

Seasonal variation in diet and nutrition of the northern-most population of *Rhinopithecus roxellana*

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There is a great deal of spatial and temporal variation in the availability and nutritional quality of foods eaten by animals, particularly in temperate regions where winter brings lengthy periods of leaf and fruit scarcity. We analyzed the availability, dietary composition, and macronutrients of the foods eaten by the northern-most golden snub-nosed monkey (*Rhinopithecus roxellana*) population in the Qinling Mountains, China to understand food choice in a highly seasonal environment dominated by deciduous trees. During the warm months between April and November, leaves are consumed in proportion to their availability, while during the leaf-scarce months between December and March, bark and leaf/flower buds comprise most of their diet. When leaves dominated their diet, golden snub-nosed monkeys preferentially selected leaves with higher ratios of crude protein to acid detergent fiber. While when leaves were less available, bark and leaf/flower buds that were high in nonstructural carbohydrates and energy, and low in acid detergent fiber were selected. Southern populations of golden snub-nosed monkey can turn to eating lichen, however, the population studied here in this lichen-absent area have adapted to their cool deciduous habitat by instead consuming buds and bark. Carbohydrate and energy rich foods appear to be the critical resources required for the persistence of this species in temperate habitat. The dietary flexibility of these monkeys, both among seasons and populations, likely contributes to their wide distribution over a range of habitats and environments.

KEYWORDS

diet selection, dietary switching, folivore, leaf scarcity, nutritional ecology

1 | INTRODUCTION

Food items differ in their nutrient content, digestibility, ease of acquisition, and spatial and temporal availability, and these factors drive diet selection and shape feeding strategies in primates (Edwards & Ullrey, 1999; Lambert & Rothman, 2015; Rothman, Dierenfeld, Hintz, & Pell, 2008). The challenges of finding a suitable diet are universal among

animals, regardless of whether they occur in tropical or temperate regions (Ganzhorn, 2002; Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2014; Tsuji, Hanya, & Grueter, 2013). Primates deal with spatial and temporal variation in food availability by using different foraging strategies, including dietary switching where lower-quality "fallback foods" may be consumed (Lambert, 2007; Marshall & Wrangham, 2007; Marshall, Boyko, Feilen, Boyko, & Leighton, 2009).

Primate dietary strategies show distinct interspecific variation among regions (Brockman & Van Schaik, 2005). Primates inhabiting tropical forests often ingest mature leaves and unripe fruits during lean-seasons when preferred foods (often young leaves and ripe fruits) are scarce (Chapman & Rothman, 2009; Marshall et al., 2009; Mitchell 1994). However, in temperate regions where deciduous tree species are common, leaves are absent or dramatically reduced in availability and quality when it is cold (Dixon, 1976; Hanya & Chapman, 2013; Tateno, Aikawa, & Takeda, 2005). Folivorous primates inhabiting temperate forests can face 4–5 months of leaf scarcity during this period, and switch their diet to items such as lichen, buds, and bark (Grueter, Li, Ren, Wei, Xiang, et al., 2009; Nakagawa, 1989, 1997).

Most colobines are found in tropical Africa and subtropical regions of southern Asia, but the snub-nosed monkeys in this study, occur in temperate eastern Asia. Many tropical and subtropical species can consume leaves (young and/or mature) year-round (Harris & Chapman, 2007; Oates 1988; Wasserman & Chapman, 2003); however, for some snub-nosed monkeys (*Rhinopithecus roxellana* and *R. bieti*), leaves are scarce from late autumn to early spring and they thus rely on alternative resources (Ding & Zhao, 2004; Grueter, Li, Ren, Wei, & Van Schaik, 2009; Ren, Li, Li, & Wei, 2010). In addition, where snub-nosed populations occur, snow may cover the ground for 3–4 months of the year making foraging difficult and the animals must deal with cold temperatures (below -10°C).

