

Age-sex analysis for the diet of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China

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Abstract Age-sex differences in diet have been reported in many nonhuman primates, and body size, reproductive costs, and growth are three mutually non-exclusive factors often proposed to explain such differences. Smaller animals tend to feed on high quality foods (high in protein/energy) more often than larger animals due to their higher metabolic requirements per body weight. Animals of different sizes tend to use different substrate levels, leading to dietary differences if food resources are unevenly distributed along substrate levels. Adult females and juveniles experience additional metabolic requirements for reproduction and growth, respectively, and tend to feed on high quality foods more frequently than adult males. We conducted an age-sex analysis for the diet of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia, China. In spite of general age-sex similarities, we found that adult males ate herbs more frequently than juveniles and adult females, most likely because they were more terrestrial. As predicted, juveniles ate high quality foods (young leaves, fruits, seeds, and buds) more frequently, and meanwhile ate low quality foods (barks and lichens) less frequently than adult males across the study year or in some seasons when these food types were eaten. However,

we found high similarities in diet between adult females and adult males. The most likely reason was that the low diversity of food sources and strong phenological synchrony did not allow adult females to select foods based on quality to cope with their higher metabolic constraints compared to adult males. Surprisingly, the only sex difference in diet except herbs was that adult females ate lichens more frequently in autumn. One plausible reason was that lactating females experienced their highest metabolic requirements in the middle period of infant care (autumn), and had to disproportionately increase the intake of lichens due to the limited availability of plant foods.

Keywords *Rhinopithecus roxellana* · Age-sex class · Diet · Body size · Reproductive cost · Growth

Introduction

Age-sex differences in dietary patterns have been observed in many nonhuman primates (Cords 1986; Boinski 1988; Rose 1994; Hemingway 1999; Agetsuma 2001; Hanya 2003; Rothman et al. 2008; Jaman and Huffman 2011). Body size, reproductive costs, and growth are three factors often proposed to explain such differences. These factors are not mutually exclusive.

Differences in body size produce variation in metabolic requirements (Sailer et al. 1985; Agetsuma 2001; Rothman et al. 2008). Smaller animals have higher requirements per body weight because metabolic rate increases with a 0.75 power of body weight (Kleiber 1987). Thus, smaller animals tend to feed on high quality foods (i.e., foods high in energy and protein) more frequently, while larger animals tend to feed on low quality foods more frequently (Rose 1994; Agetsuma 2001). In arboreal and semi-arboreal

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primates, animals of different sizes tend to use different levels of substrate due to the variation in the constraints of body mass and the vulnerability to predators (Boinski 1989; Watanuki and Nakayama 1993; Jaman and Huffman 2011). Such spatial separation may also lead to dietary differences if food resources are unevenly distributed along substrate levels (Remis 1997; Jaman and Huffman 2011).

Besides maintenance requirements, adult females and juveniles experience additional energy and nutrition requirements for reproduction (adult females) and growth (juveniles), and thus tend to feed on foods high in energy and protein more often than adult males (Rose 1994; Hemingway 1999; Hanya 2003; Rothman et al. 2008). Pregnancy and lactation increase an adult female's metabolic rate by up to 25 and 50 %, respectively, and increase her nutrient requirements as well (Portman 1970; Lee 1989). Juveniles require additional nutrients to sustain the accumulation of body mass (Rothman et al. 2008).

The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*), an endangered colobine endemic to China, inhabits temperate forests in mountainous areas at high altitudes of 1000–4100 m, which have strong seasonality with long snowy winters (Li et al. 2002a; Kirkpatrick and Grueter 2010). It exhibits striking sexual dimorphism in body size (Davison 1982; Jablonski and Pan 1995). Body weights of adult males and adult females in captivity are approximately 15.0 and 9.5 kg, respectively (Davison 1982). This species is primarily arboreal, but sometimes forages on the ground (Su et al. 1998; Ren et al. 2001; Li 2007; Zhu et al. 2015). It is a strictly seasonal breeder with conceptions concentrated between September and November and births between March and May (Zhang et al. 2000; Ren et al. 2003; Li and Zhao 2007; Qi et al. 2008).

