Diet and Food Choice of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China

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We studied the diet and food choice of 1 group of François' langurs (Trachypithecus francoisi) *from August 2003 to July 2004 in the Nonggang Nature Reserve, Guangxi province, China. The langurs consumed 90 plant species, including 14 unidentified species. Leaves constituted 52.8% of the diet (38.9% young leaves and 13.9% mature leaves). Fruits and seeds accounted for 17.2% and 14.2%, respectively. Flowers and other items— including petioles, stems, roots, and bark—contributed to 7.5% and 7.4% of the diet, respectively. The langur diet varied according to season. They fed on more young leaves from April to September. Consumption of seeds, petioles, and stems increased between October and March, when young leaves were scarce. The diet shift corresponded to higher dietary diversity during the young leaf-lean period. Though the langurs fed on many plant species, 10 species accounted for 62.2% of the diet, only 2 of which were among the 10 most common tree species in vegetation quadrants, and the percentage of feeding records on a plant species and the percentage of individuals of the species in vegetation quadrants does not correlate significantly. François' langurs fed selectively, and they did not base their diet simply on the abundance of plant species in the habitat.*

KEY WORDS: diet; food choice; François' langur; phenology; *Trachypithecus francoisi*.

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INTRODUCTION

Colobines are primarily folivorous, but fruits and seeds also contribute to a large proportion of the diet in the majority of colobine species (Oates, 1994; Yeager and Kool, 2000). For example, in lowland dipterocarp forest at Kuala Lompat in central Peninsular Malaysia, fruits and seeds accounted for 46% of the diet of *Presbytis melalophos* (Bennett, 1983). Colobine diets also show seasonal variations in response to changes in the abundance, quality, or distribution of important food resources. They feed on more low-quality, subsistence foods, such as mature leaves, when high-quality foods, such as fruits and young leaves, are scarce. They also increase dietary diversity during the lean period for high-quality foods (Bennett, 1983; Davies, 1991; Hladik, 1977; Newton, 1992).

Colobines show food choice not only in plant parts, but also in plant species (Bennett and Davies, 1994; Oates, 1994). For example, despite substantial variation in the proportion of young leaves in colobine diets (*Colobus guereza*: 65% of the total diet, Oates, 1977; *Piliocolobus badius*: 52%, Marsh, 1981; *Semnopithecus entellus*: 15%, Newton, 1992; *Trachypithecus pileatus*: 16%, Stanford, 1991; *Presbytis melalophos*: 27%, Bennett, 1983; *T. leucocephalus*: 75%, Li *et al*., 2003), colobines prefer young leaves over mature leaves, though the latter are abundant in the habitat (Bennett and Davies, 1994; Oates, 1994). In terms of food species choice, 62% of the diet of white-headed langurs (*Trachypithecus leucocephalus*) in Fusui Reserve came from 10 of 50 food species (Li *et al*., 2003). Interspecific differences of food species choice also occurred (Bennett and Davies, 1994). For example, in Sri Lanka, 2 sympatric langurs, *Semnopithecus entellus* and *Trachypithecus vetulus*, differed in food species choice. Seventy percent of the diet of *Tracgypithecus vetulus* came from only 3 tree species, while 10 out of a total of 43 species eaten provided 70% of the diet of *Semnopithecus entellus* (Hladik, 1977).

François' langur (*Trachypithecus francoisi*) is one of the least studied colobine species. They live in habitat characterized by karst topography. White-headed langurs, a close phylogenetic relative (Zhang and Ryder, 1998), also lives in a similar habitat (Huang *et al*., 2002; Li, 2000). Researchers have reported the distribution of François' langurs, their habitat, and general ecology (Huang and Huang, 1983; Li, 1993; Wu, 1983), but very little quantitative information is available concerning their diet, which is important for understanding the biology of the species and their adaptation to karst topography. We also provide important comparative information for the general study of dietary adaptation in the Colobinae.

We present quantitative data on the diet and food choice of François' langurs. We first summarize data on dietary composition, then describe

seasonal changes in the diet and diversity, and examine how seasonal changes in the availability of plant parts of interest influence the diet and diversity. Finally, we explore the relationship between food choice and floristic composition.

METHODS

Study Site

We conducted the study in the Nonggang Nature Reserve (106°42′107°4′E, 22°13′–22°33′N), Guangxi Province, China, which consists of 3 areas—Nonggang (5426 ha), Longhu (1034 ha), and Longshan (3949 ha)—separated by farmlands and villages. Our research site lies in the northwestern portion of Nonggang, and the main study area is *ca.* 200 ha. The habitat is characterized as limestone seasonal rain forest (Shu *et al.*, 1988). The habitat comprises dense limestone hills and flat lands, with altitudes of 300–700 m above sea level (Den, 1988). Around the research site, small-scale agriculture occurs, and grazing pressure from livestock (cattle) is still high.