Morphology of the gastrointestinal tract and symbiotic gut microbiota are directly related to animals' dietary spectrum (Chivers & Hladik, 1980; Ley et al., 2008) and other aspects of the animal's behavior (Matsuda, Chapman, Physilia, Sha, & Clauss, 2017). Generally, foregut-fermenting folivores (Colobinae species) have higher digestive efficiencies than hind-fermenters (Edwards & Ullrey, 1999). Colobines have evolved several physiological specializations to consume hard-to-digest food, including sharp molars, enlarged salivary glands, and enlarged and multi-chambered stomach with diverse microorganisms (Hale et al., 2017; Kay & Davies, 1994; Zhou et al., 2014). Edward and Ullrey (1999) reported the apparent digestibility and digesta passage of some captive tropical/semitemperate dwelling colobines (*Colobus guereza kikuyuensis*, *Pygathrix nemaeus*, and *Trachypithecus francoisi francoisi*), Huang (2014) and Kirkpatrick, Zou, Dierenfeld, and Zhou (2001) determined the same parameters for two temperate-living colobines, *R. roxellana*, and *R. bieti*. These comparative studies indicate that temperate-living colobines have higher digestibility of dry matter, neutral detergent fiber (NDF, total fiber fraction), and energy than tropical/semitemperate dwelling colobines (dry matter: 81.3% vs. 76.6%; NDF: 77.6% vs. 74.7%; energy: 78.9% vs. 75.6%, respectively). In addition, *Rhinopithecus bieti* have shorter transit and retention times than the tropical/semitemperate foregut fermenters (mean transit time: 27 hr vs. 37.4–43.5 hr; mean retention time: 47 hr vs. 37.6–68.6 hr). Also, *Rhinopithecus* has a different microbial community composition than other tropical/semitemperate colobines (Hale et al., 2017). These adaptations may facilitate *Rhinopithecus* living in temperate habitats.

The nutritional composition of potential foods plays an important role in their selection (Lambert & Rothman, 2015). For large primates, leaves are generally the primary source of protein

(Matsuda, Tuuga, Bernard, Sugau, & Hanya, 2013; Rothman, Pell, Nkurunungi, & Dierenfeld, 2006), whereas fruits and seeds provide more nonstructural carbohydrates (mainly water soluble carbohydrates and starch) (Houle, Conklin-Brittain, & Wrangham, 2014; Rothman et al., 2006) and lipids (Righini, Garber, & Rothman, 2017), while bark and twigs are of lower quality, containing high levels of indigestible fiber and lignin (Lambert & Rothman, 2015; Wallis et al., 2012).

Golden snub-nosed monkey (*R. roxellana*) is an endangered Asian colobine inhabiting high-altitude mountainous temperate forests (from 1,500 to 3,400 m) across central China ($31^{\circ}22' \text{ N}$ to $33^{\circ}50' \text{ N}$) (Guo, Ji, Li, & Li, 2008; Li, Pan, & Oxnard, 2002; Ren et al., 2010). This species is the northern-most colobine and exhibits a flexible diet comprising primarily leaves, but the diet also contains fruits/seeds, lichen, and bark/buds (Guo, Li, & Watanabe, 2007; Kirkpatrick, Gu, & Zhou, 1999; Li, 2006; Li, Jiang, Li, & Grueter, 2010). However, there are marked differences in diet among populations (Ren et al., 2010) (Table 1). In Shennongjia National Nature Reserve, young (19.9%) and mature leaves (16.7%) dominate the diet during spring and summer; but as leaf availability declines, they switch to eating pine seeds (*Pinus armandii*; 30.0% of the diet, 57.8% of lipid content), leaf/flower buds (16.0% of diet, 28.3% of protein content), and fructose lichen (39.5% of diet, 12.3% of water soluble carbohydrate) (Liu, Stanford, Yang, Yao, & Li, 2013). At the Baihe National Nature Reserve, they shift from eating leaves in the summer (90% of monthly diet) to lichen in the winter (51% of monthly diet) during which time leaves are only occasionally eaten (8% of monthly diet). Thus, their diets tend to be protein-rich in summer and carbohydrate-rich in winter (Kirkpatrick et al., 1999).

We examined the diet of golden snub-nosed monkeys in Zhouzhi National Nature Reserve ($33^{\circ}42' - 33^{\circ}54' \text{ N}$, $107^{\circ}45' - 108^{\circ}18' \text{ E}$, 56.39 km², altitude: 1,400–2,896 m above sea level, hereafter Zhouzhi), which is the northern-most population of this species (Li et al., 2001). Our study group has a long leaf-scarce period from December to March, at which time it is cold (-8.3°C) (Happel & Cheek, 1986; Li, Chen, Ji, & Ren, 2000) and snow covers the ground for 4–6 months a year (Li, Ma, & Hua, 1982). We quantified the diet of snub-nosed monkeys and their nutrient (particularly protein) and energy content. We specifically examine: (i) whether or not golden snub-nosed monkeys switch their foraging strategy between seasons and (ii) how they obtain sufficient protein during the leaf-scarce season.