There have been several reports on the dietary pattern at the group level of *R. roxellana* (Li 2001, 2006; Guo et al. 2007; Liu et al. 2013). Its diet is characterized by lichens, which are available year round and are an uncommon food for primates, supplemented by seasonally available plant foods, including mature leaves, young leaves, flowers, fruits, seeds, buds, and barks of woody plants, and ground herbs. However, little is known about whether and how diet varies among age-sex classes. In this paper, we conduct an age-sex analysis for the diet of this species. Since adult males have been reported to be more terrestrial than other age-sex classes (Ren et al. 2001; Li 2007; Zhu et al. 2015), we predict that adult males will eat herbs more frequently than adult females and juveniles (prediction 1). Furthermore, our recent nutritional study has suggested that this species acquires protein mainly from seasonal plant foods high in protein, including young leaves, flowers, buds, and seeds of woody plants, since the most important food source, lichens, is extremely low in protein (Liu et al. 2013). Fruits and seeds are known to be high in energy

(National Research Council 2003), while mature leaves and barks are usually considered low quality and fallback foods (Hanya 2004; Guo et al. 2007; Grueter et al. 2009; Hanya et al. 2013). Thus, we predict that juveniles and adult females will eat young leaves, flowers, fruits, seeds, and/or buds more frequently than adult males, but eat mature leaves, barks, and/or lichens less frequently (prediction 2 for juveniles, prediction 3 for adult females).

Methods

Study site and subjects

This study was conducted in the Qianjiaping area (ca. 60 km²), the most southeastern part of Shennongjia National Nature Reserve (110°03'–110°34'E, 31°22'–31°37'N), Hubei Province, China. This area is largely rugged with an elevation range of 1500–2663 m. The vegetation is characterized by temperate deciduous broadleaf and evergreen conifer, primary and secondary mixed forest (Li et al. 2002b). Grasslands and shrubs account for a small proportion of the area and are found only in wide valleys and on mountain tops. The climate is highly seasonal. At an elevation of 1700 m, the mean daily temperature is highest in July (ca. 16.3 °C) and lowest in January (ca. –5.5 °C). The annual rainfall is approximately 1800 mm, with the rainy season between July and September. Snowfalls last from November to March. According to the local climate, we defined seasons as spring from April 1st to May 31st, summer from June 1st to August 15th, autumn from August 16th to October 31st, and winter from November 1st to March 31st (the same as Li 2006).

The study group forages mainly in the study area and occasionally ranges out to the adjacent area in the south-east. The group has been semi-habituated and studied periodically since 1999 (Li 2001, 2006, 2007, 2009; Liu et al. 2013). During the study period, group size and composition were counted four times when the animals crossed open areas or when leaf fall in winter made the animals more visible. Adult females have elongated nipples, and are brownish black on the head and upper parts of the body. Adult males, larger than adult females, are grayish black on the top of the head and upper parts of the body. Their shoulders and back are covered by long golden hairs. They also have apparent tumescent warts at the corners of their mouths. Juveniles are smaller, paler, and fluffier than adult females, but with a proportionately larger head and without elongated nipples. Infants have the smallest bodies and are the palest and fluffiest (less than 1 year old). On average, the group contained $130 \pm \text{SD } 27$ individuals ($N = 4$), including $41 \pm \text{SD } 13$ adult males, $53 \pm \text{SD } 25$ adult females, $23 \pm \text{SD } 5$ juveniles, $13 \pm \text{SD } 2$ infants.

Data collection

We followed the study group from August 16th 2003 to August 15th 2004 to collect the data on feeding behaviors via instantaneous scan sampling at 15-min intervals (together with three field assistants). Observations usually began at 10 a.m. and ceased at dusk when the animals reached a sleeping site. We could approach the group to within 20–30 m. We obtained 1470–2140 scans in 15 observation days for each month except for 315 scans in 5 days for August 2003, 260 scans in 5 days for January 2004, 0 scan for February 2004, and 509 scans in 6 days for August 2004. At the beginning of each time interval, we scanned the group from one side to another with the naked eye or binoculars, and for each visible individual, excluding infants, we determined and recorded its age-sex class and behavior in 5 s. If the animal was eating, the food item was noted. Food items were classified into nine types, i.e., mature leaves, young leaves, flowers, fruits, seeds, buds, and barks of woody plants, and herbs and lichens.

