

RESEARCH ARTICLE

Foods Eaten by the Sichuan Snub-Nosed Monkey (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China, in Relation to Nutritional Chemistry

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The diet of *Rhinopithecus roxellana* is characterized by lichens, which are available year-round and an uncommon food source for nonhuman primates, supplemented by seasonal plant foods. We present the first study of foods eaten by *R. roxellana* in relation to nutritional chemistry in Shennongjia National Nature Reserve, Hubei Province, China. We analyzed the nutrients (crude protein, crude fat, and water soluble carbohydrate [WSC]) and feeding deterrents (crude fiber, condensed tannin [CT], and total phenolic [TP]) of 111 parts from 53 plant species and of 6 lichen species. Results showed that lichens were a good choice for *R. roxellana* living in habitats with limited and seasonally available plant foods. They contained higher concentrations of WSC than foliage, fat concentrations equivalent to those in plant parts (except fruits/seeds), and lower concentrations of fiber than mature leaves, flowers, and fruits. Although lichens were lower in protein than plant parts (except fruits), the monkeys could likely meet their protein requirement by eating seasonal plant foods rich in protein, including foliage, flowers, buds, and seeds. The monkeys were not observed to select foliage higher in protein, but appeared to select mature leaves higher in WSC and lower in fiber. Fruits were a good source of WSC and fat, and seeds were a good source of fat. Neither CT nor TP content showed negative effects on the selection of mature leaves or lichens. *Am. J. Primatol.* 75:860–871, 2013. © 2013 Wiley Periodicals, Inc.

Key words: *Rhinopithecus roxellana*; diet; lichen; nutritional chemistry

INTRODUCTION

Food selection by nonhuman primates is influenced by a range of ecological, morphological, and physiological factors, including specializations of the digestive system [Chivers, 1994; Milton, 1998] and food quality [Mowry et al., 1996; Remis et al., 2001], as well as feeding competition [Stanford & Nkurunungi, 2003], body size [Milton, 1984; Nakagawa, 2003], and food availability [Dasilva, 1994; Dela, 2007].

Colobines have morphological adaptations in the digestive system, among which are their enlarged and multi-chambered stomachs containing microorganisms to ferment ingested foods [Chivers, 1994]. Microbial fermentation in the forestomach helps colobines break down the indigestible building blocks (including cellulose) of plant cell walls; therefore, colobines are generally more folivorous than most other primates [Sayers & Norconk, 2008; Stanford, 1991; Struhsaker & Leland, 1987]. Evidence suggests that the fermentative digestion has the capability to detoxify or inactivate some secondary compounds that may reduce digestibility or be toxic [Gartlan et al., 1980; Hagerman & Butler, 1991].

Food choice in relation to nutritional chemistry has been studied extensively in colobines [Baranga, 1983; Dasilva, 1994; Fashing et al., 2007; Kool, 1992; Mowry et al., 1996; Oates et al., 1977]. Most studies have shown that foliage eaten by colobines contains higher concentrations of protein, lower concentrations of fiber, or higher ratios of protein to fiber than

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foliage that is not eaten [Fashing et al., 2007; Wasserman & Chapman, 2003; Yeager et al., 1997]. Protein concentrations decrease and fiber concentrations increase with leaf maturity; therefore, young leaves are usually preferred to mature leaves [Baranga, 1983; Mowry et al., 1996]. Whether plant secondary compounds affect colobine food choice is controversial, however. Some species, for example, were found to eat foods with low tannin concentrations [*Colobus satanas*: McKey et al., 1981; *Procolobus verus*: Oates, 1988], while no correlation was found between tannin (or phenol) concentrations and food choice in several other species [*Ptilocolobus rufomitratu*s: Mowry et al., 1996; *Ptilocolobus tephrosceles*: Chapman & Chapman, 2002; *Presbytis rubicunda*: Davies et al., 1988]; this confusion may be in relation to the methods used [Rautio et al., 2007; Rothman et al., 2009].

The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) is a China-endemic endangered colobine species. It lives in temperate forests at the elevations of 1,000–4,100 m in the isolated mountainous areas on the eastern edge of the Qinghai-Tibet Plateau [Kirkpatrick & Grueter, 2010; Li et al., 2002a; Ren et al., 1998]. Its diet is diverse and strongly seasonal; flowers, young leaves, mature leaves, fruits, seeds, and buds become available and become main dietary components subsequently [Guo et al., 2007; Li, 2006; Li et al., 2010]. Lichens, an uncommon food source for nonhuman primates and other mammals, compose an important part of its diet, especially in winters with limited availability of plant foods [Guo et al., 2007; Li, 2006].

This article presents the results of the first systematic study of foods choice in relation to nutritional chemistry in a group of *R. roxellana* in Shennongjia National Nature Reserve, Hubei Province, China. We hypothesized that foods eaten by *R. roxellana* were higher in nutrients and lower in feeding deterrents than those uneaten. The nutritional basis of food choice is of great importance to understand its other ecological aspects, and to apply conservation and management strategies.

METHODS

Study Site

This study was conducted in the Qianjiaping area (about 60 km²) of Shennongjia National Nature Reserve (110°03'–110°34' E, 31°22'–31°37' N), Hubei Province, China. This area has a rugged topography with an elevational range of 1,500–2,663 m. The climate is highly seasonal. There is a conservation station at the elevation of 1,700 m, where the monthly mean temperature was highest in July (16.3°C) and lowest in January (–5.5°C) during the study period [Liu et al., unpublished data]. Snowfalls lasted from early November to middle March. The

annual rainfall was approximately 1,800 mm, with the rainy season between July and September. The vegetation is characterized by deciduous broadleaf and evergreen conifer mixed forest. There were 75 woody plant species (evergreen: seven species) and 12 arboreal lichen species (four species of fruticose: branched and beard-like; eight species of foliose: leaf-shaped with lobes, the whole body tightly attached to the substrate) in the forest [Liu et al., unpublished data].