2 | METHODS

2.1 | Study site and subjects

This study was conducted in Yuhuangmiao region, northeast of Zhouzhi, on the northern slopes of Qinling Mountains, which is the most northern location of any colobine. The reserve has a semi-humid montane climate that supports a diversity of vegetation types depending on altitude—deciduous broadleaf (1,400–2,200 m), mixed deciduous broadleaf and conifer (2,200–2,600 m), and conifer (>2,600 m). During our study the highest monthly mean temperature

TABLE 1 Diets of *Rhinopithecus roxellana* at different study locations, all dietary data were based on the percent proportion of feeding records

| Site | Period | Leaves | Lichens | Fruits/Seeds | Buds | Bark | Others | Reference |
|-------------------|----------|--------|---------|--------------|------|------|--------|---------------------------|
| BNNR | June | 90 | 8 | | | | | Kirkpatrick et al. (1999) |
| | November | 43 | 51 | | | | | |
| SNNR | | 32.22 | 43.28 | 14.57 | 5.36 | 1.36 | 4.22 | Li (2006) |
| ZNNR ^a | | 24.0 | 29.0 | 29.4 | 4.2 | 11.1 | 1 | Guo et al. (2007) |
| QNNR | Summer | 25 | | 72.2 | | | | Li et al. (2010) |
| | Winter | 73 | | 5.6 | | | | |
| ZNNR ^b | | 37.2 | 1.3 | 22.5 | 16.2 | 13.5 | 9.3 | This study |

BNNR, Baihe National Nature Reserve, Sichuan Province; SNNR, Shengnongjia National Nature Reserve, Hubei Province; ZNNR^a, West Ridge Troop of Zhouzhi National Nature Reserve, Shaanxi Province; QNNR, Qingmichuan National Nature Reserve, Shaanxi Province; ZNNR^b, East Ridge Troop of Zhouzhi National Nature Reserve, Shaanxi Province.

was in July (20.8 °C) and the lowest was in January (-2.5 °C; assessed with a CR200X Datalogger, Campbell Scientific; Vaisala Weather Transmitter, WXT520, Vaisala, Finland) and the annual rainfall was 690 mm. Temperatures were typically below 0 °C from November to March. The snowfall level is not available in our site. The group has been studied continuously since 2001 and observers can watch the animals from a distance of 3–10 m without any sign of disturbance (Zhang, Watanabe, Li, & Tan, 2006). The group contains 13 adult males and multiple females units (OMUs) with 135 individuals. The group is provisioned for 5 months each year (April to May and October to December). To provision the animals we searched for the group starting at 6:00 a.m. and then led them to provisioning site. We provided 10 kg of corn grain and 5 kg freshly sliced radish by spreading the food across a 30 × 50 m flat area (1,419 m above sea level). Not all OMUs came to the site, but of those that did (6 to 10 units), we estimate that they ate 150 g per individual per day. To decrease the effect of provisioning on diet selection, the group was not provisioned for 10 consecutive each month and diet data was only collected 80 hr after provisioning stopped for 7 successive days. This 80 hr criteria was based on the retention time of *Rhinopithecus bieti* (47 ± 17 hr mean ± standard deviation; Kirkpatrick et al., 2001).

2.2 | Field data collection and phytochemical analysis

Dawn to dusk observations were conducted by RH from July 2012 to June 2013 for 7 to 12 days per month. Food items eaten (part and species) were recorded during instantaneous scan samples of 5 min duration and an interval of 15 min. During each scan, diet data was recorded on as many adult males, adult females, and juveniles as was possible and on average 17.3 ± 6.5 individuals (range 12–33) were observed per 5-min scan, average 9.14 hr (±0.12, standard error) per day were followed and 868 hr in total. If an individual was holding, chewing, or otherwise processing a food item, this was considered as feeding behavior. We categorized food items into 13 classes: young leaf, mature leaf, seed, ripe fruit, bark, bud (including leaf bud and flower bud), lichen, twig, fungus, flower, grass, insect, and clay. The monkeys not observed to consume unripe fruit. We divided the study into four seasons: spring (March to May), summer (June to August), autumn (September to November), and winter (December to February).

To determine food availability, we sampled 32 plots (50 × 50 m²) randomly distributed in the group's core area (1% of the home range) (Huang, 2015). We identified and measured the girth of all trees with diameter at breast height (DBH) ≥ 15 cm, recording 8,298 trees and 1,518 woody lianas. To quantify monthly phenology, we selected 10 trees per species from the 25 most abundant species and recorded food item abundance on a 0–4 scale. Subsequently, we calculated a seasonal food availability index (FAI) by multiplying the seasonal phenology score (mean score of 3 months) by the density of tree species (number of stem/ha) (Guo et al., 2007).

To determine the nutritional value of food items, we collected samples from at least 10 plants that the animals were seen feeding from within two days of the observed feeding bout (Chapman, Chapman, Rode, Hauck, & McDowell, 2003). Only the exact plant part ingested by the monkeys was collected (e.g., leaf with petiole or not, bark with periderm or not, seed with husk or not; Rothman, Chapman, & Van Soest, 2012). Because of the high dietary diversity, rarely eaten food (<0.5% of feeding time) and low-density foods were not sampled. Some uneaten plant parts were also collected and analyzed for comparison (leaves *N* = 11, bark *N* = 13). The same foods consumed in different seasons were analyzed separately. Samples were weighed within 0.2–3 hr of collection and dried to constant weights in a drying oven (45 °C) and then sealed for later phytochemical analysis at Northwest University, Xi'an by RH.

