton et al., 2005):

RD = number of individuals of the species *i* /total number of individuals in all the plots;

- RF = number of plots with the species i/ total number of plots;
- RC = sum of the basal area of species i / sum of the basal areas of all the species.

Based on previous studies of langurs (Zhou et al., 2006) and our two-month pilot study, 32 plant food species were selected for phenology monitoring. Then, 10 individuals of each species were randomly selected and tagged in the main study area, and a total of 320 trees were monitored. In addition, the data from the vegetation surveys and plant phenology were combined to obtain appropriate estimates of food availability. During the monthly phenology surveys, all the tagged trees were visually inspected for the presence of young leaves, flowers, and fruit, and their abundance (% of crown cover) was scored with a five-point scale: 0, absent; 1, 0.1–25%; 2, 25.1–50%; 3, 50.1–75%; and 4, 75.1–100%. The monthly food availability index (FAI) was calculated for the main food items (young leaves, flowers, and fruits) by integrating the density, basal area, and phenology score of the plant species. The formula was as follows:

$FAI = \sum_{i=1}^{n} D_i B_i P_i,$

where Di is the density of the tree species *i* (number of stems/ha), Bi is the average basal area of tree species $i(m^2/ha)$, and Pi is the mean phenology score of the particular food item in the crown of species *i* in a given month (Albert et al., 2013).

2.3 Field data collection

Behavioral data of the target langur group were collected for a full day and many other partial days throughout the study. During each full-day follow, the observations were recorded from when the monkeys left their sleeping sites to when they reentered their sleeping sites at the end of the day. During each partial-day follow, the data collection began when we first encountered the focal group and ended when they disappeared for over 30 min or entered a sleeping site.

The food items eaten (part and species) were recorded during instantaneous scan samples of 5 min with an interval of 15 min. During each scan, to avoid sampling bias toward certain individuals, the diet data were recorded for as many individuals as possible. If an individual was holding, chewing, or processing a food item, this was considered to be a feeding behavior. Additionally, the plant species that were eaten by the monkeys were recorded via *ad libitum* sampling; these records were used in a food species list but not for assessing the contributions to the monthly diet.

2.4 Data analysis

The percentages of the different plant species in the diet of each study group were calculated using the total feeding records. Similarly, the percentages of the different plant parts in the monthly diet of each study group were calculated using the monthly total feeding records. The Shannon-Wiener index was used to compare the food diversity index (FDI) of the langurs. The formula was as follows:

$FDI = H' = \sum_{i=1}^{n} P_i \operatorname{Ln} P_i$

where H' is the Shannon-Wiener diversity index, and P_i is the percentage of the feeding records of the plant species i. Similarly, the diet composition was expressed as the percentage of the feeding time spent on specific food items or food species. Generalized linear mixed models (GLMMs) were used to examine the influence of season on the diet. Specifically, the number of food species per month and diversity index were tested as the response variables, the seasons were set as fixed factors, and the sample size was set as a random factor. Season was considered a key factor when it influenced the goodness-of-fit of the model and the p-value was lower than 0.05, which indicated a significant difference in the diet between the dry and rainy seasons.

Then, generalized linear models were constructed to examine the influence of ecological factors on the FAI. diet, and dietary diversity. The monthly food availability (including young leaves, flowers, fruits, and mature leaves) was set as the response variable, and climatic factors (including rainfall and temperature) were set as explanatory variables to test the impact of climatic factors on food provision. Similarly, the monthly food species and diversity index was set as the response variable, and food availability (including young leaves, flowers, fruits, and mature leaves), climatic factors (including rainfall and temperature), and diet composition (including young leaves, flowers, fruits, and mature leaves) were set as explanatory variables to examine the influences of diet composition and ecological factors on the langurs' diet. The models considered all possible combinations of all the predictors (total ranked according to their Akaike information criterion [AIC] values). The relative importance of each predictor (Wip) was obtained by summing the Akaike weights for each model. The models with the lowest AIC values were considered to be the top models, and the models within two AIC units (ΔAIC [?] 2) of the top models were considered to be highly supported (Burnham & Anderson, 2002). Model-averaged regression coefficients (β) with 95% confidence intervals were used to estimate the effect of each predictor in the models, and the predictors in the highly supported models were determined to be the most important factors affecting the response variables when their 95% confidence intervals for the β -values did not overlap with zero (Xu et al., 2017).