Data analysis

We calculated the proportions of feeding records on various food types out of total feeding records across the study year and each season for each age-sex class (i.e., adult females, adult males, and juveniles) to represent the annual and seasonal diets, respectively.

We first employed a chi-square test to analyze whether the frequency of eating each food type was different among age-sex classes across the study year. Because the diet was clearly seasonal and there may be interaction effects of

seasonality and age-sex class on the diet, we also compared the differences in dietary patterns among age-sex classes on a seasonal basis. Specifically, for each season, we examined whether the frequency of eating each food type was different among age-sex classes using a chi-square test. If chi-square tests were significant in the above analyses, we used Fisher's exact tests to perform pairwise comparisons. All tests were two-tailed, with a significance level of 0.05 for chi-square tests and a Bonferroni adjusted significance level of 0.017 ($=0.05/3$) for Fisher's exact tests, respectively. In the analyses for each season, we did not perform statistical tests for the food types that were not or nearly not eaten in a season.

Results

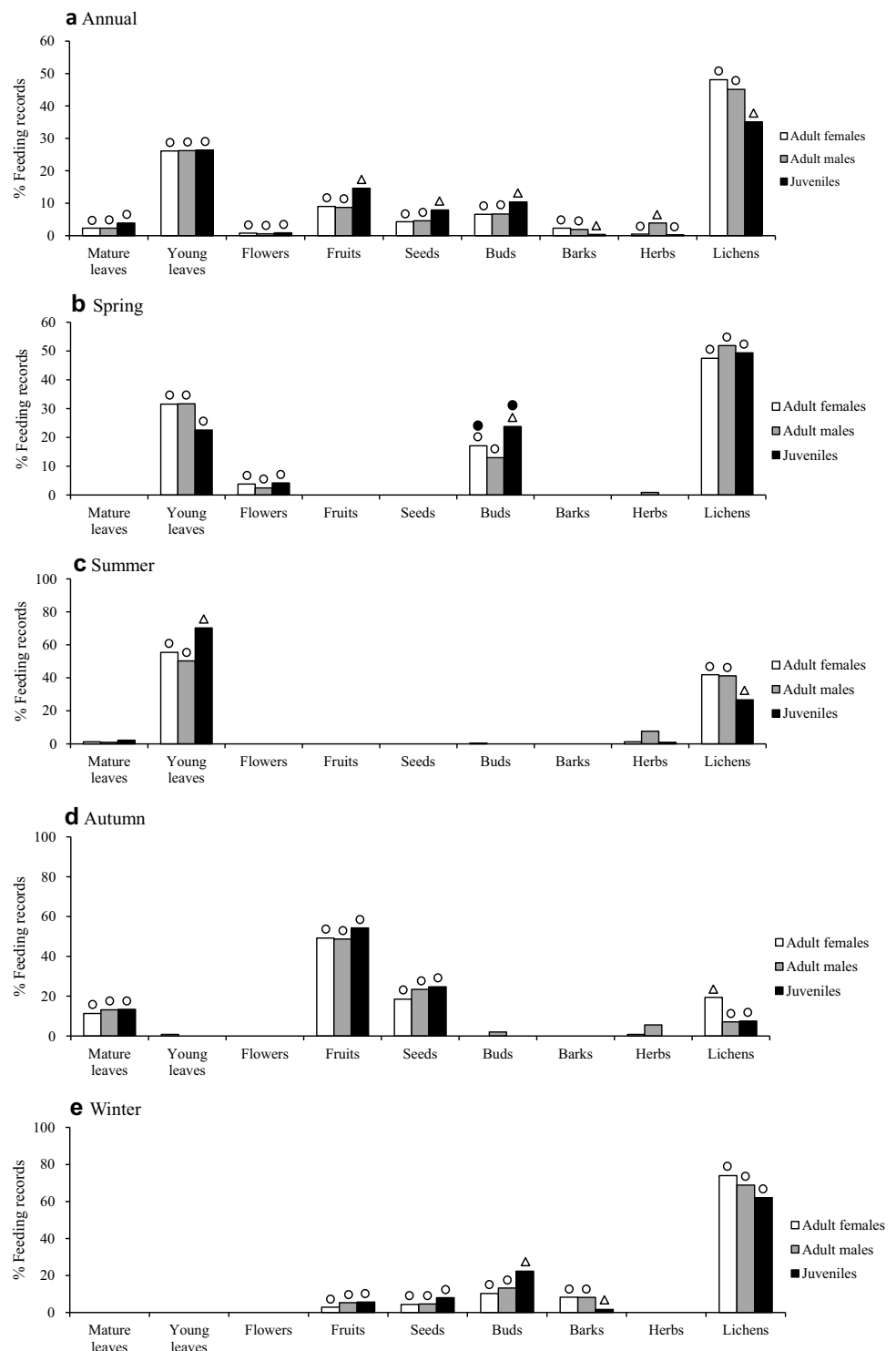
The annual diet and age-sex comparisons

During the study year, we obtained 744, 1292, and 760 feeding records for adult females, adult males, and juveniles, respectively (Table 1). The annual diet had a similar composition for all age-sex classes (Fig. 1a). Lichens composed the largest proportion in the annual diet for all age-sex classes; they accounted for 48.1, 45.1, and 35.1 % of the diet for adult females, adult males, and juveniles, respectively. Young leaves composed the next largest proportion in the annual diet for all age-sex classes; they occupied 26.1, 26.2, and 26.4 % of the diet for adult females, adult males, and juveniles, respectively. Other food types including mature leaves, flowers, fruits, seeds, buds, barks, and herbs were also observed to be eaten by all

Table 1 Numbers of feeding records on various food types for different age-sex classes in a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China (study year: August 16th 2003–August 15th 2004)