We analyzed the content of each of the food samples, including crude protein (CP), lipids, water soluble carbohydrate (WSC), starch, neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL, lignin), and ash. Cellulose was calculated taking the difference between ADF and ADL, while hemicellulose was scored as the difference between NDF and ADF. All samples were ground and sieved through a 1-mm screen.

Nitrogen content was determined with the standard Kjeldahl method (BUCHI, K-360, Switzerland), and crude protein was calculated by multiplying N (nitrogen content) by 6.25 (Maynard & Loosli, 1969; Van Soest, 1994). Petroleum ether was used to extract total lipids with a FOSS Soxtec machine (ST-310 Extraction Unit, Sweden, AOAC, 1990). Water-soluble carbohydrate was assayed with anthrone reaction using a glucose standard and starch was calculated via Fehling's solution and 1% hydrochloric acid hydrolysis

(Lawler, Aragonés, Berding, Marsh, & Foley, 2006). Fiber fractions (NDF, ADF, and ADL) were determined sequentially via an ANKOM A2000i fiber analyzer (USA) (Rothman et al., 2012). We then burned plant samples in a muffle furnace for 3.5 hr at 550 °C to obtain ash content (Rothman et al., 2012). Three to five replications were performed for all analyses. Total nonstructural carbohydrate (TNC) was calculated after subtracting the percentage of CP, lipids, NDF, and ash from the total dry mass (Rothman et al., 2012). All nutritional components are reported as percent dry matter.

2.3 | Data analysis

Metabolizable energy (ME) of each food item was calculated using the summation of crude protein, lipids, total nonstructural carbohydrate, and fiber with conversion factors of 17 kJ/g for CP, 37 kJ/g for lipids, and 16 kJ/g for TNC (Conklin-Brittain, Knott, & Wrangham, 2006). Snub-nosed monkeys can ferment fiber in the foregut to obtain energy, thus we took the energy from fiber (cellulose and hemicellulose) into account. Since cellulose and hemicellulose are carbohydrates that could theoretically use conversion factor (16 kJ/g), and nearly 4 kJ/g of energy derived from digest/ferment fiber is used by anaerobic microbes (Conklin-Brittain et al., 2006). In addition, Huang (2015) reported the NDF digestibility (74.3%) of *R. roxellana* in captivity, thus the physiological fuel value from fiber was estimated as $0.743 \times 12 = 9$ kJ /g.

We compared the diversity of food species among seasons (top 15 food species of each season were selected) using the Shannon-Wiener index (H') (Krebs, 1999). The relationships between feeding time and food availability and nutritional properties were evaluated with a Spearman Rank Correlation. We computed Vanderploeg and Scavia's electivity index, E^* (Lechowicz, 1982) to estimate the preferences of food choice. The food items and tree species we chose to estimate the electivity index that accounted for more than 88% of the total annual diet. The electivity index was calculated as

$$E^* = ((r_{is}/p_s)/\sum_i(r_{is}/p_s) - 1/n)/((r_{is}/p_s)/\sum_i(r_{is}/p_s) + 1/n)$$

where r_{is} is the percentage of food items i belonging to species s in the diet (based on the feeding records), p_s is the availability of food item i belonging to species s , and n is number of food items or tree species.

Kruskal-Wallis tests were used to test if the nutritional component and metabolizable energy differed among mature/young leaves, bark, buds, and lichen and if there was a significant difference, we conducted pairwise comparisons using the Steel-Dwass test. We also contrasted the nutritional constituents between consumed and unconsumed foods, both young and mature leaves using t -test. t -tests were also used to compare variation in seasonal FAI for all plant parts between leaf-abundant and leaf-scarce periods. Paired t -test was used to compare seasonal variation (summer and winter) in all variables for the mature leaves of the same species. Steel-Dwass test was run in JMP Pro 13, while other tests were performed in SPSS V21.0.

3 | RESULTS

3.1 | Seasonal diets

The overall diet of the golden snub-nosed monkeys in Zhouzhi comprised 20.1% young leaves, 17.1% mature leaves, 13.6% seeds, 8.9% ripe fruits, 16.2% buds, 13.5% bark, 4.5% twigs, 2.4% flowers, 1.3% lichens, and 2.4% other items (0.6% for insects, 1.0% for fungi, and 0.8% for clay), but there was considerable seasonal fluctuation in the plant parts eaten (Figure 1). Leaves were primary food consumed from April to November (mean \pm standard deviation: $53.2 \pm 13.8\%$; Figure 1). As the proportion of leaves (young and mature) in the diet declined, there was an increase in the proportion of buds/bark consumed ($r_s = -0.818$, $N = 12$, $p = 0.001$). Seeds from *Quercus* spp. (oak) formed a large part of the diet from September to March ($15.1 \pm 4.1\%$). The diversity of food species (Shannon-Wiener index, H') differed between seasons with the most diverse diet occurring in the spring ($H' = 2.46$) and the least diverse diet in summer ($H' = 2.20$), when the monkeys had a higher proportion of leaves in their diet. In the remaining seasons the diet was intermediate in diversity (autumn: $H' = 2.31$, and winter: $H' = 2.36$).