Study Group

The study group had been semi-habituated and studied periodically since 1999 [Li, 2006, 2007; Li et al., 2002b]. The monkeys sometimes (often in summer) ranged to the area of two other counties adjacent to the study site. Group size was counted eight times during the study period, when the monkeys crossed open areas or rivers, or during winters when the leaves of deciduous plants fell. On average, the group contained 236 ± SD 38 individuals (N = 8), including 106 ± SD 12 adult males, 77 ± SD 18 adult females, 35 ± SD 10 juveniles, and 18 ± SD five infants [age sex class definition: Li, 2007].

Data Collection

We followed the group from August 2006 to July 2008 (except December 2006–February 2007 and February 2008) to collect behavioral data via instantaneous scans at 30-min intervals with the naked eyes or with a binocular (27–151 scans on 6–28 days per month; 1,489 scans on 317 days in total). We could approach the group within 20–30 m. For each visible individual (excluding infants) in each scan, the behavior was determined and recorded in 10 sec. If the monkey was eating (defined as plucking or manipulating food items by hands or mouth, or chewing food items), food species and food part were noted. If the animal was eating lichens, food part was assumed as the whole body, and lichen form (i.e., fruticose or foliose) was also recorded. The proportions of eating records on food species or parts represented dietary composition.

Samples of plant parts (i.e., mature leaves, young leaves, flowers, buds, bark, fruits, and seeds) and lichens were collected opportunistically over the study period from the home range of the study group. Samples were taken from several individuals of a given species to represent its spatial distribution. Samples were weighed fresh, dried to constant weights at 65–70°C in an electric oven (a potential issue because overheating may alter some components; a temperature less than 60°C has been recommended [Rothman et al., 2012]), and then packaged in airtight bags in the field. Water content was measured as (fresh weight–dry weight)/(fresh

weight). The dried samples were taken to laboratories for the analysis of nutrients (crude protein, CP; crude fat, CFA; water soluble carbohydrate, WSC) and feeding deterrents (crude fiber, CF; condensed tannin, CT; total phenolic, TP). All samples were ground using a 1-mm mill and dried again to constant weights to remove atmospheric moisture before analysis. CP was determined using the standard macro-Kjeldahl method (CP = Nitrogen \times 6.25) [No. 7.015 in AOAC, 1984]. CFA was determined via ether extraction using the Tecator Soxtec System HT 1034 Extraction Unit [Hanson et al., 2006]. WSC was measured with a standard of sucrose using the method of Dubois et al. [1956] and Rothman et al. [2006]. CF, containing cellulose, hemicellulose, and lignin, was measured by the standard method [No. 7.060 in AOAC, 1984]. Samples were extracted with 50% methanol to determine TP with Folin-Denis technique [Mowry et al., 1996]. Samples were extracted with 70% acetone to measure CT with butanol-HCL technique [Rothman et al., 2006]. The contents of CP, CFA, WSC, and CF were expressed as proportions of dry matter. For CT and TP, instead of actual concentrations, we reported the absorbance at five levels: I (<0.1), II ($\geq 0.1, <0.5$), III ($\geq 0.5, <1.0$), IV ($\geq 1.0, <2.0$), and V (≥ 2.0); assuming a higher level indicated more CT or TP present [Rothman et al., 2006, 2009].

The research protocols were reviewed and approved by the Animal Care Committee of the Department of Forestry of Hubei Province, China. The observations confirmed to the regulatory requirements of Shennongjia National Nature Reserve, China. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Data Analysis

We used Kruskal-Wallis tests to see whether there were differences in each component among plant parts/lichens, and whether there were differences in the ratio of CP to CF among mature/young leaves and lichens. If a test was significant, we conducted pairwise comparisons using Steel-Dwass tests. We then compared each component between food and non-food plant parts/lichens and between food plant parts and food lichens using Mann-Whitney U-tests. Similarly, the comparison of the ratio of CP to CF was made only for food and non-food mature/young leaves, and lichens. For CT and TP, the levels of absorbance were used in all statistical analyses. The variables with sample sizes of less than three were excluded in statistical analyses. Steel-Dwass tests were performed in R 2.14.2, and other tests were performed in SPSS 17.0. We reported results with a significance level of 0.05, as well as a marginal significance level of 0.10 because of small sample sizes.

RESULTS

Diet

Fruticose lichens were the most eaten food, accounting for 38.4% of the overall diet, while no foliose lichen was observed to be eaten (Tables I and II). In addition to fruticose lichens, the monkeys ate various parts from at least 15 plant species. Seeds (only of *Pinus armandii*) occupied 20.8% of the overall diet, young leaves 13.5%, fruits 9.5%, mature leaves (including ground herbs) 8.9%, and buds 5.8%. Flowers, bark, and insects accounted for very small proportions ($<2.0\%$ in sum) of the overall diet.

The diet showed clear seasonality (Table II). Flowers were mainly eaten from March to April, young leaves from April to July, mature leaves from May to September, fruits from June to October, seeds from September to March, and buds from December to April. Fruticose lichens were eaten through the year, ranging from 24.0% in October to 48.0% in April of the monthly diet.

Nutritional Chemistry

We analyzed the chemical components of 111 parts from 53 woody plant species and of 6 lichen species, among which 32 parts from 14 plant species and 3 lichen species were observed to be eaten during the study period (see Appendix I). The contents of CP, CFA, WSC, and CF were summarized by plant part and lichen (Fig. 1). For CT and TP contents, the numbers of plant/lichen species were counted by plant part/lichen and absorbance level (Table III).

Among Plant Parts and Lichens

Crude Protein

CP concentrations differed among plant parts and lichens ($\chi^2 = 34.56$, $df = 5$, $P < 0.001$). Flowers and buds contained more CP than mature leaves and young leaves, which further contained more CP than fruits and lichens, respectively (Table IV).