We collected climatic data, including rainfall and maximum and minimum temperatures, daily from August 2003 to July 2004 (Fig. 1). The
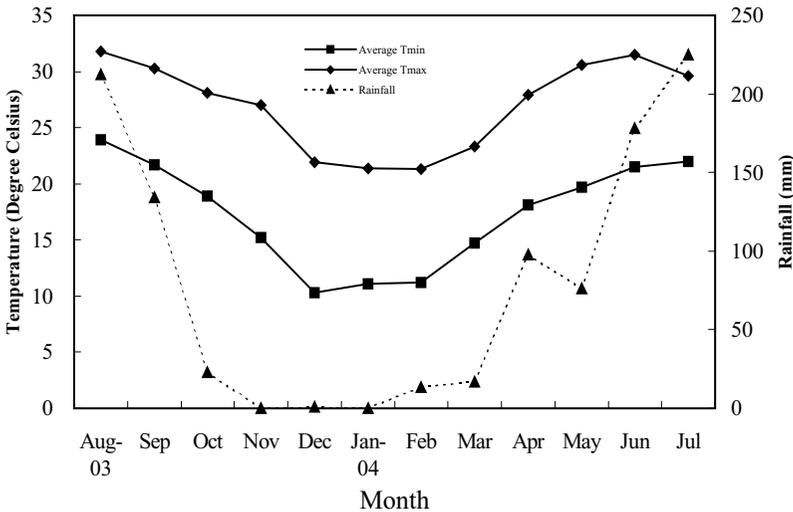

Fig. 1. Monthly average temperature (maximum and minimum) and rainfall in the Nonggang Nature Reserve between August 2003 and July 2004.

total rainfall was 977 mm. There were 2 seasons: a dry season from October 2003 to March 2004 with <50 mm monthly rainfall and a rainy season in the remainder of the year with >50 mm monthly rainfall. Mean annual temperature was 22° C, ranging from a mean monthly minimum of 10° C in December 2003 to a mean monthly maximum of 32° C in August 2003.

Study Groups

Two groups of langurs inhabited the study area. Group 1 consisted of 12 individuals (4 adult males, 5 adult females, and 3 immatures) at the start of our study, but declined to 10 individuals by the end, owing to the disappearance of an adult female and her infant. Group 2 comprised 10 individuals (7 adults and 3 immatures). Because of temporal and logistic constraints, we could not determine the sex ratio of group 2. Group 1 ranged nearest to our camp and was semihabituated to observers at the onset of detailed behavioral data collection. Thus, we collected behavioral data only on them.

Ecological Sampling

We set up 13 (50 m × 10 m) vegetation quadrants: 4 at the valley basins and 9 on the hillsides. We determined the locations of the quadrants by vegetation types (Shu *et al.*, 1988), and the quadrants covered most of the vegetation types in the study area. Within the quadrants, we tagged all trees with ≥ 5 cm diameter at breast height (DBH). We collected plant specimens in the field with the help of a local assistant and later identified in the Guangxi Institute of Botany, Chinese Academy of Sciences (Guilin, Guangxi). We recorded the circumference at breast height (CBH) of each tagged tree and converted it to diameter, which we used to calculate the basal area. We calculated the relative density, relative frequency, and relative coverage for each species in the vegetation quadrants by the following formulae:

Relative density = number of stems of species *i*/total number of stems in all quadrants;
Relative frequency = number of quadrants of species *i*/total number of quadrants; and
Relative coverage = sum of basal areas of species *i*/sum of basal areas of all species.

To examine the relative abundance and size of each species in vegetation quadrants, we calculated the dominance of each species via relative density + relative frequency + relative coverage (Brower *et al*., 1990).

We collected phenological data from the vegetation quadrants. We checked all tagged trees ($n = 312$) by visual inspection at monthly intervals for the presence of young leaves, fruit, and flowers from August 2003 to July 2004 and used the data to calculate a tree index, expressed simply as the percentage of trees bearing the plant parts of interest each month, regardless of the size of the canopy. Though the method cannot reflect the real abundance of food resources, it provides an estimate of food availability (Britt *et al.*, 2002; Estrada *et al.*, 1999).

Behavioral Data Collection

We collected dietary and behavioral data for an average of 10 d of each month between August 2003 and July 2004. Each day we observed the langurs via binoculars (10×60) at a distance of 10–200 m. Observation began when we first encountered the focal study group or at 0600 h, if we could locate the subjects' sleeping site in the previous evening, and ended when the langurs entered the sleeping site. We made few observations in July 2004 because many places were flooded, and used only 11 mo of data for analysis in the study. Because the langurs often hid in dense vegetation during midday or moved to places where observers could not follow them, we could not conduct full-day consecutive behavior sampling on many observation days. We collected a total of 739 h of behavioral data.

On each day of observations, we collected behavioral data via instantaneous 5-min scan sampling (Altmann, 1974) at 15-min intervals. During a scan, we recorded the age, sex class (adult male, adult female, and immature), and activity of each individual. We watched each individual for 5 s after we detected it, and recorded the predominant activity during the interval. To avoid sampling bias toward certain individuals or a particular age-sex class, we collected behavioral records on as many different individuals as possible during a scan to include all individuals in the focal group but sampled no individual more than once. Some individuals, hid in dense vegetation; thus, we could sample only a fraction of the group during most scans (mean $= 4.2$, SD $= 2.29$, range $= 1$ to 10, $n = 2961$).