Periods	Age-sex classes	Mature leaves	Young leaves	Flowers	Fruits	Seeds	Buds	Barks	Herbs	Lichens	Total
Annual	Adult females	17	194	6	67	32	49	17	4	358	744
	Adult males	30	338	8	112	60	86	25	50	583	1292
	Juveniles	30	201	7	111	60	79	3	2	267	760
Spring	Adult females		50	6			27			75	158
	Adult males		102	8			42		3	167	322
	Juveniles		38	7			40			83	168
Summer	Adult females	3	143				1		3	108	258
	Adult males	4	236						36	193	469
	Juveniles	5	163						2	62	232
Autumn	Adult females	14	1		61	23			1	24	124
	Adult males	26			96	46	4		11	14	197
	Juveniles	25			101	46				14	186
Winter	Adult females				6	9	21	17		151	204
	Adult males				16	14	40	25		209	304
	Juveniles				10	14	39	3		108	174

Fig. 1 Variation in the consumption of various food types among age-sex classes in a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China (study year: August 16th 2003–August 15th 2004). Chi-square tests with a significance level of 0.05 were used to compare the frequencies of eating various food types among age-sex classes and, if significant, Fisher's exact tests with a Bonferroni adjusted significance level of 0.017 ($=0.05/3$) were used for pairwise comparisons. Columns with the same symbols represent no difference (no statistical test for the cases without symbols due to small sample sizes; for buds in spring: different between juveniles and adult males, but not between adult females and adult males or between adult females and juveniles)



age-sex classes, while their proportions in the annual diet were much lower than those of lichens and young leaves.

There was no difference in the frequencies of eating mature leaves, young leaves, or flowers among age-sex classes, whereas significant differences were detected in the frequencies of eating all other food types (Table 2;

Fig. 1a). Specifically, juveniles ate fruits, seeds, and buds more frequently (fruits $P = 0.001$, $P < 0.001$; seeds $P = 0.004$, $P = 0.003$; buds $P = 0.010$, $P = 0.003$), and barks and lichens less frequently (barks $P = 0.001$, $P = 0.003$; lichens $P < 0.001$ for both) than adult females and adult males, while no difference was found in the

Table 2 Comparisons for the intake of various food types among age-sex classes in a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China (chi-square tests: $df = 2$; study year: August 16th 2003–August 15th 2004)