To improve linearity and normality, the numeric variables, such as food availability, were $\log 10(X + 1)$ transformed (Xu et al., 2017), and the variables expressed in percentages, such as the feeding time, were $\log (X + 0.00001)$ -transformed because the raw data for the nonfood species were zero (Warton & Hui, 2011). In addition, Spearman's rank correlation was used to estimate the relationship among the variables. The normality of all the variables was examined using a one-sample Kolmogorov-Smirnov test. The GLMMs were performed using the lime4 package in R version 4.0.4 (R Core Team, 2021). The model averaging was performed using the dredge and model.avg function in the MuMIn package (Bartoń, 2019). All the analyses were conducted using R version 4.2.1. All the tests were two-tailed, with significance levels of 0.05 (R Core Team, 2023).

3 Results

3.1 Forest composition and food availability

In the vegetation plots, a total of 150 plant species from 46 families were recorded. The dominance value of the 10 most important tree species ranged from 0.06 to 1.09 (Table 1). The five most dominant species were *Delavaya toxocarpa* Franch., *Ficus virens* Aiton., *Bischofia javanica* Blume, *Pistacia weinmanniifolia* J. Poiss. ex Franch., and *Cipadessa cinerascens* (Pellegr.) Hand.-Mazz. Moreover, the 10 most dominant families were Fabaceae, Lauraceae, Euphorbiaceae, Rhamnaceae, Lauraceae, Rutaceae, Anacardiaceae, Annonaceae, Arecaceae, and Tiliaceae, which accounted for 60.67% of the total stems (range: 2.0–14.0%).

TABLE 1 The	top 10	species in	Encheng	National	Nature	Reserve,	China ^a
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Species	Family	Density (individuals/ha)	Mean DBH (cm)	Relative density
Delavaya toxocarpa	Sapindaceae	983.75	13.62	0.16
Ficus virens	Lauraceae	71.25	12.28	0.01
Bischofia javanica	Euphorbiaceae	47.5	18.09	0.01
Pistacia weinmannifolia	Anacardiaceae	208.75	13.43	0.03
Cipadessa cinerascens	Meliaceae	278.75	13.00	0.05
Ficus tinctoria	Lauraceae	48.75	12.56	0.01
Desmos chinensis	Annonaceae	202.5	9.50	0.03

Species	Family	Density (individuals/ha)	Mean DBH (cm)	Relative density
Hainania trichosperma	Tiliaceae	133.75	10.71	0.02
Caesalpinia sinensis	Fabaceae	463.75	12.52	0.08
Flueggea virosa	Euphorbiaceae	73.75	12.29	0.01
^a Ranked by Dominance	^a Ranked by Dor			

The production of young leaves, fruits, and flowers varied considerably among the months (P < 0.05). The minimum availability of the mature leaves and fruits occurred in April and January, respectively. The maximum availability of the young leaves, flowers, and fruits occurred during the rainy season, which was April, June, and September, respectively (Figure 3). The phenology also changed significantly between the seasons. In the dry season, the FAI of the young leaves and flowers was significantly lower than that in the rainy season (YL: $\chi^2 = 10.80$, P < 0.05, FL: $\chi^2 = 7.51$, P < 0.01). However, there was no significant change in the availability of the fruits and mature leaves (FR: $\chi^2 = 2.48$, P = 0.12, MF: $\chi^2 = 2.04$, P = 0.15). Furthermore, a significant positive relationship was documented between the abundance of young leaves and rainfall ($\beta = 0.382$, Wip = 0.98). Similarly, there was a significant positive relationship between the abundance of flowers and rainfall ($\beta = 0.274$, Wip = 0.80).



FIGURE 3 Monthly availability of the mature leaves, young leaves, fruits, and flowers in the main study area in Encheng National Nature Reserve

3.2 Overall diet and seasonal variations

During the study, the langurs consumed 101 plant species from 43 families. Among the 101 identified tree species, 58.26% were trees (n = 67), and 2.61% were herbaceous (n = 3), accounting for 66.13% and 1.19% of the foraging records, respectively. Additionally, the langurs consumed 29 species of lianas, accounting for 22.66% of the diet and six of the top 20 species consumed. Furthermore, the langurs consumed two species of parasitic plants, accounting for 7.39% of the diet and two of the top 20 species consumed. The langurs also ate nest material, a food that has not been recorded in other studies, accounting for about 0.29% of the total foraging record (n = 2249). In addition, at least one insect was eaten (n = 2249, 0.04%; Table 2).