We divided activities into 6 general categories: feeding, resting, moving, grooming, playing, and other. We defined feeding as manually or orally handling a food item, and bringing it into the mouth. We recorded plant species and parts eaten, including leaves, fruit, flowers, seeds, stems, petioles, roots, and bark. We also tried to distinguish between young and mature leaves and fruits. When we could not discern the food items, we scored them as unknown. We marked all food species and collected specimens for later identification.

Data Analysis

We determined the percentage of different food items in the monthly diet of the study group by calculating the percentage of feeding records devoted to them among monthly total feeding records. We obtained annual dietary composition by averaging the monthly percentages. The method may result in not entirely independent data, but researchers still commonly use it in determining colobine diets (Li *et al.*, 2003; Oates, 1977; Stanford, 1991; Struhsaker, 1978), which allows comparisons with other colobine studies.

To examine seasonal variation in dietary diversity, we used the Shannon-Weaver diversity index, calculated as follows:

$$H' = \sum P_i \times \ln P_i$$

where in P_i is the proportion of feeding records of the ith plant species. To explore the food species selection, we calculated the selection index (S-index) (Clutton-Brock, 1977; Li *et al.*, 2003; Nunes, 1998), using the ratio of the percentage of feeding records to the percentage of individuals of the species in vegetation quadrants. We used Mann-Whitney's U test to compare the monthly average of the percentage of feeding records for various food items and the number of food species from 5 rainy season months vs. the 6 dry season months. We used the Spearman rank correlation coefficient test to test the correlations between various variables (Dytham, 1999).

RESULTS

Forest Composition and Phenology

There were 312 trees with ≥ 5 cm DBH within the 13 vegetation quadrants, comprising 56 tree species belonging to 37 genera from 30 families. The 10 most dominant tree species within the quadrants (Table I) account for 57.6% of the total individual trees, but made up only 17.9% of the total number of tree species. The most dominant family, Euphorbiaceae, comprised 38.1% of the total number of individuals.

Availability of young leaves peaked in April and May 2004. Fruit production was highest in September 2003 and June 2004. The highest level of flower availability occurred in March and May 2004 (Fig. 2). The availability of young leaves and fruit in the forest varied seasonally (Mann-Whitney U test $Z = -2.887$, $p < .01$ for young leaves, and $Z = -2.419$,

Table I. Frequency, density, and dominance of the 10 most dominant tree species found ≤ .65 ha of vegetation quadrants in main study area in the nonggang nature reserve[a]

Species	Family	Number	Density (individuals/ha)	Dominance
Deutzianthus tonkinensis	Euphorbiaceae	63	96.9	1.1638
Bischofia javanica	Euphorbiaceae	37	56.9	1.0325
Clausena anisum	Rutaceae	11	16.9	.5301
Cleistanthus saichikii	Euphorbiaceae	13	20.0	.5240
Litsea monopetala	Annonaceae	17	26.2	.4821
Pithecellobium clypearia	Mimosaceae	7	10.8	.4445
Ficus fistulosa	Moraceae	9	13.8	.4397
Dracontomelom duperreanum	Anacardiaceae	6	9.2	.4126
Burretiodendron hsienmu	Tiliaceae	10	15.4	.3576
Ficus microcarpa	Moraceae	7	10.8	.3422

[a]Species are in order of dominance.

$p < .05$ for fruit). Further, there are significant and positive relationships between rainfall and the availability of young leaves (Spearman rank correlation coefficient $r_s = .820$, $n = 12$, $p < .01$), and fruit ($r_s = .785$, $n = 12$, $p < .01$). Based on young leaf abundance, we defined a young leaf-lean period, and a young leaf-rich period, corresponding to the dry season and rainy season, respectively.
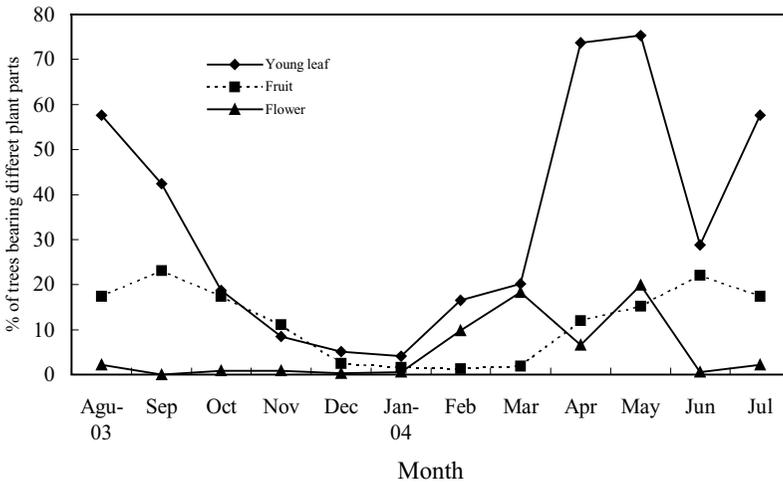

Fig. 2. Monthly availability of young leaves, fruit, and flowers in the Nonggang Nature Reserve between August 2003 and July 2004.