3.2 | Relationship between diet and food availability

Plant parts varied in availability among seasons, except for bark (Figure 2). Leaves were less available during winter and early spring (leaf-scarce period—December 2012 to March 2013; leaf FAI <200) than in other months (leaf-abundant period, from April to November, leaf FAI was >200; $t = 3.060$, $df = 40$, $p = 0.006$) and the peak of seasonal leaf consumption (Figure 1) and availability (Figure 2) were in summer. No difference in bud availability was found between the leaf-abundant and leaf-scarce periods ($t = 0.580$, $df = 24$, $p = 0.567$), nor did bud consumption vary seasonally ($t = -1.301$, $df = 24$, $p = 0.206$). When leaves became scarce, the monkeys switched to feeding on bark and buds (36.7% and 32.7%, respectively), and the bark consumption was higher in the leaf-scarce period than the leaf-abundant period ($t = -3.104$, $df = 24$, $p = 0.005$). Seed availability and consumption did not differ between leaf-abundant and leaf-scarce period ($t = 0.827$, $df = 10$, $p = 0.428$ for availability; $t = 0.516$, $df = 10$, $p = 0.619$ for consumption). In contrast, fruit availability and consumption during leaf-abundant period was greater than in leaf-scarce period

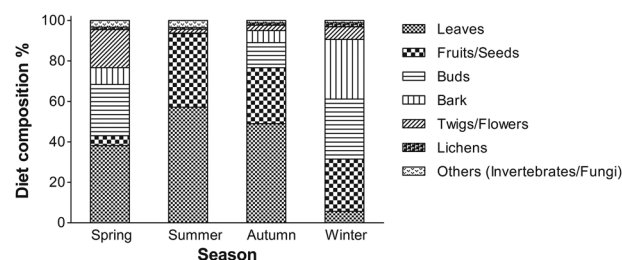


FIGURE 1 Diet composition of *Rhinopithecus roxellana* in Zhouzhi National Nature Reserve, China

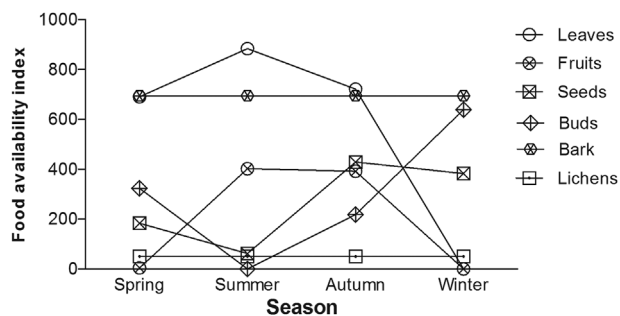


FIGURE 2 Food Availability Index (FAI) for the species studied of leaves, fruits, seeds, buds, barks, and lichens in Zhouzhi National Nature Reserve, China recorded from July 2012 to June 2013

($t = 2.439$, $df = 18$, $p = 0.037$ for availability; $t = 0.639$, $df = 18$, $p = 0.044$ for consumption).

The 25 food species that we monitored constituted 88.7% of the snub-nosed monkey's diet. *Celastrus orbiculatus* and *Quercus aliena* (oak) were the species with the greatest FAI scores, accounting for 33.3% and 20.1% of total FAI respectively (Supplementary Table S1). Overall, foods that were more available were eaten more ($r_s = 0.508$, $N = 118$, $p < 0.001$). *Quercus* trees were common in the monkey's habitat, comprising 35% of the stems >15 cm DBH and their seeds were important foods. As the availability of *Quercus* seeds increased, so did its consumption ($r_s = 0.972$, $N = 12$, $p < 0.001$); however, availability and time spent eating their seeds did not differ between leaf-abundant and leaf-scarce period ($t = 1.338$, $df = 10$, $p = 0.211$ for availability; $t = 2.062$, $df = 10$, $p = 0.066$ for consumption).