Crude Fat

CFA concentrations did not differ among plant parts and lichens ($\chi^2 = 8.34$, $df = 5$, $P = 0.14$).

Water Soluble Carbohydrate

WSC concentrations differed among plant parts and lichens ($\chi^2 = 8.34$, $df = 2$, $P < 0.05$). Lichens contained more WSC than mature leaves and young leaves, respectively, and mature leaves contained more WSC than young leaves (Table IV).

Crude Fiber

CF concentrations differed among plant parts and lichens ($\chi^2 = 17.62$, $df = 5$, $P < 0.05$). Lichens contained less CF than mature leaves, flowers, and fruits, respectively (Table IV).

TABLE I. Food Species and Their Proportions in the Overall Diet of *Rhinopithecus roxellana* in Shennongjia, China (August 2006 to July 2008)

Food species	Flowers	Young leaves	Mature leaves	Fruits	Seeds	Buds	Bark	Total
<i>Actinidia chinensis</i>		0.1						0.1
<i>Aralia chinensis</i>		1.6	0.3			0.2		2.1
<i>Cerasus szechuanica</i>	0.2	1.0		1.8		0.1		3.1
<i>Cornus controversa</i>				0.5				0.5
<i>Crataegus hupehensis</i>		1.5	0.8	0.1				2.4
<i>Decaisnea fragesii</i>		0.3	0.3				0.1	0.7
<i>Euonymus alatus</i>		1.6	0.5				0.1	2.2
<i>Lindera obtusiloba</i>	0.5	4.0	1.3	1.5		4.9		12.2
<i>Litsea ichangensis</i>	0.4	0.9		1.5		0.5		3.3
<i>Malus hupehensis</i>	0.1	0.3		0.1				0.5
<i>Morus alba</i>		1.2	0.2					1.4
<i>P. armandii</i>					20.8			20.8
<i>Salix wallichiana</i>	0.1	0.5				0.1		0.7
<i>Schisandra glaucescens</i>		0.2	0.6	0.4				1.2
<i>Sorbus hupehensis</i>		0.3		3.6				4.9
Fruticose lichens								38.4
Ground herbs			4.9					4.9
Insects								0.4
Unknown								1.4
Total	1.3	13.5	8.9	9.5	20.8	5.8	0.2	

Condensed Tannin

There were differences in the absorbance level in the assay of CT among plant parts and lichens ($\chi^2 = 16.44$, $df = 4$, $P < 0.05$). The absorbance level in lichens was lower than that in mature leaves and flowers, respectively (Table IV).

Total Phenolic

No difference in the absorbance level in the assay of TP was detected among plant parts and lichens ($\chi^2 = 7.01$, $df = 4$, $P = 0.14$).

Protein / Fiber Ratio

The ratio of CP/CF differed among mature and young leaves, and lichens ($\chi^2 = 5.85$, $df = 2$,

$P = 0.05$). Lichens had a lower ratio of CP/CF than young leaves (Table IV).

Between Food and Non-Food Plant Parts/lichens

Food mature leaves contained more WSC and less CF than non-food mature leaves (Table V). Food lichens (i.e., fruticose) contained less CP than non-food lichens (i.e., foliose).

Between Food Plant Parts and Food Lichens

Food lichens contained less CP than any food plant part except food fruits, and less CF than any food plant part except food young leaves (Table V). Food lichens

TABLE II. Monthly Diet Composition of *Rhinopithecus roxellana* in Shennongjia, China (August 2006 to July 2008)

	Flowers	Young leaves	Mature leaves	Fruits	Seeds	Buds	Bark	Fruticose lichens	Insects	Unknown
Jan					26.7	29.1	1.2	43.0		
Mar	13.2		1.9		5.7	32.1		45.3		1.9
Apr	6.4	17.9	2.3	1.7	0.6	20.8		48.0		1.7
May	0.9	48.5	7.0	3.9		0.4		36.7	0.9	1.8
Jun		24.6	14.8	14.8				45.3		0.5
Jul		7.7	38.9	15.0				43.4		1.8
Aug		0.9	20.5	23.1				35.9	2.6	10.3
Sep			9.5	27.2	29.1			32.9	1.3	
Oct			4.0	11.8	69.3			24.0		0.7
Nov				2.0	51.4		0.7	36.1		
Dec					60.0	6.3		33.7		
Overall	1.3	13.5	8.9	9.5	20.8	5.8	0.2	38.4	0.4	1.4