Overall Diet

We collected 3668 feeding records in total during the study period (Table II), of which there were 3372 records of identified food species and 3528 of identified food items. We identified 90 plant species as the food resources of *Trachypithecus francoisi* (Table III). Not counting 14 unidentified species, the foods included 70 genera from 43 families, with 61 species of trees, 24 species of vines, 4 species of herbs, and 1 species of epiphyte. Tree species account for 79.4% of all feeding records, vines for 18.1%, herbs for 1.2%, and epiphyte for 1.3%. The relationship between the cumulative number of food species eaten and observation time is in Fig. 3. The curve reached a clear plateau at the end of the study, suggesting that the list of food species in the langur diet was fairly complete.

Langurs are relatively folivorous, and their monthly diet comprises 52.8% leaves on average (Table II). Young and mature leaves account on average for 38.9% and 13.9% of monthly feeding records, respectively. Fruit consumption averages 17.2% of monthly feeding observations, and the majority of fruits in the diet come from only 4 plant species: *Ficus nervosa*, *F. microcarpa*, *Securidaca inappendiculata*, and *Tetrastigma cauliflorum*, which account for 82% of 607 fruit feeding records. Based on 552 fruit feeding records (91% of the total fruit feeding records) in which we could determine the fruit maturity, immature fruits account for 93.1%. Except for a few species, e.g., *Dracontomelom duperreanum*, of which only the fresh fruit pulp was ingested, individuals ingested most fruits, e.g. *Ficus nervoca*, entirely. Langurs fed on seeds almost exclusively from 4 plant species—*Pithecellobium clypearia*, *Bauhinia* sp., *Acacia pennata*, and *Wrightia pubescens* (99% of 638 seed feeding records). Monthly seed consumption averaged 14.2% of feeding records. The average monthly consumption of flowers was low, consisting of 7.5% of monthly feeding records. Other items—petioles, stems, roots, and bark—contributed to 7.4% of monthly feeding records on average.

On several occasions, we observed François' langurs licking rock surfaces in cliffs, possibly for minerals. Further, we often observed them closely inspecting rock surfaces and manually putting objects into their mouths. Perhaps they were foraging for small insects such as ants.

Seasonal Variation in Diet

The number of plant species that the langurs ate each month varied from 10 species in August 2003 to 47 species in March 2004, with an average of 22.5 species monthly (Table II). They consumed more plant species

Table II. Monthly number of food species, diversity index, percentage of feeding records devoted to different plant parts, and number of feeding records between August 2003 and June 2004

Month	No. species eaten	Diversity index	Young leaf	Mature leaf	Mature fruit	Immature fruit	Flower	Seed	Petiole	Stem	Root	Bark	Unkown	No. feeding records
Aug	10	1.5	70.5	18.7	0	6.6	4.2	0	0	0	0	0	0	165
Sept	17	2.3	56.5	14.6	0	24.6	4.3	0	0	0	0	0	0	321
Oct	18	2.2	27.9	9.3	0	34.9	17.0	9.6	0	0	0	0	1.0	344
Nov	25	2.5	19.5	14.2	3.0	26.0	4.7	20.4	7.0	2.4	0	0	3.6	374
Dec	29	2.6	5.0	29.6	2.7	11.0	0	39.4	6.5	5.4	0	0	.4	498
Jan	21	2.6	5.8	27.3	5.8	0	0	38.0	5.0	14.9	2.5	.8	0	126
Feb	34	2.5	11.1	14.3	.4	9.5	0	34.4	18.0	1.4	3.4	1.9	5.6	587
Mar	47	2.9	48.5	8.1	1.3	13.9	5.3	14.9	5.1	.8	1.6	.1	.4	769
Apr	19	2.3	71.6	4.7	0	5.5	14.4	0	3.8	0	0	0	0	236
May	16	2.2	58.8	10.6	0	20.0	10.6	0	0	0	0	0	0	180
June	11	2.1	52.2	1.5	0	23.9	22.4	0	0	0	0	0	0	68
Mean	22.5	2.3	38.9	13.9	1.2	16.0	7.5	14.2	4.1	2.3	.7	.3	1.0	333
SD	10.9	.4	25.6	8.7	1.9	10.7	7.6	16.4	5.4	4.5	1.2	.6	1.9	213

Table III. Plant species consumed by François' langurs in the Nonggang Nature Reserve between August 2003 and June 2004