	Mature leaves		Young leaves		Flowers		Fruits		Seeds		Buds		Barks	
	χ^2	<i>P</i> value	χ^2	<i>P</i> value	χ^2	<i>P</i> value	χ^2	<i>P</i> value	χ^2	<i>P</i> value	χ^2	<i>P</i> value	χ^2	<i>P</i> value
Annual	5.40	0.067	0.02	0.989	0.62	0.733	18.08	<0.001	11.71	0.003	10.25	0.006	9.93	0.007
Spring			3.47	0.176	1.16	0.559					7.62	0.022		
Summer			10.99	0.004										
Autumn	0.30	0.859					0.68	0.713	1.32	0.518				
Winter							1.96	0.376	2.97	0.227	10.25	0.006	8.41	0.011
			Herbs				Lichens							
			χ^2		<i>P</i> value		χ^2		<i>P</i> value					
Annual			41.95		<0.001		16.72		<0.001					
Spring							0.43		0.805					
Summer							10.03		0.007					
Autumn							13.27		0.001					
Winter							1.96		0.376					

frequencies of eating these food types between adult females and adult males (fruits $P = 0.808$; seeds $P = 0.741$; buds $P > 0.999$; barks $P = 0.628$; lichens $P = 0.197$). In addition, adult males fed on herbs more frequently than adult females and juveniles ($P < 0.001$ for both), whereas no difference was detected between adult females and juveniles ($P = 0.448$).

Seasonal diet and age-sex comparisons

In general, the diet exhibited a similar trend of seasonal changes, and the dietary composition in each season was similar for adult females, adult males, and juveniles (Table 1; Fig. 1b–e). Lichens were one of main dietary components in all seasons for all age-sex classes. Besides lichens, other main components included young leaves, flowers, and buds in spring, young leaves in summer, mature leaves, fruits, and seeds in autumn, and fruits, seeds, buds, and barks in winter for all age-sex classes. Furthermore, in many cases, no significant difference was detected in the frequencies of eating various food types in the age-sex comparisons on a seasonal basis (Table 2; Fig. 1b–e).

Nevertheless, there were differences in the frequencies of eating some food type(s) in every season among age-sex classes (Table 2; Fig. 1b–e). Specifically, in spring, juveniles ate buds more frequently than adult males ($P = 0.003$), while no difference was detected between adult females and adult males ($P = 0.268$) or between adult females and juveniles ($P = 0.170$). In summer, juveniles fed on young leaves more often ($P = 0.001$, $P < 0.001$) and lichens less often ($P < 0.001$ for both) than

adult females and adult males, whereas there was no difference in the frequencies of eating these two food types between adult females and adult males (young leaves $P = 0.214$; lichens $P = 0.875$). In autumn, adult females spent more time feeding on lichens than adult males ($P = 0.001$) and juveniles ($P = 0.003$), but no difference was detected in the time allocated for eating lichens between the latter two classes ($P > 0.999$). Finally, in winter, juveniles fed on buds more frequently ($P = 0.002$, $P = 0.011$) and barks less frequently ($P = 0.005$, $P = 0.004$) than adult females and adult males, but no sex difference was detected (buds $P = 0.404$; barks $P > 0.999$). In addition, although no statistical test was done due to small sample sizes, it was obvious that adult males fed on herbs more frequently in summer and autumn than adult females and juveniles.

Discussion

To our knowledge, this study is the first attempt to analyze the dietary pattern of *R. roxellana* by age-sex class. In general, we found that the diet exhibited a similar pattern of composition and seasonality for adult males, adult females, and juveniles. As reported on the diet at the group level of the study population (Li 2006), the annual diet was mainly composed of lichens and young leaves for all age-sex classes, while other food types, especially mature leaves, fruits, seeds, and buds, were also seasonally important. It has been shown that the dietary pattern of *R. roxellana* is strongly influenced by the seasonality of food availability (Li 2006).

In spite of the general similarities, we found that adult males ate ground herbs more frequently compared to adult females and juveniles, consistent with our prediction 1. This was most likely because adult males were more terrestrial than adult females and juveniles (Ren et al. 2001; Li 2007; Zhu et al. 2015). For the study population, Li (2007) reported that adult males spent 5.4 % of their time on the ground, whereas adult females and juveniles spent only 1.4 and 0.6 % of their time on the ground, respectively. The larger body size of adult males apparently restricted their use of upper supports. Simultaneously, adult males were less vulnerable to terrestrial predators, allowing them to spend more time on the ground than other age-sex classes. Several terrestrial carnivorous and omnivorous mammals have been suggested to be the predators of *R. roxellana*, including leopards (*Panthera pardus*), wolves (*Canis lupus*), dholes (*Cuon alpinus*), and black bears (*Ursus thibetanus*) (Su et al. 1998; Li 2007; Huang et al. 2014). The finding that adult males are more terrestrial than adult females and juveniles has also been reported in other primates, such as white-faced capuchins (*Cebus capucinus*: Rose 1994) and Yunnan snub-nosed monkeys (*Rhinopithecus bieti*: Grueter et al. 2013).