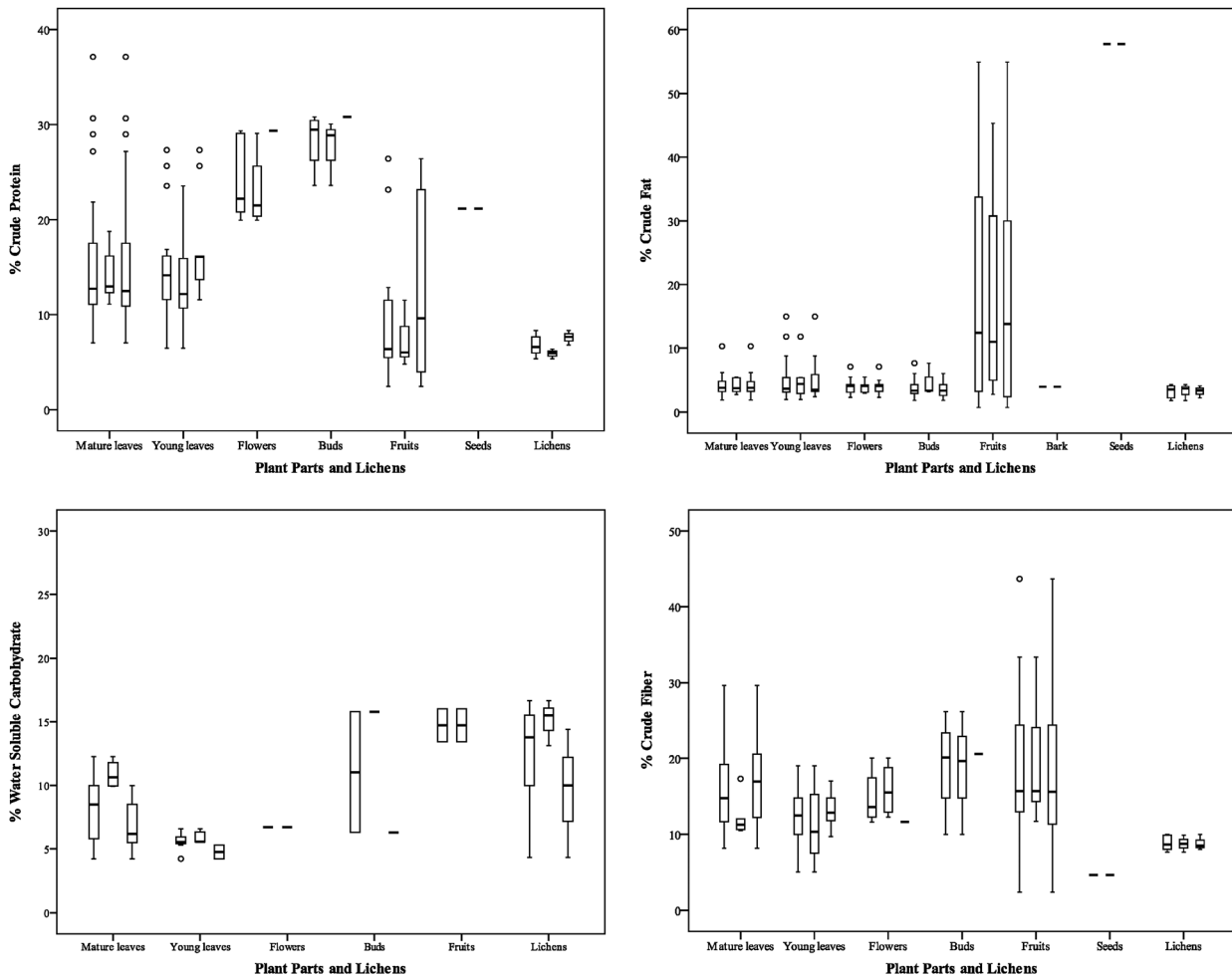


Fig. 1. Boxplots for the concentrations (% dry matter) of crude protein, crude fat, water soluble carbohydrate, and crude fiber measured in plant parts and lichens collected from the habitat of *Rhinopithecus roxellana* in Shennongjia, China (For each component in each item of plant part/lichen, the first box for combined food and non-food, the second for food, and the third for non-food).

TABLE III. The Numbers of Plant/Lichen Species at Different Absorbance Levels in the Assays (Dry Matter Based) of Condensed Tannin and Total Phenolic in the Habitat of *Rhinopithecus roxellana* in Shennongjia, China

		Condensed tannins					Total phenolics				
		I	II	III	IV	V	I	II	III	IV	V
Mature leaves	Food		1	2				1	1	1	
	Non-food		5	7	6	2	1	10	4	3	2
Young leaves	Food		2	2				2	2		
	Non-food		1							1	
Flowers	Food			2				1		1	
	Non-food		1	4	1	1		4	2		1
Buds	Food	1						1			
	Non-food		4	2	1		2	4		1	
Fruits	Food		1							1	
	Non-food				1					1	
Lichens	Food	1	2					3			
	Non-food	1	2					3			

Note: I: <0.1; II: ≥0.1, <0.5; III: ≥0.5, <1.0; IV: ≥1.0, <2.0; V: ≥2.0.

TABLE IV. Pairwise Comparisons for the Concentrations (% Dry Matter) of Chemical Components in Plant Parts and Lichens Collected From the Habitat of *Rhinopithecus roxellana* in Shennongjia, China (Steel-Dwass Tests)

	CP		WSC		CF		CT		CP/CF	
	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value	Statistic	P-value
ML vs. YL	0.48	0.997	2.11	0.087	2.05	0.315	1.74	0.408	1.81	0.167
ML vs. FL	2.71	0.073			<0.01	>0.999	0.22	0.999		
ML vs. BD	2.72	0.072			1.11	0.879	1.94	0.296		
ML vs. FR	3.03	0.029			0.80	0.967				
YL vs. FL	2.62	0.091			1.21	0.830	1.53	0.540		
YL vs. BD	2.87	0.048			1.93	0.386	0.16	>0.999		
YL vs. FR	2.87	0.048			2.03	0.325				
FL vs. BD	1.47	0.684			0.98	0.924	1.58	0.508		
FL vs. FR	2.61	0.094			0.54	0.994				
BD vs. FR	2.83	0.053			0.34	0.999				
LI vs. ML	3.76	0.002	2.01	0.102	3.32	0.011	3.20	0.012	1.02	0.564
LI vs. YL	3.36	0.010	2.14	0.081	2.17	0.252	1.91	0.309	2.42	0.042
LI vs. FL	2.74	0.068			2.74	0.068	2.86	0.035		
LI vs. BD	2.56	0.101			2.35	0.176	1.58	0.508		
LI vs. FR	0.09	>0.999			2.89	0.044				

Note: The contents of CFA and TP were excluded because overall comparisons were not significant. See Appendix I for abbreviations.

contained more WSC, and had a lower ratio of CP to CF than food mature leaves and food young leaves, respectively. In addition, food lichens contained less CFA than food fruits, and had a lower absorbance level in the assay of CT than food mature leaves.