Family	Species	Life[a] form	Part(s) eaten[b]	Number of month used	%(F)[c]	%(V)[c]	S-index[d]
Anacardiaceae	Brassaiopsis glomerulata	T	FR, U	3	1.18		
	Pistacia weinmannifolia	T	YL, ML	11	.88		
	Spondia lakonensis	T	FR, B	3	.39	.95	.43
	Dracontomelom duperreanum	T	FR	1	.18	1.90	.10
Annonaceae	Miliusa chunni	T	YL, ML, F	5	5.31	0.95	5.87
	Fissistigma glaucescens	V	YL	1	.06		
Apocynaceae	Wrightia pubescens	T	YL, ML, F, S	5	1.81	1.58	1.20
Araceae	Epipremnum pinnatum	V	P	1	.12		
Aristolochiaceae	Aristolochia kwangsiensis	V	ML	1	.03		
Asclepiadaceae	Hoya carnosa	T	S	2	.09		
Bambusoiceae	Indocalamus calcicolus	T	P	1	.03		
Begoniaceae	Begonia peltatifolia	H	R	3	.97		
Bignoniaceae	Orocylon indicum	T	YL	2	.15	.63	.25
Caesalpiniaceae	Bauhinia sp.	V	YL, S	4	4.59		
	Zenia insignis	T	YL	2	1.51	.32	5.00
	Bauhinia aurea	V	YL, ML	2	.09		
Caprifoliaceae	Lonicera confusa	V	YL	1	.27		
Convolvulaceae	Cuscuta chinensis	E	FR, F, ST	3	1.30		
	Argyreia capitata	V	YL, ST	2	.12		
Ebenaceae	Diospyros siderophyllus	T	YL, FR	5	1.15		
Euphorbiaceae	Bischofia javanica	T	YL	2	.18	11.71	.02
	Deutzianthus tonkinensis	T	YL	2	.12	19.94	.01
	Prosartema stellaris	T	ML	1	.09	.32	.30
Gnetaceae	Gnetum montanum	V	YL, ML, S	2	.54		
Gutticeae	Garcinia paucinervis	T	P	6	6.28	.32	20.81
Icacinaceae	Apodytes dimidiata	T	YL	4	1.33	.63	2.20
	Iodes ovalis	V	S	1	.18		
Lauraceae	Cinnamomum burmanni	T	F	1	.24	4.43	.06
	Cinnamomum saxatile	T	YL	1	.12	.63	.20
	Litsea monopetala	T	F	1	.03	5.38	.01
Linaceae	Tirpitzia ovoidea	T	YL, F	5	2.50		

Table III. Continued

Family	Species	Life[a] form	Part(s) eaten[b]	Number of month used	%(F)[c]	%(V)[c]	S-index[d]
Melastomaceae	*Memecylon scutellatum*	T	YL	1	.03		
Meliaceae	*Cipadessa cinerascens*	V	YL, FR	4	.51		
Menispermaceae	*Pericampylus glaucus*	V	YL	2	.60		
Mimosaceae	*Pithecellobium clypearia*	T	YL, ML, S	6	13.82	2.22	6.54
	Ormosia glaberrima	T	YL, ML, F	8	1.99	.63	3.30
	Acacia pennata	T	S	4	1.51		
	Albizia kalkora	T	ML	1	.12	.32	.40
Moraceae	*Ficus nervosa*	T	YL, ML, FR	11	9.72		
	Ficus microcarpa	T	YL, ML	4	5.46	2.22	2.59
	Ficus glaberrima	T	YL, ML, FR, P	6	2.14	1.58	1.42
	Cudrania cochinchinensis	T	YL, ML	5	1.45		
	Ficus sp.	T	YL	1	.24		
	Ficus fistulosa	T	YL	1	.24	2.85	.09
	Broussonetia papyrifera	T	ML, F	1	.09		
	Ficus sp.	T	YL	1	.06		
	Ficus sp.	T	YL	1	.06		
	Malaisia scandens	V	ML	1	.03		
Myrsinaceae	*Embelia scandens*	V	YL, ML	4	.72		
	Embelia subcoriacea	V	P	3	.15		
Myrtaceae	*Syzygium* sp	T	ML	1	.03		
Opiliaceae	*Urobotrya latisquama*	V	YL, ML, P	5	.54	.32	1.80
Orchidaceae	*Cymbidium pendulum*	H	U	1	.15		
	Dendrobium loddigesii	H	YL	1	.09		
Papilionaceae	*Pueraria thunbergiana*	V	YL, ML, S	5	.69		
	Bowringia callicarpa	V	YL	1	.12		
Pittosporaceae	*Pittosporum pulchrum*	T	YL	1	.33		
Polygalaceae	*Securidaca inappendiculata*	V	YL, ML, FR, U	4	5.19		
Rhamnaceae	*Sageretia theezans*	T	FR	1	.45		
	Zizyphus yunnanensis	T	ML	1	.06		
Rosaceae	*Pyrus calleryana*	T	YL	1	.09	.32	.30
Rubiaceae	*Canthium dicoccum*	T	YL, ML, F	9	3.41	.63	5.65
	Randia spinosa	T	YL, ML, FR	4	1.60	.63	2.65