For *R. roxellana*, we could not exclude the effect of displacement by adult males, who are more competitive, on the lower frequency of eating herbs in adult females and juveniles. The monkeys mainly ate one herb species, *Heracleum hemsleyanum*, whose leaves are rich in protein (21.5 % of dry matter) (Li 2007). Herbs, as a protein source, appear to be important with respect to the extremely low concentrations of protein in some main food types, particularly fruits and lichens (Liu et al. 2013). Protein concentrations of fruits and lichens (means 7.3 and 5.9 % of dry matter, respectively) consumed by *R. roxellana* in Shennongjia are much lower than those (15–22 % of dry matter) recommended by the National Research Council for feeding nonhuman primates (National Research Council 2003).

Our prediction 2 was also generally supported. We found that juveniles fed on young leaves, seeds, and buds more frequently, and meanwhile fed on barks and lichens less frequently than adult males across the study year or in some seasons when these food types were eaten. This was in line with previous reports on the group-level feeding behaviors of this primate (Li 2006; Guo et al. 2007; Liu et al. 2013). Young leaves, fruits, seeds, and buds are usually preferred when available, while the intake of barks and lichens, the fallback foods, is increased when the availability of preferred foods is limited. As mentioned above, our nutritional study has confirmed that young leaves, fruits, seeds, and buds are high in energy/protein, while lichens are very low in protein (Liu et al. 2013). Similar findings that juveniles eat high quality foods more

frequently and low quality foods less frequently than adult males have also been reported in many other primates, such as redbell monkeys (*Cercopithecus ascanius*: Cords 1986) and Japanese monkeys (*Macaca fuscata*: Agetsuma 2001). In some studies, foliage (both mature and young leaves) was considered a low quality food and juvenile primates fed on foliage less frequently compared to adult males (*Cercopithecus mitis*: Rudran 1978; *M. fuscata*: Agetsuma 2001, Hanya 2003). This was because juveniles of these species had other food choices, particularly insects, which contained protein concentrations much higher than foliage. Although flowers consumed by *R. roxellana* are also rich in protein and thus can be considered a high quality food (Liu et al. 2013), we did not detect significant differences in the frequency of eating flowers between juveniles and adult males. This was likely because flowers occupied only a very small proportion in the diet for both juveniles and adult males (Table 1; Fig. 1).

Contrary to our prediction 3, we found high similarities in diet between adult females and adult males, and the only sex difference except herbs was that adult females ate lichens more frequently than adult males in autumn, when lichens played the least important role through the year (Fig. 1). Even after we combined young leaves, flowers, fruits, seeds, and buds as high quality foods, and barks and lichens as low quality foods across the study year, there was also no sex difference in the frequencies of eating high (chi-square test for overall comparison $\chi^2 = 20.01$, $df = 2$, $P < 0.001$; Fisher's exact tests for pairwise comparisons $P > 0.999$) or low (chi-square test $\chi^2 = 21.27$, $df = 2$, $P < 0.001$; Fisher's exact tests $P = 0.154$) quality foods. However, adult female *R. roxellana* should experience higher metabolic constraints compared to adult males in light of the great sex differences in body size and reproductive costs. Adult males are 1.5–2.0 times heavier in body mass than adult females (Davison 1982; Jablonski and Pan 1995). Furthermore, in this seasonal breeder, the inter-birth interval is approximately 2 years, the length of gestation is 6–7 months, and weaning occurs when infants reach 1–1.5 years old (Zhang et al. 2000; Ren et al. 2003; Qi et al. 2008). These reproductive parameters suggest that most adult females are likely to be either pregnant or lactating in any given period of the year. Many previous studies have documented that adult females eat high quality foods more frequently and low quality foods less frequently than adult males (Boinski 1988; Rose 1994; Agetsuma 2001; Vasey 2002).