DISCUSSION

Although colobines are well known for their high intake of foliage and fermentative forestomach

[Stanford, 1991; Struhasker & Leland, 1987], recent studies have showed that some colobine species have diverse diets with much seasonal variations [Dela, 2007; Sayers & Norconk, 2008]. In this study, the diet of *R. roxellana* in Shennongjia was diverse with strong seasonality, confirming previous findings for this species at our study site and in the Qinling Mountains [Guo et al., 2007; Li, 2001, 2006; Li et al., 2010]. We believed that the lack of data in February did not affect this seasonal pattern of diet.

TABLE V. Comparisons for the Concentrations (% Dry Matter) of Chemical Components Between Food and Non-Food Plant Parts/Lichens, and Between Food Plant Parts and Food Lichens in the Study of *Rhinopithecus roxellana* in Shennongjia, China (Mann-Whitney U-tests)

	F ML vs. NF ML		F YL vs. NF YL		F FL vs. NF FL		F BD vs. NF BD		F FR vs. NF FR		F LI vs. NF LI	
	U-stat	P-value	U-stat	P-value	U-stat	P-value	U-stat	P-value	U-stat	P-value	U-stat	P-value
CP	62.0	0.775	21.0	0.149					17.0	0.568	0.0	0.050
CFA	125.0	0.915	42.0	0.806	22.0	0.947	10.0	0.398	22.0	0.749	4.0	0.827
WSC	1.0	0.011									1.0	0.127
CF	36.0	0.102	25.0	0.290					19.0	0.775	4.0	0.827
CT	19.5	0.307									4.5	>0.999
TP	24.5	0.588									4.5	>0.999
CP/CF	45.5	0.263	35.0	0.923							2.0	0.275

	F LI vs. F ML		F LI vs. F YL		F LI vs. F FL		F LI vs. F BD		F LI vs. F FR	
	U-stat	P-value	U-stat	P-value	U-stat	P-value	U-stat	P-value	U-stat	P-value
CP	0.0	0.025	0.0	0.014	0.0	0.034	0.0	0.050	8.0	0.569
CFA	7.0	0.606	8.0	0.309	6.0	0.655	4.0	0.827	3.0	0.087
WSC	0.0	0.025	0.0	0.025						
CF	0.0	0.025	8.0	0.414	0.0	0.034	0.0	0.050	0.0	0.017
CT	1.0	0.099	2.0	0.115						
TP	4.0	0.121	3.0	0.180						
CP/CF	1.0	0.053	2.0	0.041						

Note: F, food; NF, non-food; see Appendix I for other abbreviations.

It is suggested that the diet of *R. roxellana* well reflected the seasonal availability of plant foods [Li, 2006]. Besides seasonal plant foods, *R. roxellana* ate a year-round available item, lichens, occupying 38.4% of the overall diet with a range of 24.0–48.0% in any given month. The Qinling population of *R. roxellana* was also reported to include a large proportion of lichens in the diet (29.0% varying from 1.6% in summer and 62.3% in winter) [Guo et al., 2007]. Lichens played a more important role in the diet of another China-endemic snub-nosed monkey species, *Rhinopithecus bieti*; dietary proportions of lichens varied across populations (Tacheng: 60% with a monthly range of 40–82%; Xiaochangdu: 74.8% with a monthly range of 30.7–98.2%; Wuyapiya: 85.9% with a monthly range of 64.3–97.8%) [Ding & Zhao, 2004; Grueter et al., 2009; Kirkpatrick, 1996; Xiang et al., 2007]. *Colobus angolensis*, a colobine living in the Nyungwe Forest, Rwanda, was observed to eat lichens, but lichens occupied only 5% of its overall diet [Fimbel et al., 2001]. Reindeers (*Rangifer tarandus*) may be the most well-known lichen-eating mammal, and lichens accounted for up to 26% of its diet in winter [Mathlesen et al., 2000]. Overall, however, lichens are an uncommon food source for nonhuman primates and other mammals.

Lichens were previously considered a low-quality or fallback food to supplement limited and seasonally available plant foods [Grueter et al., 2009; Li, 2006]. Indeed, compared to plant parts (except fruits), lichens in the Shennongjia forest could provide much less protein for *R. roxellana*. Food lichens contained even less protein than non-food lichens (means: 5.90% vs. 7.59% of dry matter), which were not eaten probably because their whole bodies attached to plant surface tightly and were difficult to be harvested. Protein concentrations in lichens were much lower than those (15–22% of dry matter) recommended by the National Research Council for feeding nonhuman primates [NRC, 2003]. Less protein in lichens relative to plant parts was also reported in a nutritional study of *R. bieti* at Wuyapiya [Kirkpatrick, 1996]. In reindeer, protein deficiency as a result of lichen eating in winter may lead to a temporary decrease in body weight because the animals need to break down muscles to compensate for the low-protein diet [Reimers & Ringberg, 1983]. For all populations of *R. roxellana* and *R. bieti*; however, lichens were one of main dietary components throughout (or almost) the year, suggesting that these monkeys relied on seasonal plant foods to meet their protein requirement.

Foliage is a major source of protein for nonhuman primates living in forests [Waterman, 1984], and many colobines are found to eat foliage to increase the consumption of protein [Fashing et al., 2007; Fimbel et al., 2001; Mowry et al., 1996; Yeager et al., 1997]. Foliage was eaten by *R. roxellana* in Shennongjia

from April to September. Contrary to previous studies, mature leaves (and young leaves) *R. roxellana* ate had equivalent protein concentrations to those uneaten. Even if we lumped mature leaves and young leaves as foliage, there was also no difference in protein concentrations between food and non-food foliage (Mann-Whitney $U = 208.5$, $P = 0.564$). This result, however, was consistent with previous finding for the silver leaf monkey (*Trachypithecus auratus*) at Pangandaran, which did not select foliage higher in protein [Kool, 1992]. At our study site, protein concentrations measured in foliage (means: 15.51% of dry matter in mature leaves, 15.30% of dry matter in young leaves) appeared to meet the minimum protein requirement of the monkeys according to the recommendation of the National Research Council [NRC, 2003], though this may be a conservative estimate [Oftedal, 1991].