Table III. Continued

Family	Species	Life[a] form	Part(s) eaten[b]	Number of month used	%(F)[c]	%(V)[c]	S-index[d]
	Paederia scandens	V	YL	1	.09		
	Adina racemosa	T	YL	1	.03		
Rutaceae	Zanthoxylum scandens	V	F	2	.30		
	Citrus grandis	T	YL	1	.12		
	Clausena emarginata	T	YL	1	.06		
Sapindaceae	Boniodendron minor	T	YL, ML	6	2.29	3.16	.76
	Dimocarpus longan	T	ML	1	.03	.95	.03
Sapotaceae	Sinosideroxylon pedunculatum	T	YL	5	5.94		
	Mastichodendron wightianum	T	YL	2	.06		
Sterculiaceae	Eriolaena kwangsiensis	T	YL	3	.51		
	Sterculialanceolata	T	YL	1	.03	.32	.10
Tiliaceae	Burretiodendron hsiennu	T	FR,F	3	1.27	3.16	.42
Umaceae	Celtis philippinensis	T	YL, ML	5	.33	.95	.35
Urticaceae	Maoutia puya	T	F	1	.06		
Verbenaceae	Vitex kwangsiensis	T	YL	1	.03		
Vitaceae	Tetrastigma cauliflorum	V	YL, FR, ST, P	4	2.08	3.80	.01
	Tetrastigma caudatum	V	ML,ST,P	3	.27		
	Species 1	V	YL, ML, F	4	.97		
	Species 2	T	YL, B	3	.78		
	Species 3	V	YL	2	.69		
	Species 4	V	ST	1	.15		
	Species 5	T	YL	2	.09		
	Species 6	T	F	1	.09		
	Species 7	V	ML, F	2	.06		
	Species 8	T	P	1	.03		
	Species 9	H	U	1	.03		
	Species 10	V	F	1	.03		

[a]Plant type: T = tree; V = vine; H = herb; E = epiphyte.
[b]Parts eaten: YL = young leaf; ML = mature leaf; FR = fruit; S = seed; F = flower; P = petiole; ST = stem; R = root; B = bark; U = unknown.
[c]%(F): percentage of total feeding records; %(V): percentage of individuals of each species represented in the vegetation quadrants.
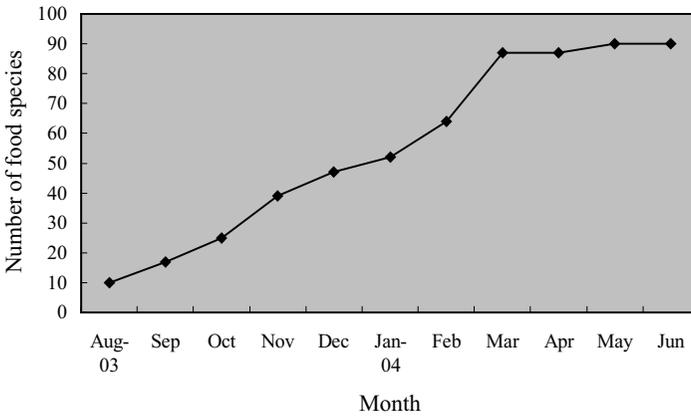[d]S-index: % (F)/%(V).

Fig. 3. Relationship between the cumulative number of food species and observation time.

during the dry season—young leaf-lean period—than in the rainy season: young leaf-rich period (Mann-Whitney U test $Z = -2.556, p < .01$).

Among all food species the langurs used only 3 (3.3% of 90 food species) in ≥ 9–12 mo—*Pistacia weinmannifolia*, *Ficus nervosa*, *Canthium dicoccum*—and 13 (14.4% of 90 food species) in $\geq 5 \leq 8$ months. They used the remainder in $\geq 1 \leq 4$ mo (82.3% of 90 food species) (Table III). There is a significant and positive relationship between number of months and the percentage of feeding records per food species (Spearman rank correlation coefficient $r_s = .833, n = 90, p < .001$; Table III). There is substantial variation in the top 5 food species between months (Table IV). *Ficus nervosa* was the only food langurs consumed in quantities in both rainy and dry seasons. They used *Sinosideroxylon pedunculatum*, *Boniodendron minor*, and *Burretiodendron hsienmu* in quantities only in the rainy season; in the dry season, *Pithecellobium clypearia*, *Ficus microcarpa*, *Bauhinia* sp., *Acacia pennata*, and *Cuscuta chinensis* became important foods. Seeds of *Pithecellobium clypearia* contributed an average of 18.2% to the monthly diet in 5 of the 6 mo during the dry season.