Each month, the langur group consumed between 24 species (April) and 49 species (January), with a monthly average of 38 (standard deviation [SD] 6.64; Table 2). The monthly dietary diversity varied from 2.2 (August) to 3.4 (January), with an average of 3.08 (SD 0.35; Table 2). Additionally, the monthly dietary diversity and the number of food species that were consumed varied seasonally during the study period (species number: $\chi^2 = 6.33$, P < 0.05; dietary diversity: $\chi^2 = 3.52$, P < 0.05). The langurs consumed more species and obtained a higher dietary diversity in the dry season than in the rainy season.

									Number of	Food diver-
	Dietary	Dietary	Dietary	Dietary	Dietary	Dietary	Dietary	Dietary	food	sity
Month	composit	ioncomposit	ioncomposit	ioncomposit	ioncomposit	ioncomposit	ioncomposit	ioncompositi	orspecies	index
	Young	Mature	Flowers	Fruits	Seed	Barks	Stems	Others		
	Leaves	Leaves								
Jul-19	87.2	3.3	2.5	1.7	0.0	0.0	4.6	0.8	39.0	3.3
Aug	47.4	0.0	0.8	51.0	0.0	0.0	0.5	0.3	37.0	2.2
Sep	64.7	1.6	6.5	21.2	0.0	0.0	5.4	0.5	34.0	3.1
Oct	19.8	45.5	4.8	16.6	4.8	1.1	3.7	3.7	40.0	3.1
Nov	22.9	42.2	5.5	20.6	3.2	0.0	5.1	0.5	41.0	3.4
Dec	21.7	50.2	5.1	13.4	4.7	0.4	4.7	0.0	46.0	3.4
Jan-	30.6	53.3	1.3	5.9	3.6	2.0	1.0	2.3	49.0	3.4
20										
Apr	73.3	0.0	6.2	10.6	0.0	1.9	8.1	0.0	24.0	2.7
May	72.4	3.9	1.8	15.9	0.0	0.0	6.0	0.0	36.0	3.2
Jun	70.8	0.9	22.3	2.2	0.0	0.0	3.9	0.0	33.0	3.0
Annual	51.1	20.1	5.7	15.9	1.6	0.5	4.3	0.8	37.9	3.1
mean	05.0	24.0		14.0		0.0		1.0	0.0	0.4
SD	25.6	24.0	6.2	14.2	2.2	0.8	2.2	1.2	6.6	0.4
Dry-	23.7	47.8	4.2	14.1	4.1	0.9	3.6	1.6	28.4	2.4
season										
mean			1.0	6.0		0.0	1.0		110	
SD	4.7	4.9	1.9	6.2	0.8	0.9	1.8	1.7	14.6	1.4
Rainy-	69.3	1.6	6.7	17.1	0.0	0.3	4.7	0.3	26.1	2.2
season										
mean										
SD	13.0	1.7	8.0	18.3	0.0	0.8	2.5	0.3	12.7	1.1

TABLE 2 Monthly percentages of the feeding records for the different plant parts, number of food species, and food diversity of the study group

Fifteen species of plants, including *Ficus concinna* (Miq.) Miq., *Cuscuta chinensis* Lam., and *Boniodendron* minus(Hemsl.) T. C. Chen, were consumed in large quantities throughout the year, accounting for 61.29% of the total records and being the main food of François' langur. Eight species of plants, including *Taxillus* sutchuenensis (Lecomte) Danser, *Henslowia frutescens* Benth., and *Apodytes dimidiate* E.Mey. ex Arn., contributed to a relatively high proportion of the annual feeding records (more than 1%) but were only consumed by the langurs for a few months. For the parasitic vines, the proportion of the annual foraging records was relatively high (1.68%), especially in January, accounting for up to 12.93% of the monthly foraging records. In addition, plants, such as *Ligustrum lucidum* W. T. Aiton and *Cinnamomum burmanni* (Nees & T.Nees) Blume, were only sporadically recorded throughout the year and were often rare.

There was no significant correlation between the consumption of the food species and the mature leaves, flowers, and abundance of mature leaves and flowers (mature leaves: $\beta = 0.03$, Wip = 0.68; flowers: $\beta =$ -0.102, Wip = 1.00; FAI of mature leaves: $\beta = 2.52$, Wip = 1.00; FAI of fruits: $\beta = -0.28$, Wip = 1.00), and there was no significant correlation between the consumption of food species and the dietary composition and ecological factors (Table 3). There was also no significant correlation between the dietary diversity and the mature leaves (mature leaves: $\beta = 0.02$, Wip = 0.52), and there was no significant correlation between the consumption of the food species and the dietary composition and ecological factors (Table 3).