The only foliage in winter was the grass *Glechoma longituba*, which was not common, and it only accounted for 4.6% of the feeding time in winter. Two foliose lichens, *Ramalina sinensis*, and *Parmelia* sp., were eaten year-round, but accounted for only a small proportion of the group's annual diet ($1.3 \pm 0.05\%$), which was in accordance with their low availability (Figure 2). Our study showed these monkeys preferred some food items from specific species, such as leaves of *Morus australis*, buds of *Populus purdomii*, leaves of *Prunus armeniaca*, and fruits of *Bothrocaryum controversum*. These plant species, plus *Padus asiatica*, are top five most preferred food species (Table S2) accounting for 23.1% of monkeys' diet. The electivity index of some food species varied with season, which correlated with the fluctuation of food availability, and nutrients (see Table S2).

3.3 | Nutritional properties

We collected 167 food items from 82 plant species and evaluated their nutritional properties (Figure 3). Young leaves contained more protein than other plant parts ($p < 0.05$, Table S2), leaves (young and mature) contained less NDF, ADF, ADL than bark ($p < 0.05$), and bark had higher cellulose content than mature leaves ($p = 0.005$). Lichens had more hemicellulose than any other plant parts ($p = 0.011$). However, no difference in ME was found between bark and other plant parts ($p > 0.05$) except ripe fruits contained higher ME than bark ($p < 0.001$; Tables S3 and S4). The ratios of CP/ADF differed among plant parts ($H = 97.712$, $df = 9$, $p < 0.001$, Table 2) with leaves (young and mature)

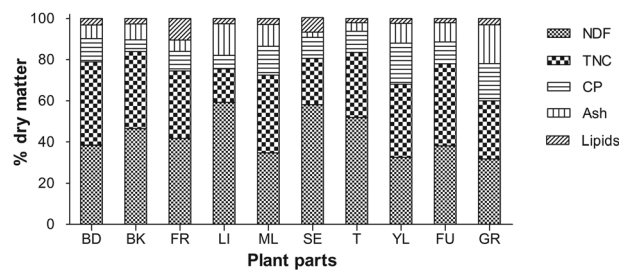


FIGURE 3 Nutritional components of the plant parts consumed by *Rhinopithecus roxellana* in Zhouzhi National Nature Reserve, China. CP, crude protein; TNC, total nonstructural carbohydrate; NDF, neutral detergent fiber; BD, buds; BK, bark; FR, fruits; LI, lichens; ML, mature leaves; SE, seeds; T, twigs; YL, young leaves; FU, fungi; GR, grass

having a larger CP/ADF ratio than all other plant parts ($p < 0.05$) except foliose lichens ($p > 0.05$, Table S3). Young leaves contained more CP, CP/ADF, and starch than mature ones (t -test: CP: $t = -5.429$, $p < 0.001$; CP/ADF: $t = -3.642$, $p < 0.001$; starch: $t = -3.489$, $p < 0.001$), while the latter contained more WSC than the former (WSC: $t = 2.379$, $p = 0.017$, Table S4). Consumed leaves had more protein (t -test: $t = 2.123$, $df = 35$, $p = 0.041$) and lower lignin ($t = -2.523$, $df = 35$, $p = 0.016$) than non-consumed ones and while consumed bark showed higher TNC, WSC, and ME than unconsumed bark (TNC: $t = 2.685$, $df = 36$, $p = 0.011$; WSC: $t = 3.772$, $p = 0.001$; ME: $t = 2.968$, $p = 0.005$), the unconsumed bark had more fiber (NDF, ADF, and cellulose) compared with consumed bark (Table S4).

The concentrations of protein, lipids, cellulose and CP/ADF in mature leaves decreased from summer to autumn (paired t -test $p < 0.05$, statistical result in Table 3). In contrast, ADL, WSC, and starch in mature leaves increased from summer to autumn (Paired t -test $p < 0.05$, Table 3). There was no difference in other nutritional properties in mature leaves consumed in the two seasons ($p > 0.05$, Table 3).

We found that snub-nosed monkeys selected foods with a high CP to ADF ratio ($r_s = 0.690$, $N = 12$, $p = 0.013$, Table 4) in the summer, whereas lignin appeared to be avoided in this period ($r_s = -0.630$, $N = 12$, $p = 0.028$; Table 4). In addition, monkeys fed on leaves the most (57.2%) in summer and had a higher CP to ADF ratio than autumn (mean ratio: 0.77 vs. 0.64).