There is also seasonal variation in the percentage of feeding records for each food item (Table II). Young leaves are a significantly higher percentage of feeding records during the young leaf-rich period than during the young leaf-lean period (Mann-Whitney U test $Z = -2.739, p < .01$). Conversely, during the young leaf-lean period, the consumption of mature leaves is higher, but the difference is not statistically significant (Mann-Whitney U test $Z = -0.913, p > .05$). Fruit consumption peaked during the transitional period (October) between rainy and dry seasons,

Table IV. Top 5 species consumed by François' langurs each month in the Nonggang Nature Reserve between August 2003 and June 2004[a]

Family	Species	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June
Anacardiaceae	Brassaiopsis glomerulata							5.8				
Annonaceae	Miliusa chunni		7.3						7.2	38.4		
Apocynaceae	Wrightia pubescens											7.5
Caesalpiniaceae	Bauhinia sp.				20.6	16.3						19.4
	Zenia insignis									8.6		
Convolvulaceae	Cuscuta chinensis						14.3					
Ebenaceae	Diospyros siderophyllus			5.7								14.9
Guttiferae	Garcinia paucinervis				8.6	8.8		15.2	5.9			13.4
Icacinaceae	Apodytes dimidiata	17.8	8.6									
Linaceae	Tirpitzia ovoidea	16.6		20.2								
Mimosaceae	Acacia pennata						20.6					
	Ormosia glaberrima										6.3	
	Pithecellobium clypearia		11	12.6		21.1	10.3	32.6	14.4			
Moraceae	Cudrania cochinchinensis						5.5		21.3			
	Ficus microcarpa	14		4.9								
	Ficus microcarpa		11									
	Ficus nervosa	21	9.3	32.7	26.1		10.3	6.9			6.3	25.4
Myrsinaceae	Embelia scandens											
Polygalaceae	Securidaca inappendiculata				5.8		5.6					
Rubiaceae	Canthium dicoccum			4.9	6.5			9.9	13.4	8.2	11.3	
	Randia spinosa					8.4						
Sapindaceae	Boniodendron minor	21										
Sapotaceae	Sinosideroxylon pedunculatum	57.3	29.9									
Tiliaceae	Burretiodendron hsienmu									9.9	12	
Vitaceae	Tetrastigma cauliflorum					9.7						
	Species 1									4.3		
	Species 2										13.2	

[a]Numbers are the percentages of feeding records for each species.

and had no significant seasonal variation ($Z = -.365$, $p > .05$). There is also no significant seasonal variation in the percentage of feeding records for flowers ($Z = -1.290$, $p > 0.05$). Langurs consumed seeds only during young leaf-lean period ($Z = -2.872$, $p < 0.01$), with a peak between December 2003 and February 2004. Likewise, consumption of petiole and stem occurred only during the young leaf-lean period ($Z = -2.298$, $p < .05$ for petiole and $Z = -2.489$, $p < .05$ for stem), except that the langurs still consumed petioles at the beginning of the rainy season.

The consumption of young leaves correlates positively with their availability (Spearman rank correlation coefficient $r_s = .955$, $n = 11$, $p < .001$), but there is no significant relationship between the consumption and the availability of fruit ($r_s = .483$, $n = 11$, $p > .05$) and flower ($r_s = .207$, $n = 11$, $p > .05$).

Dietary Diversity and Food Choice

Annual dietary diversity was 3.56, and monthly dietary diversity varied from 1.49 (August 2003) to 2.87 (March 2004) (SD $= 0.36$) (Table II). Dietary diversity was significantly higher during young leaf-lean period than during young leaf-rich period (Mann-Whitney U test $Z = -.2191$, $p < .05$). Dietary diversity correlates negatively with the percentage of feeding records for young leaves (Spearman rank correlation coefficient $r_s = -0.645$, $n = 11$, $p < .05$), and positively with that for seeds ($r_s = .763$, $n = 11$, $p < 0.01$). There is no significant relationship between dietary diversity and the percentage of feeding records for mature leaves ($r_s = .318$, $n = 11$, $p > .05$), fruits ($r_s = -.14$, $n = 11$, $p > .05$), and flowers ($r_s = -0.514$, $n = 11$, $p > .05$). Dietary diversity correlates significantly negatively with the availability of young leaves and fruit ($r_s = -0.627$, $n = 11$, $p < 0.05$; and $r_s = -0.729$, $n = 11$, $p < .05$). There is no significant relationship between dietary diversity and the availability of flowers ($r_s = -0.064$, $n = 11$, $p > .05$).

Though the langurs consumed a large number of plant species, only 25 species (28% of 90 food species) account for >1% each of all feeding records, of which 13 species (14%) each account for >2% of total feeding records, and only 7 species (8%) each account for >5% of all feeding records (Table III). A large proportion of the total diet (62.2%) came from only 10 species: *Pithecellobium clypearia*, *Ficus nervosa*, *Garcinia paucinervis*, *Sinosideroxylon pedunculatum*, *F. microcarpa*, *Miliusa chunni*, *Securidaca inappendiculata*, *Bauhinia* sp., and *Canthium dicoccum*. Thus, François' langurs concentrated on a few species, but opportunistically consumed a large number of other plant species.