TABLE 3 Effect of diet composition and ecological factors on the number of food species and

dietary diversity of the langurs in Encheng National Nature Reserve based on the results of the model averaging

Variables

(Intercept)
Mature leaves
Young leaves
Flowers
Friuts
(Intercept)
FAI(Mature leaves)
FAI(Young leaves)
FAI(Flowers)
FAI(Friuts)
Rainfall
Taverage
β , model-averaged regression coefficients; 2.5%CI/97.5%CI, the 95% confidence intervals of regression coefficients β · Wip, regression coefficients (β · Wip, regression coefficients)

Using all the records in which the food types were confirmed (n = 2249), the diet of the study group consisted of slightly more leaves than fruit. Leaves accounted for about 67.7% of the food eaten by the langurs (young leaves 43.9%; mature leaves 23.8%). Fruits and flowers constituted 24.93% of the diet (20.74% fruits and 4.19% flowers), stems and seeds accounted for 6.1% of the diet (4.0 and 2.1%, respectively), and bark and other plant parts constituted 0.24% and 0.97%, respectively (Table 2). Notably, the stems that the langurs consumed were almost all dodder, a parasitic plant. The langurs were very fond of feeding on all the components of the dodder, especially the stems (Yao Wei, personal observation).

There was significant seasonal variation in the types of foods that the langurs consumed most frequently. They are significantly more mature leaves and seeds and fewer young leaves in the dry season than in the rainy season (mature leaves: $\chi^2 = 6.51$, P < 0.05; young leaves: $\chi^2 = 22.45$, P < 0.01; seeds: $\chi^2 = 68.67$, P < 0.01). The mature leaf consumption was negatively correlated ($\beta = -8.68$, Wip = 0.39) with the abundance of fruits, and the young leaf consumption was positively correlated ($\beta = 4.76$, Wip = 0.15) with the abundance of young leaves. The flower consumption was positively correlated with the abundance of flowers and fruits (FAI of the flowers: $\beta = 3.28$, Wip = 1.00; FAI of the fruits: $\beta = 2.67$, Wip = 1.00; Table 4).

TABLE 4 Effect of the ecological factors on the diet composition of the langurs in EnchangNational Nature Reserve based on the results of the model averaging

Variables

(Intercept) FAI(Mature leaves) FAI(Young leaves) FAI(Flowers) FAI(Friuts) Rainfall Taverage Variables

(Intercept) FAI(Mature leaves)

Variables		
FAI(Young leaves)		
FAI(Flowers)		
FAI(Friuts)		
Rainfall		
Taverage		
β , model-averaged regres	ssion coefficients; 2.5% CI/97.5%CI, the 95% confidence intervals of regression coefficients β ·Wi	p, re

3.3 Food choice

The langurs showed significant selectivity in their diet composition throughout the year. Among the 115 food species (including three non-plant components and 11 plants whose species names could not be identified) that François' langur consumed throughout the year, only 23 plants (20%) accounted for more than 1% of the total foraging records but contributed to 72.99% of the foraging records. Among the 23 species of plants, *Ficus concinna, Cuscuta chinensis, Boniodendron minus, Pittosporum pulchrum* Gagnep., *Flueggea virosa* (Roxb. ex Willd.) Royle, *Pithecellobium clypearia* (Jack) Benth., *Pericampylus glaucus* (Lam.) Merr., *Vitex kwangsiensis* C. Pei, *Cudrania cochinchinensis*(Lour.) Yakuro Kudo & Masam., and *Erythropalum scandens* Blume were among the top 10, contributing to 49.06% of the foraging records.

The François' langurs did not consume plants within each family evenly. They used 68 (45.3%) of the 150 plant species marked by the vegetation surveys in the overall foraging record, which accounted for 89.04% of the total foraging record (Table 5). Among the top ten tree species in the vegetation surveys, only *Flueggea virosa* accounted for more than 2% of the total foraging records. The correlation analysis showed that there was no significant correlation between the foraging ratio and relative density of these 68 plants (Spearman Rank Correlation Coefficient rs = 0.146, n = 68, P > 0.05), indicating that there was no strong correlation between the François' langur's food choice and the number of plants in the environment.