4 | DISCUSSION

Golden snub-nosed monkeys inhabiting Zhouzhi National Nature Reserve had a very flexible diet, exhibiting marked seasonal differences in the plant species and parts eaten compared to more southern populations (Kirkpatrick et al., 1999; Li, 2006; Li et al., 2010). When this population faced 4 months of leaf scarcity and they were not able to switch to feeding on lichens, which is the strategy open to some southern groups (e.g., 29.5% Baihe National Nature Reserve Kirkpatrick et al., 1999; 38.4–43.3% Shennongjia National Nature Reserve (Li, 2006; Liu et al., 2013), the population ate bark and leaf/flower buds. *Rhinopithecus* species have gut morphology that allows

TABLE 2 Chemical concentration of the plant parts (% dry matter) eaten by *Rhinopithecus roxellana* in Qinling Mountains (Kruskal–Wallis tests)

| | CP | Lipids | WSC | Starch | Ash | ME | CP/ADF | TNC |
|-----------------|--------|--------|--------|-----------|---------------|--------|--------|--------|
| <i>H</i> | 98.353 | 23.213 | 19.714 | 44.113 | 65.895 | 35.718 | 97.712 | 12.340 |
| df | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 0 |
| <i>p</i> -value | 0.000 | 0.006 | 0.020 | 0.000 | 0.000 | 0.000 | 0.000 | 0.195 |
| FIBER | | | | | | | | |
| | NDF | ADF | ADL | Cellulose | Hemicellulose | | | |
| <i>H</i> | 44.592 | 57.974 | 37.971 | 20.440 | 17.454 | | | |
| df | 9 | 9 | 9 | 9 | 9 | | | |
| <i>p</i> -value | 0.000 | 0.000 | 0.042 | 0.015 | 0.042 | | | |

CP, crude protein; WSC, water soluble carbohydrate; ME, metabolizable energy; CP:ADF, crude protein:acid detergent fiber; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; ME, metabolizable energy.

them to eat a diversity of foods when leaves are scarce. For example, *R. brellichi* eat buds and evergreen mature leaves (Xiang, Liang, Nie, & Li, 2012), while *R. bieti* eat fruticose lichens (Grueter, Li, Ren, Wei, Xiang, et al., 2009).

Foliage is an important protein source for many primates (Lambert & Rothman, 2015; Oftedal, 1991; Waterman, Ross, Bennett, & Davies, 1988), especially for those large-bodied species that cannot easily capture sufficient high protein insects (Rothman, Raubenheimer, Takahashi, Bryer & Gilbert, 2014). Golden snub-nosed monkeys have large body mass (adult males >20 kg, RH unpub data) and occasionally preys on birds, *Turdus merula* (Zhao, Wang, Watanabe, & Li, 2008), and invertebrates (Huang, 2015) to obtain protein from sources other than leaves; however, leaves are still the primary protein resources for these folivores. In our study, the mean protein concentration of leaves was higher (17.0%) than other plant parts (Figure 3), matching protein levels (15–22%) recommended by the National Research Council for primates in captivity (N.R.C., 2003). Leaves dominated the diet from spring to autumn suggesting that protein is not a limiting resource at this time. However, during winter, when leaves from deciduous trees are unavailable, leaf/flower buds are the alternative protein source this population turns to (mean concentration = 11.3%, range = 6.8–22.0%; see also *R. bieti*—Grueter, Li, Ren, Wei, Xiang, et al., 2009 and *Macaca fuscata*—Sakamaki, Enari, Aoi, & Kunisaki, 2011). These buds also contain lipids, total nonstructural carbohydrate, and fiber (NDF, cellulose, and hemicellulose) at levels similar to leaves (Figure 3),

making them a suitable substitute to leaves. However, buds are small, widely scattered, and at low density, thus the animals must move longer distances and expend more energy than when feeding on leaves. Guo et al. (2007) suggested that this species conserves energy through its activity pattern in the winter, characterized by longer feeding times and shorter resting and moving times. In addition, cold temperatures present a substantial challenge for these animals. *Quercus* seeds, which are available when it is cold, represent an available energy source (starch content: 53.0%). However, *Quercus* does not fruit every year, thus this population turns to eating bark at times when *Quercus* seeds are not available.

Bark is not very nutritious being low in protein and high in indigestible fiber fractions and lignin, which may be why bark is rarely consumed by other primates, including snub-nosed monkeys in more southern regions. Therefore, given its ready availability and energy content, bark can be a fallback food in leaf-scarce periods for this northern colobine species. A similar pattern of bark use is reported in Japanese macaques that increase bark/buds consumption to support 60% of energy expenditure in the winter (Hanya et al., 2006; Nakagawa 1997). The nutritional content of bark selected by these monkeys is similar to the lichens selected by Shennongjia groups, in that both foods are high in water soluble carbohydrates and low in fiber (Liu et al., 2013). Consuming a relatively carbohydrate-rich bark diet in winter may represent part of a strategy used by *R. roxellana* to persist in a cold environment.