Flowers were eaten by *R. roxellana* in Shennongjia from March to April, and buds from December to April. The monkeys could obtain protein from these two parts, which had higher protein concentrations than foliage. Flowers consumed by lemurs [Yamashita, 2008] and orangutans [Hamilton, 1994] also contained high concentrations of protein, while buds were seldom considered a protein source in the diets of nonhuman primates in previous studies. In addition, seeds of *P. armandii* eaten from September to March contained higher protein concentrations (21.15% of dry matter) than foliage on average, although statistical tests could not be made due to the small sample size of seeds (Appendix I, Fig. 1). This was consistent with some studies showing that seeds contained high concentrations of protein, such as *Colobus polykomos* on Tiwai Island [Dasilva, 1994; Sourd & Gautier-Hion, 1986] and *T. auratus* at Pangandaran [Kool, 1992]. Thus, although lichens contained limited protein, *R. roxellana* in Shennongjia could likely obtain enough protein from seasonal plant foods. Oftedal [1991] claimed that protein deficiency was not a problem for most primates, according to his calculation on the protein requirement for the maintenance and reproduction of primate populations.

Fiber is often considered a negative index of leaf quality. Colobines can digest some fiber components, but not others (e.g., lignin) [Waterman & Kool, 1994]. Increasing concentrations of fiber can slow the rate of digestion and reduce the intake of protein [Milton, 1998]. Consistent with previous findings for *C. angolensis* [Fimbel et al., 2001] and *C. polykomos* [Mowry et al., 1996], mature leaves eaten by *R. roxellana* in Shennongjia contained less fiber than those uneaten. If we lumped mature leaves and young leaves as foliage, the difference in the concentrations of fiber between food and non-food foliage was more significant ($U = 132.0$, $P = 0.021$). Mature leaves usually contain more fiber than young leaves [Mowry et al., 1996], but this difference was not found in this study. Many studies have shown

that colobines select foliage with higher protein to fiber ratios [Chapman et al., 2004; Fashing et al., 2007; Mowry et al., 1996; Yeager et al., 1997]. But we did not detect any difference in the protein to fiber ratio between food and non-food mature leaves (or young leaves). The protein to fiber ratio also did not differ between food and non-food foliage (lumped mature and young leaves) ($U = 178.0$, $P = 0.205$). Fiber was a better index than the protein to fiber ratio for the selection of foliage by *R. roxellana* in Shennongjia. Interestingly, both this study of *R. roxellana* and Kirkpatrick's [1996] study of *R. bieti* found that lichens contained less fiber compared to plant parts (except young leaves and buds for this study), which was probably one of nutritional aspects making lichens a good potential food source for these monkeys living in habitats with limited availability of plant foods.

Another nutritional aspect for lichens as a food source was that they were rich in WSC relative to mature and young leaves. In the nutritional study of *R. bieti*, lichens were also reported to contain more nonstructural carbohydrate (including WSC and starch) than foliage [Kirkpatrick, 1996]. Mature leaves with higher concentrations of WSC were selected by *R. roxellana* in Shennongjia. Foliage is not often considered a source of WSC. There are some studies, however, showing that mature leaves eaten by folivorous primates contained more WSC than those uneaten [*Gorilla gorilla*: Ganas et al., 2008]. Fruits are known to contain high concentrations of WSC [Conklin-Brittain et al., 1998], while few nutritional studies in colobines have included this assay because fruits are usually not as important as foliage in diets. Consistent with previous findings for some folivorous-frugivorous non-colobine primates [*Alouatta pigra*: Silver et al., 2000; *G. gorilla*: Remis et al., 2001; *Lemur catta*: Yamashita, 2008], fruits contained more WSC (mean: 14.71% of dry matter) than other plant parts, although statistical tests were not conducted due to small sample sizes (Appendix I, Fig. 1).

Fat is an important energy source for primates [NRC, 2003], whereas few nutritional studies in colobines have included this assay because the staple food (i.e., foliage) is usually low in fat. But fruits and seeds, two of main dietary components of *R. roxellana*, are known to be high in fat [Milton, 2008; Waterman & Kool, 1994]. In this study, mean fat concentrations measured in fruits (18.91% of dry matter) and seeds (57.72% of dry matter) were much higher than those in other plant parts and lichens (<5.10% of dry matter) (statistical insignificance for fruits was probably due to small sample sizes; no statistical analysis for seeds) (Appendix I, Fig. 1).

Consistent with some previous studies in colobines [Chapman & Chapman, 2002; Davies et al., 1988; Mowry et al., 1996], neither CT or TP content showed

negative effects on the selection of mature leaves or lichens by *R. roxellana* in Shennongjia. Actually, if we interpreted an absorbance value of <0.10 to be the absence of CT or TP as in Rothman et al. [2006], the prevalence of both compounds was very high among plant parts and lichens (CT was absent only in buds of one plant species and two lichen species; TP was absent only in mature leaves of one plant species and buds of two plant species) (Table III). *R. roxellana* were tolerant to these compounds probably due to the inactivation or detoxification capability of the fermentative forestomach. Alternatively, there is increasing evidence that some plant secondary compounds may be helpful to the health of mammalian herbivores. Tannin, for example, can regulate iron metabolism by absorbing the excessive food iron leading to pathological iron storage diseases [Gaffney et al., 2004; Roy & Mukherjee, 1979]. Phenolic is suggested to be helpful to maintain the microbe population in the gut healthy [Sahoo & Soren, 2012].