Langurs expoited only 54% of tree species among 56 identified from the vegetation quadrants (Table III). Likewise, we found only 54% of food tree species in vegetation quadrants. There were only 2 tree species (*Pithecellobium clypearia*, *Ficus microcarpa*), which each accounted for $>5\%$ of all feeding records, belonging to the 10 most predominant tree species in vegetation quadrants, and only 2 tree species (*Pithecellobium clypearia*, *Ficus microcarpa*) among the 10 most predominant tree species in quandrats were highly preferred foods according to the S-index. We used the 30 tree species, which were found both in the diet and vegetation quadrants, to test the association between the percentage of specific feeding records (*F*%) and the percentage of individuals of the species in quadrants (*V*%) (Table III). There is no significant correlation between *F*% and *V*% (Spearman rank correlation coefficient $r_s = -.014, n = 30, p > .05$).

DISCUSSION

Seasonal Changes in the Diet of François' Langurs

Primates appear to adjust their diets in response to seasonal shortage in their preferred foods (Bennett, 1983; Davies, 1991; Hladik, 1977; Newton, 1992). François' langurs in the Nonggang Nature Reserve, like other folivorous primates (Chapman, 1988; Yamagiwa *et al.*, 1994), varied the consumption of different food items according to season. They increased consumption of young leaves during young leaf-rich period. When the foods were scarce, they increased seed, petiole, and stem consumption. The dietary shift corresponded to more food species and higher dietary diversity during the young leaf-lean period than during the young leaf-rich period. It may be a strategy for the François' langurs to deal with fluctuations in the availability of preferred foods. For example, frugivorous *Lophocebus albigena* increased the consumption of seeds and leaves during fruit-lean periods (Poulsen *et al.*, 2001). At Kanha, India, *Semnopithecus entellus* fed on mature leaves in large quantities during the cold season when fruits, flowers, and young leaves were scarce (Newton, 1992). *Presbytis melalophos* at Kuala Lompat, Malaysia, tended to include a larger number of different species when few favored foods were available (Bennett, 1983).

Seasonal change in the availability of potential food resources is one of multiple factors determining seasonal variation in the diet of primates (Hanya, 2004; McConkey *et al.*, 2003; Newton, 1992; Poulsen *et al.*, 2001; Silver *et al.*, 1998). In the Nonggang Nature Reserve, the availability of young leaves and fruit exhibited significant seasonal changes. When the

availability of young leaves was high, François' langurs increased consumption of them; thus, they preferred young leaves in response to their increased availability. There was also a tendency for an increase in the percentage of feeding records for fruits as they became more available, but the relationship is not significant statistically. Accordingly, fruits seemed to be less preferred than young leaves, even though they may also be a preferred food, a conclusion that is also supported by the fact that the consumption of young leaves still remained high when fruits were plentiful.

Though we did not test the relationship between seed consumption and seed availability, seeds clearly were important food resources in the dry season, when young leaves and fruits were scarce. Between December 2003 and February 2004, François' langurs largely specialized on the seeds of *Pithecellobium clypearia*, and visited the same feeding tree on several consecutive days; during this period, seeds of *Pithecellobium clypearia* constituted the highest proportion of the diet. The species appeared to play a crucial role in François' langur feeding ecology during the lean period. *Pithecellobium clypearia* are large-canopied, emergent trees that produce seeds synchronously during the few months of low availability of young leaves and fruit. Seeds are rich in fats and starch, and form one of the most important energy resources for animals (Richard, 1985), and they can provide enough alternative high quality food during the seasonal scarcity of other important resources in the seasonal rain forests of the karst regions. Other researchers have reported that primates consumed seeds in large quantities during the lean period for preferred foods (Kaplin *et al*., 1998; Poulsen *et al*., 2001; Strier, 1999).

Food Choice of François' Langurs

Many field studies have documented that food choice among primates is likely constrained by food availability (Bennett, 1983; Li *et al*., 2003; Oates *et al*., 1980). For François' langurs in the Nonggang Nature Reserve, 62.2% of the diet came from only 10 species, of which only 2 belonged to the 10 most dominant tree species in the habitat. Similar findings come from other colobine studies. At Kuala Lompat, Malaysia, 5 species, which accounted for only 9.6% of the trees in the forest, provided 45% of the diet of *Presbytis melalophos* (Bennett, 1983). White-headed langurs in the Fusui Reserve fed on 50 out of 164 available species, of which as much as 61.8% of the diet came from 10 plant species, only 1 of which was among the 20 most common species in the habitat (Li *et al*., 2003). Though *Trachypithecus johnii* at Kakachi used 115 species as foods, only 3 species contributed to 45% of the diet, and 2 species belonging to the most common trees in

the habitat provided only 5% of the diet (Oates *et al.*, 1980). In keeping with other studies of colobines, François' langurs did not select their favored foods based on the abundance of the species in the habitat. Common species provided little food, and food choice does not correlate with the relative abundance of species in the habitat. Food choice among primates is also determined by other factors, including spatial distribution of resources and food nutritional characters such as fiber or toxins (Di Fiore, 2004; Waterman and Kool, 1994). Clearly François' langurs have feeding behavior similar to that of other colobines, with a preference for young leaves, selection in the species from which foods are chosen, and greater diversity of diet when resources are poorer.

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