TABLE 5 The top 10 food species, plant parts, and selection ratios for François' langur (n = 10 months) from July 2019 to June 2020 in the Encheng National Nature Reserve, China

Species
Ficus concinna
Cuscuta chinensis
Boniodendron minus
Pittosporum pulchrum
Flueggea virosa
Pithecellobium clypearia
Pericampylus glaucus
Vitex kwangsiensis
Cudrania cochinchinensis
Erythropalum scandens
^a Plant type: T,tree; H,herb; V,vine; E, Parasitic plants. ^b Parts eaten: YL,young leaves; ML,mature leaves; FL,flowers; FR

4 Discussion

Our results provide new evidence of the underexplored dietary ecology of François' langurs in the fragmented limestone habitat. By documenting the foraging data from unique geographical populations using instantaneous scanning sampling methods, we qualitatively assessed the flexibility and adaptability of François' langurs. The data revealed that the François' langurs' diet has a high degree of flexibility with seasonal variations, which could be advantageous for adapting to current habitat changes. In addition, the François' langurs' diet showed a high degree of selectivity, suggesting that their diet was highly dependent on important species in the habitat.

4.1 Dietary characteristics of the fragmented limestone-living François' langur

Species foraging strategies are closely related to their behavior and ecological plasticity. The same species may adopt different foraging strategies in response to different habitats, which helps them adapt to changes in habitat quality due to different natural or anthropogenic disturbances. In this study, the Francois' langur ate 101 plant species. When compared with three other different geographical populations of similar latitude and climatic conditions, the langurs living in ECNNR feed on more plant species (Nonggang: 84 species/90 species; Fusui: 56 species/51 species, Table 6), and their diet had a high diversity (3.08). This result did not support our first hypothesis. Previous studies have shown that there are significant differences in the diet of the different geographical populations of François' langurs, and this difference is likely related to the local vegetation composition (Li et al., 2016). The results of this study support this finding. High-quality habitat often means more food variety but it can also result in a high abundance of a single plant species. Animals can adjust their diet according to their food preferences and consume more of their preferred plant species. This has been confirmed in other studies of colobus monkeys, where only some of the species are consumed despite the high diversity of the plant species in the forests. Similar conclusions have been found for other langurs; for instance, white-headed langurs (Trachypithecus leucocephalus Tan, 1957) selectively use some plants in their habitat (Zhang et al., 2017). However, when the number of preferred foods is insufficient, monkeys can expand their diets and eat more alternative foods to overcome the lack of their preferred foods (Zhou & Huang, 2021). The high level of food diversity in the ECNNR may also be evidence of this strategy. According to the vegetation survey, the diversity of the plant species in the study area reached 145 species/ha (DBH [?] 5 cm). This is much larger than the abundance in Fusui of 70 species/ha (DBH [?] 1.2 cm; Li et al., 2015). Thus, even though the habitats are extremely fragmented, many of the fragmented habitats may act as safe havens, where relatively rich vegetation conditions are preserved locally. This provides an adequate food source for the langurs. This suggests that Francois' langurs not only have a wide dietary composition but can also adjust their dietary composition according to the differences in the plant species in the habitat, and foraging flexibility is one of the important reasons for their survival in various habitats (Garber et al., 2009; Chaves & Bicca-Marques, 2013).

TABLE 6 The number of plant species in the different sites that were consumed by the four geographic populations of Francois' langur

Site								
NG								
NG								
FS								
EC								
L: leaves; YL: You	ing leaves; ML:	Mature leaves;	FR: Fruits; I	FL: Flowers; S	SD: Seed; ST	: Stem; P: I	Petiole; O:	Other; T: Tre

4.2 Dietary response to phenology change

The quantity and quality of food resources are not always evenly distributed in space and time (Fryxell, 1991). Seasonal changes in temperature and precipitation often result in changes in primate foraging strategies by altering the availability of food resources (Oates, 1987). In this study, François' langurs expanded their food intake in the dry season (dry season: 44 species; rainy season: 33 species), which effectively alleviated the foraging pressure caused by food scarcity. This may be a coping strategy for François' langurs when there is food scarcity. Therefore, François' langurs broaden the richness of their diet by increasing the food diversity and food variety to get enough food. This finding is consistent with other studies (Li et al., 2003). For instance, Luo (2000) found that in the Mayanghe area of Guizhou, the François' langurs fed on more food

species in the spring and autumn (42 species) than in the winter and summer (24 species). In the Nonggang area of Guangxi, François' langurs also increased the number of foraging plant species during the dry season to cope with the lack of their preferred food (Zhou et al., 2006). Additionally, in the Chongzuo region of Guangxi, white-headed langurs increased their intake of plant species during the dry season (Zhou & Huang, 2021), while in Malaysia, *Presbytis femoralis* fed on more types of food during the food shortage season (Bennett, 1983). This trait was also seen in other food-eating primates, such as *Lophocebus albigena*, which increased their food diversity during the months when the fruit abundance was lower (John et al., 2001). These studies all supported the suggestion that primates can survive periods of food scarcity by adjusting the food diversity of their diet.