The results of this study must be interpreted cautiously due to three major limitations. First, food samples were collected over the study period from the study site, not just when the monkeys were eating the food plants/lichens individuals and items. Previous studies have shown that there may be variations in the nutritional value among tree individuals and time periods [Chapman et al., 2003]. Secondly, CF contains cellulose, hemicellulose, and lignin, whereas the fiber content considered to be negatively correlated with food selection is the fraction of acid detergent fiber, only containing cellulose and lignin [Rothman et al., 2012; Van Soest et al., 1991]. Thirdly, except foliage, sample sizes were relatively small, which prevented us from conducting some statistical analyses and may have introduced bias in some others. Future studies using better techniques and more precise sample collecting methods are needed to obtain a better understanding of nutritional chemistry of foods eaten by *R. roxellana*.

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Appendix I. Nutritional composition of individual plant parts and lichens in the habitat of *Rhinopithecus roxellana* in Shennongjia, China.

Species	Part	H ₂ O	CP	CFA	CF	WSC	CT	TP
<i>Abies fargesii</i>	ML	62.73	9.63	10.28	23.18	9.29		
<i>Acer oliverianum</i>	ML	70.35	15.70	3.57	17.78	5.35	III	III
<i>A. oliverianum</i>	YL	67.49	13.70	3.27	16.79			
<i>Actinidia chinensis</i>	ML	60.00		5.38			III	IV
<i>Aralia chinensis</i>	ML ^a	66.71		5.48				
<i>Betula albosinensis</i>	ML	62.50	13.89	3.91	18.60		III	IV
<i>B. albosinensis</i>	YL	68.19	16.17	8.82	11.80			
<i>Betula ermanii</i>	ML	60.00		5.09				
<i>Betula utilis</i>	ML	69.66	11.75	2.65	17.07	6.35		
<i>B. utilis</i>	YL	72.83	16.09	4.91	10.22	4.22		
<i>Carpinus fargesiana</i>	ML	57.84	12.47	3.15	22.28			
<i>Castanea seguinii</i>	ML	58.14	12.48	6.16	19.13			
<i>C. seguinii</i>	FR	47.53	2.46	1.60	11.33			
<i>Cerasus szechuanica</i>	ML	56.07	7.01	1.88	8.27		II	II
<i>C. szechuanica</i>	YL ^a	53.18	6.45	1.97	7.80			
<i>C. szechuanica</i>	FL ^a	85.47	29.07	4.27	12.26			
<i>C. szechuanica</i>	BD ^a	74.38	28.87	7.68	10.00			
<i>Cetralia delavayana</i> ^b	LI		7.65	2.22	8.51	4.33	II	II
<i>Cinnamomum glanduliferum</i>	ML	73.63	27.17	4.08	9.60			
<i>Cornus controversa</i>	ML	67.85	11.93	4.10	12.23	7.72	IV	II
<i>C. controversa</i>	YL	68.10	14.14	3.30	9.70			
<i>C. controversa</i>	FR ^a	45.86	5.51	25.13	31.79	13.41		
<i>Cornus hemsleyi</i>	ML	64.95		2.85				
<i>Cornus walteri</i>	ML	63.39	10.34	3.80	9.95			
<i>C. walteri</i>	FR	59.95	6.36	13.81	43.67			
<i>Crataegus hupehensis</i>	ML ^a	59.21	12.32	3.21	10.48	9.92	III	III
<i>C. hupehensis</i>	YL ^a	74.53	23.54	2.91	10.64			
<i>C. hupehensis</i>	FL	75.00		2.88			III	III
<i>C. hupehensis</i>	FR ^a	64.16	4.81	2.76	33.35			
<i>Decaisnea fargesii</i>	ML ^a	72.44	18.77	5.38	10.64	12.25		
<i>D. fargesii</i>	YL ^a	75.00		11.79		6.34	II	II
<i>Dendrobenthamia japonica</i>	ML	73.00		3.60			IV	II
<i>D. japonica</i>	FL	79.00		2.29				
<i>Elaeagnus pungens</i>	ML	61.25		2.66			II	I
<i>Euonymus alatus</i>	ML ^a	62.44	11.10	2.74	12.03	11.30		
<i>E. alatus</i>	YL ^a	75.56	10.26	2.77	5.05	5.57	II	II
<i>E. alatus</i>	BK ^a	57.14		3.96	13.41			
<i>Fagus engleriana</i>	ML	55.56	10.24	4.38	25.62	5.62	IV	IV
<i>F. engleriana</i>	FL	53.33		3.26			III	III
<i>F. engleriana</i>	BD	72.16	30.82	2.99	20.60			
<i>F. engleriana</i>	FR	57.40	26.40	26.03	14.02			
<i>Heterodermia</i> spp. ^b	LI	12.01	6.79	3.40	10.01	9.99	II	II
<i>Juglans cathayensis</i>	ML	63.18		3.79				
<i>Lindera obtusiloba</i>	ML ^a	65.96	12.96	3.89	17.34	10.01	III	IV
<i>L. obtusiloba</i>	YL ^a	70.39	14.97	3.33	14.69	5.53		
<i>L. obtusiloba</i>	FL ^a	72.06	20.78	3.12	20.06	6.72	III	IV
<i>L. obtusiloba</i>	BD ^a	74.86	30.07	3.35	19.64	15.79		
<i>L. obtusiloba</i>	FR ^a	56.04	10.22	36.35	11.71	16.01		
<i>Liriodendron chinense</i>	ML	77.80	28.98	4.12	12.15			
<i>Litsea ichangensis</i>	ML	75.05	15.14	5.80	19.24		II	III
<i>L. ichangensis</i>	YL ^a	65.33	12.75	5.44	10.00	6.59		
<i>L. ichangensis</i>	FL ^a	81.54	19.95	5.51	13.59			
<i>L. ichangensis</i>	BD ^a	73.38	23.59	3.20	26.17		I	II
<i>L. ichangensis</i>	FR ^a	54.28	11.52	45.32	13.00		III	IV
<i>Magnolia biondii</i>	FL	89.71		7.12			II	II
<i>M. biondii</i>	BD	60.00		2.90			II	I
<i>Malus hupehensis</i>	ML	57.64	10.71	6.17	9.25			
<i>M. hupehensis</i>	YL ^a	63.09	11.59	4.42	7.22	5.55	III	III
<i>M. hupehensis</i>	FL ^a	80.00		4.11			III	II
<i>M. hupehensis</i>	BD	77.50		6.06			III	II
<i>M. hupehensis</i>	FR ^a	59.12	6.00	3.72	15.73			
<i>Meliosma veitchiorum</i>	ML	62.50		5.18			V	V