There can be three potential explanations for the high sex similarities in diet. First, the proportions of feeding records on food types are just a crude proxy measure for food composition (Chivers 1998; Nakagawa 2009). The rates of energy and nutrition intake, for example, play an essential role in the estimation of food composition since

they may vary largely for different specific food items (reviewed in Nakagawa 2009). While we could not exclude the influences of this factor, many studies examined the sex differences in dietary composition by the proportions of feeding records on food types (Cords 1986; Boinski 1988; Rose 1994; Agetsuma 2001; Prates and Bicca-Marques 2008).

Second, as *R. roxellana* is primarily a lichen-eater (Li 2006; Liu et al. 2013; Yang et al. 2014; this study), the low floristic diversity of food species and strong phenological synchrony may not have allowed adult females to cope with their higher metabolic constraints compared to adult males by selecting foods based on quality. At the study site, the availability of plant foods is strongly seasonal with any food type available in only 1–2 seasons (Li 2006). More importantly, apart from lichens, the diet is composed of only a small number of plant species (Li 2006; Liu et al. 2013; Yang et al. 2014). In Liu et al.'s (2013) study, for example, the 5 most important plant species accounted for 81 % of the rest of the annual diet. In Yang et al.'s (2014) study, 76 % of the diet apart from lichens was attributed to only 1 most important species in autumn, 90 % attributed to 2 species in winter, and 79 and 68 % attributed to 5 species in spring and summer, respectively. Indeed, several studies have shown that the low diversity of food sources can lead to high sex similarities in dietary patterns (Bicca-Marques and Calegario-Marques 1994; Pavelka and Knopff 2004; Prates and Bicca-Marques 2008). Juvenile *R. roxellana* in this study could still be able to select foods based on quality compared to adult males probably because they have lower metabolic requirements on an absolute basis (Kleiber 1987), and thus are less limited by food availability.

Third, adult female primates may adopt the alternative way to cope with their metabolic constraints compared to adult males, i.e., increasing feeding time for more dry matter (Boinski 1988; Rose 1994; Rothman et al. 2008; Li et al. 2014), especially when the diversity of food sources is low (Bicca-Marques and Calegario-Marques 1994). Indeed, the study on time budgets of *R. roxellana* (the same study group and period as this study) has shown that adult females spend much more time feeding than adult males: 23.2 versus 13.9 % for overall, 23.1 versus 15.4 % for spring, 26.4 versus 18.3 % for summer, 20.7 versus 9.5 % for autumn, and 23.9 versus 13.0 % for winter (Li 2009). Thus, we conclude that the high sex similarities in dietary pattern in this study most likely resulted from the very low diversity of food sources at the study site, and adult females had to cope with their higher metabolic constraints compared to adult males by increasing feeding time to obtain more dry matter.

It was a surprising but interesting finding that adult female *R. roxellana* ate lichens, a presumed low quality

food, more frequently than adult males in autumn. The reasons for this result are not readily apparent. We believe that this was not due to the monopolization of high quality foods by adult males who are more competitive than other age-sex classes, since juveniles generally fed on high quality foods more frequently than adult males. Alternatively, in several primates, the metabolic requirements of lactating females first increase steadily until infants begin to walk independently, and then decrease until weaning, suggesting the significant costs for infant carrying (*Chlorocebus aethiops*: Lee 1987; *C. capucinus*: McCabe and Fedigan 2007). Previous studies of *R. roxellana* have also shown that for infants immediately after about 6 months old (in late autumn), there is a significant increase in time for moving freely, and meanwhile a significant decrease in time for sucking (Li et al. 2011; Luo et al. 2011). Thus, we tentatively propose that probably because lactating female *R. roxellana* experienced the highest metabolic requirements for infant care in autumn, and they had to disproportionately increase the intake of lichens, readily available, due to the limited availability of plant foods (as mentioned above), this led to the sex difference in the frequency of eating lichens. The lichen intake of adult females relative to adult males can be estimated by $(\% \text{ lichens in diet} \times \% \text{ feeding time for adult females}) / (\% \text{ lichens in diet} \times \% \text{ feeding time for adult males})$. The value is much larger in autumn (5.95) than in other seasons (1.37 in spring, 1.47 in summer, 1.98 in winter) ($\% \text{ lichens in diet}$ from Table 1; $\% \text{ feeding time}$ from the above paragraph, Li 2009).

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