François' langurs also survive long dry seasons by adjusting their food composition (Zhou et al., 2018). The results of this study showed that the François' langurs increased their feeding on mature leaves when the feed intake of the young leaves decreased during the dry season when compared with that during the rainy season, and most of the seed and bark records occurred in the dry season (seed: 100%, bark: 85.6%). This was supported by other studies. According to Zhou et al. (2006), during the dry season when the food was scarce, the Nonggang François' langur consumed mature and young leaves as an alternative food to solely young leaves. In Fusui, Li et al. (2009) found that François' langurs also increased their intake of mature leaves in the dry season. In Chongzuo, Guangxi, white-headed langurs fed on more young leaves during the dry season but increased their intake of mature leaves (Li & Rogers, 2006). On the island of Kaba in Vietnam, Kaba langurs (*Trachypithecus delacouri* (Osgood, 1932)) consumed more leaves during the dry season and correspondingly reduced their fruit intake (Workman, 2010). Moreover, the long-tailed langur (*Semnopithecus entellus* (Dufresne, 1797)) in the Kanha region of India will eat mature leaves in large quantities when there is a shortage of young leaves, fruits, and flowers (Newton, 1992).

4.3 Food choice

Previous studies have shown that primates are selective about the types and components of their food. including the selection of plant species and food portions (Zhou et al., 2018). This selectivity is influenced by factors, such as the quality and quantity of food (e.g., nutrients, cellulose, mineral elements, secondary toxicants, and food availability) and water content (Zhou et al., 2021). The findings of this study were consistent with previous studies, and the Encheng Francois' langur had obvious food selectivity. However, food selection is not strictly based on the number of plants in the habitat. In this study, 72.99% of the total foraging records of the François' langurs consisted of 23 plant species. They used 68 of the 150 plant species marked by the vegetation surveys in the overall foraging record, which accounted for 89.04% of the total foraging record. The top 10 tree species in the vegetation survey included Pittosporum pulchrum and Vitex kwangsiensis, which accounted for more than 2% of the total foraging records. This was similar to the findings of other studies. In the Van Long Nature Reserve in Vietnam, the 10 most commonly consumed plants by Trachypithecus delacouri accounted for 82% of the total foraging records (Workman, 2010). In Madhupur, Bangladesh, the caped langur (Trachypithecus pileatus (Blyth, 1843)) feeds on only 35 species of trees and vines during the year (John et al., 2001). In Sri Lanka, long-tailed langurs used a total of 43 plant species, of which 70% of their food consisted of 10 species, none of which were dominant species (Newton, 1992). In the Kuala Lumpur area, 45% of the diet of the black-crowned langur consists of five plant species, which make up only 9.6% of the forest tree species (Bennett, 1983). François' langurs and white-headed langurs showed selectivity in the plant species they ate, and the 10 plants that were most consumed accounted for 51%-90%of the food composition (Zhou & Huang, 2021). In summary, François' langurs living in the ECNNR have similar feeding behaviors to other primates, their choice of food is independent of the number of plant species in the habitat, and the most common tree species in the habitat are only consumed in a small amount.

Overall, we found the François' langurs in the fragmented limestone forest in southwest China had a similar feeding ecology to other François' langurs in distinct habitats. However, there were also some differences. The langurs in this study ate a higher number of food species throughout the year when compared with other species, maintained a high level of food diversity, and ate more vines. These François' langurs might have a slightly different feeding strategy than the other François' langur populations, although we suspect that these

dietary differences are mainly due to environmental conditions. We concluded that François' langurs exhibit a flexible feeding strategy, and thus they are an ecological generalist that inhabits fragmented limestone forests. Further research is needed to better understand the langurs' feeding ecology, especially in southwest China.

CRediT authorship contribution statement

Qi-Hai Zhou and Peng-Lai Fan conceived the ideas and designed methodology; Wei Yao, Jia-Xin Zhao, Rong Huang, Wen-Hua Li collected the data; Wei Yao and Cheng-Ming Huang analysed the data and wrote the manuscript. All authors contributed critically to the draft and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data that support the findings of this study are openly available in the zenodo Repository at https://doi.org/10.5281/zenodo.10597573.

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