Appendix I. Continued

Species	Part	H ₂ O	CP	CFA	CF	WSC	CT	TP
<i>Morus alba</i>	ML ^a	71.32	16.17	3.61	11.28		II	II
<i>Parmelia</i> spp. ^b	LI		8.33	4.21	8.02	14.41	I	II
<i>Platycarya strobilacea</i>	ML	54.00		2.73				
<i>Pinus armandii</i>	ML	63.91	9.37	4.28	29.62			
<i>P. armandii</i>	YL	67.50		14.96			II	IV
<i>P. armandii</i>	SE ^a	29.27	21.15	57.72	4.63			
<i>Populus simonii</i>	ML	54.54	13.49	5.56	17.00			
<i>P. simonii</i>	YL	59.28	11.57	5.89	17.04			
<i>Populus wilsonii</i>	ML	79.63	37.11	3.07	13.36			
<i>P. wilsonii</i>	YL	87.62	27.32	3.24	14.81			
<i>Prunus vaniotii</i>	ML	71.84	20.65	3.15	13.64			
<i>Pterocarya hupehensis</i>	ML	55.00		3.32			III	III
<i>Pterocarya insignis</i>	ML	65.33		3.74				
<i>Quercus glauca</i>	ML	56.72	10.13	3.47	21.83		IV	II
<i>Q. glauca</i>	BD	47.87		3.73				
<i>Q. glauca</i>	FR	68.40	3.99	0.71	2.36			
<i>Quercus spinosa</i>	ML	50.00		2.64			IV	II
<i>Quercus variabilis</i>	ML	63.53	12.18	2.22	21.85	6.01	IV	II
<i>Q. variabilis</i>	YL	79.46	16.10	2.42	13.76	5.29		
<i>Q. variabilis</i>	BD	68.66		3.97			II	II
<i>Q. variabilis</i>	FR	35.08	23.14	54.90	17.26			
<i>Ramalina americana</i> ^b	LI ^a	11.53	5.37	1.80	9.91	16.65	II	II
<i>Rhododendron</i> spp.	FL	85.56		4.12			IV	V
<i>Rhododendron</i> spp.	BD	39.29		1.87		6.30		
<i>Rosa henryi</i>	ML	62.50		4.99			V	II
<i>R. henryi</i>	FL	85.00		3.61			V	II
<i>R. henryi</i>	BD	70.00		1.82			IV	II
<i>R. henryi</i>	FR	62.50		3.25			IV	II
<i>Rhus potaninii</i>	ML	72.15		3.50				
<i>Rhus verniciflua</i>	ML	69.83	18.78	3.52	13.18			
<i>R. verniciflua</i>	YL	76.79	25.64	3.67	12.88			
<i>R. verniciflua</i>	FR	53.43	12.86	33.71	24.40			
<i>Salix wallichiana</i>	ML	59.82	14.86	4.38	15.47		III	IV
<i>S. wallichiana</i>	YL ^a	68.37	16.87	4.79	19.02			
<i>S. wallichiana</i>	FL ^a	78.37	22.19	2.95	17.49			
<i>Sapindus mukorossi</i>	ML	79.50	30.66	3.43	8.15			
<i>Schisandra glaucescens</i>	FR ^a	76.79	5.65	10.98	16.32			
<i>Schoepfia jasminodora</i>	ML	72.96	21.83	4.17	14.12			
<i>Sorbus hupehensis</i>	ML	65.82	11.08	4.82	17.14	4.20		
<i>S. hupehensis</i>	YL ^a	68.21	11.12	5.38	15.86		III	III
<i>S. hupehensis</i>	FL	78.17	29.36	4.99	11.63			
<i>S. hupehensis</i>	FR ^a	65.18	7.29	6.26	15.65			
<i>Stranvaesia davidiana</i>	ML	61.54		3.64			II	II
<i>Sulcaria sulcata</i> ^b	LI ^a	10.42	6.37	3.69	8.77	13.11	II	II
<i>Symplocos paniculata</i>	ML	83.00		4.71			II	II
<i>S. paniculata</i>	FL	75.00		4.30			II	II
<i>Tilia oliveri</i>	ML	67.47	16.26	3.60	23.30		III	IV
<i>T. oliveri</i>	BD	80.00		2.60			III	V
<i>Usnea aciculifera</i> ^b	LI ^a	11.08	5.95	4.31	7.67	15.51	I	II
<i>Viburnum utile</i>	ML	68.00		6.21				
<i>Vitis flexuosa</i>	BD	76.00		4.31			II	II
<i>Weigela japonica</i>	ML	70.22	11.47	2.88	12.23	9.99	III	II
<i>W. japonica</i>	YL	73.80	11.81	3.03	12.51			
<i>W. japonica</i>	FL	80.00		4.12			III	II
<i>W. japonica</i>	BD	75.00		4.30			II	I

Note: ML, mature leaves; YL, young leaves; FL, flowers; BD, buds; FR, fruits; SE, seeds; BK, bark; LI, whole bodies of lichens. H₂O (water): % fresh weight; CP (crude protein): % dry matter; CFA (crude fat): % dry matter; CF (crude fiber): % dry matter; WSC (water soluble carbohydrate): % dry matter; CT (condensed tannin) and TP (total phenolic): level of absorbance (I: <0.1; II: ≥0.1, <0.5; III: ≥0.5, <1.0; IV: ≥1.0, <2.0; V: ≥2.0).

^a Food parts.

^b Lichen species.