TABLE 3 Pairwise comparison of the nutritional properties (% dry matter) of mature leaves in the diet of Golden snub-nosed monkey of Qinling Mountains, China in summer and autumn (paired *t*-test)

| | CP | Lipids | WSC | Starch | TNC | NDF | ADF | ADL | Cellulose | Hemicellulose |
|-----------------|---------|--------|--------|--------|--------|--------|--------|--------|-----------|---------------|
| <i>t</i> | 5.480 | 2.787 | -3.539 | -2.853 | -1.748 | -0.659 | -0.708 | -2.639 | 2.409 | -0.389 |
| <i>p</i> -value | 0.001 | 0.024 | 0.008 | 0.021 | 0.119 | 0.266 | 0.528 | 0.499 | 0.043 | 0.707 |
| | CP/ADFF | Ash | ME | | | | | | | |
| <i>t</i> | 2.807 | -1.197 | 5.368 | | | | | | | |
| <i>p</i> -value | 0.022 | 0.266 | 0.001 | | | | | | | |

CP, crude protein; WSC, water soluble carbohydrate; ME, metabolizable energy; CP:ADF, crude protein:acid detergent fiber; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; ME, metabolizable energy.

TABLE 4 The relationship (spearman correlation coefficients [r_s]) between food nutrition and the diet of Golden snub-nosed monkey during the summer at Qinling Mountains, China

| | CP | Lipids | WSC | Starch | NDF | ADF | Cellulose | Hemicellulose | TNC |
|------------|--------|--------|--------|--------|-------|--------|-----------|---------------|--------|
| r_s | 0.357 | 0.459 | -0.067 | 0.189 | 0.427 | -0.560 | -0.130 | 0.417 | -0.168 |
| p -value | 0.254 | 0.134 | 0.837 | 0.556 | 0.166 | 0.058 | 0.680 | 0.178 | 0.601 |
| N | 12 | 12 | 12 | 12 | 12 | 12 | 12 | 12 | 12 |
| | ADL | CP/ADF | Ash | ME | | | | | |
| r_s | -0.630 | 0.690 | 0.007 | 0.382 | | | | | |
| p -value | 0.028 | 0.013 | 0.983 | 0.221 | | | | | |
| N | 12 | 12 | 12 | 12 | | | | | |

CP, crude protein; WSC, water soluble carbohydrate; ME, metabolizable energy; CP: ADF, crude protein: acid detergent fiber; NDF, neutral detergent fiber; ADF, acid detergent fiber; ADL, acid detergent lignin; ME, metabolizable energy.

The long and cold winter is a substantial challenge for *R. roxellana* and adults lose body weight during this period (RH unpub. data). Consequently, the protein and energy obtained from non-leaf sources is extremely important in the winter, particularly for infants and lactating females (Nakagawa, 1989, 1997). To maintain their macronutrient and energy requirements, golden snub-nosed monkeys living in this temperate region shift their diet seasonally, choosing diverse plant species and parts in response to their availability. This dietary flexibility, both among seasons and populations contributes significantly to their persistence over a wide range of habitats and environments. But with projected temperature changes the question is how long will such populations be able to respond to future environmental challenges.

The Intergovernmental Panel on Climate Change (IPCC) estimates that the earth warmed by 0.85 °C between 1880–2012 (IPCC, 2014) and under most of their scenarios, temperatures are projected to increase by at least 1.5 °C by 2100 (IPCC, 2014). Gao, Bai, Zhang, and He (2012) reported that average annual temperature and rainfall in northern slope of Qinling Mountains was increased between 1959–2009, with temperature increasing by 0.24 °C per decade and precipitation increasing of 16 mm. In addition, Zhang, Bai, Yuan, and Ma (2013) predicted the mean annual temperature of Qinling Mountains are projected to increase exceed 2 °C by 2070, and 3–4 °C by 2099. Some of the populations at greatest risk from climate change are those on mountains because as temperature rises the only direction to move is upslope, and thus habitat limited. In addition to climate change, the vegetation cover on the northern slope of the Qinling Mountains has decreased of 1.0% per decade (data from 2000 to 2015) (Deng et al., 2018). Recent models of vegetation shifts in Qinling Mountains suggest range contraction and elevation shifts in a number of plant species, associated with increased fragmentation (Shen et al., 2015; Tuanmu et al., 2013). Planning for climate change and vegetation loss will be a challenge in the coming decades.

Numerous documented shifts in the distribution, population abundance, and life history of species highlight the significance of climate change in altering species and community characteristics (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hannah et al., 2002; Parmesan & Yohe 2003). *R. roxellana* appears to be capable of substantial dietary flexibility, but projecting the response of a number of their major food species and modeling their future distribution is a priority in future research so that

informed conservation plans can be formulated. If necessary corridors could be planted in degraded areas to facilitate the colonization of new areas with a greater range of habitat options (Chapman, 2018). In 2001, it was estimated that there were only 3,800–4,000 *R. roxellana* remaining in the Qinling Mountains (Li et al., 2001), such a small population requires careful conservation and management planning.

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CONFLICTS OF INTEREST

The authors acknowledge no conflict of interest in the submission.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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