**Lichen fallback food in nonhuman primates at high altitudes, a**

**unique ecological adaptation and evolutionary development**

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## Abstract

Fallback foods (FBF), classified into staple and filler types, are low-quality food resources chosen by animals due to a shortage of preferred food during a specific period. The selection of lichens as FBF for Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) represents a unique ecological adaptation and evolutionary development in the animal kingdom. This study investigates the yearly dietary selection of five *R. bieti* groups to address the issues and elucidate the nutritional value and ecological selection of lichens for this monkey species, which resides at the highest altitude among nonhuman primates. The results indicate that the consumed lichens serve as the staple FBF. Two main lichen species taken by the monkeys are *Bryoria* spp. and *Usnea longissimi*, with *Bryoria* spp. being the primary choice (67.25 ± 12.20% compared to 15.79 ± 11.66% from *U. longissimi*). *Bryoria spp*. provides a higher level of digestible fiber (NDF) and a lower level of tannin, fat, ADF, and energy compared to *U. longissimi*, which offers higher availability. Lichens are the dominant food and nutritional resource for the monkey species during the dry season, while they serve as a primary food source rather than a nutritional resource during the wet season. Therefore, they compensate for nutrients from other food types, such as fruits, seeds, and leaves. Compared to other Asian colobine counterparts, this species consumes the highest amount of lichens but the lowest proportions of leaves, flowers, and seeds. This dietary pattern demonstrates a specific type of ecological selection and evolutionary development during the Quaternary. The biomass of lichens in the monkeys’ habitat has significantly decreased due to environmental degradation. This study also provides evidence and information to develop or amend conservation strategies and guidelines for the dietary management of captive Yunnan snub-nosed monkeys.

**Keyword:** Yunnan snub-nosed monkeys; Dietary selection; Nutritional requirement; Conservation

**Introduction**

Animals’ dietary selection critically depends on environmental changes, ecology, evolutionary development, climate, habitats, and air pollution. They, together, have affected animals’ survivability and prospective development (Cao 1989, Wang et al. 2020, Heiduck 1997). Thus, it is necessary to study such selection mechanisms, reveal the strategies to adopt different food resources and ecology (Litvaitis 2000), and explore factors influencing such selection (Chapman 1990). Such exertion can also help us identify the intensity of inter and intra-specific competition for food and analyze population division, fusion, and fluctuation, affected by natural resources, environment, ecology and habitats under the principles and regulations of natural selection and environment adaptation (Kirkpatrick 1996, Van Noordwijk and Van Schaik 1988). It also enhances the understanding of other ecological aspects of animals for maintaining tangible conservation and management strategies (Liu et al. 2013).

Such exploration in nonhuman-primate (primates thenceforth) has provided valuable information to understand their dietary preference, resource demand, and habitat-carrying capacity (Grueter et al. 2009a, Grueter et al. 2009b), and guide the construction and management of their habitat and strengthen their conservation (Marshall et al. 2009).

Fallback food (FBF) is a low-quality food resource chosen by animals due to the shortage of preferred food in a specific period (Marshall and Wrangham 2007, Marshall et al. 2009). It has been considered to have two types – “staple” and “filler;” the former is consumed year around and seasonally can constitute up to 100% of the diet, and the latter never constitutes 100% (Marshall and Wrangham 2007). Lichen consumed by *R.* *bieti* has been regarded as the FBF (Grueter et al. 2009b, Huang et al. 2017), a specific habitat-depended evolutionary selection.

Primates in temperate and cold regions face severe challenges because of low plant productivity in harsh habitats and chronic seasonal food shortages (Cramer et al. 1999, Grueter et al. 2009b, Latham and Ricklefs 1993). They frequently adjust their feeding strategies to adapt to such challenges, including FBF selection (García-Castillo and Defler 2018, Grueter et al. 2009b, Harrison and Marshall 2011). Current research on FBF of primates focuses mainly on the definition, function, ecologic and evolutionary adaptation of different species (Constantino and Wright 2009, Laden and Wrangham 2005, Lambert et al. 2004, Marshall et al. 2009, Marshall and Leighton 2006, Marshall and Wrangham 2007, Grueter et al. 2009b). Nevertheless, attention to nutritional and chemical components that are different among FBF species and periodic variation seems to have not been seen. Their identification and amounts consumed from specific food are gravely required to understand animals’ specific demands to maintain a normal metabolism (Mattson Jr 1980, Schoener 1971), especially regarding protein, fat, fibers from which carbohydrate comes, and vitamin (Raubenheimer and Simpson 2016, Hale et al. 2018). On the other hand, the exact demands for each item recorded from a given wild animal taxon provide essential guidelines for its captivity feeding (Hansell, Asberg and Laska 2020).

Among primates, food choice in colobines (Colobinae) has been considered to primarily consists of leaves, fruits, flowers, and seeds (Huang et al. 2010, Kirkpatrick 1996, Oates, Waterman and Choo 1980). Asian colonies’ evolutionary development from Africa to Asia during the Miocene and Plioce has shaped them dramatically in morphology, ecology, and dietary selection (Zhang et al. 2022). Their phylogenetic development and distribution expansion in East and Southeast Asia have allowed them to adapt to the alternative environment, ecology, and habitats and display a significant variation of altitudinal range from sea coastlines to more than 4,000m in Mt. Hengduan and the Qinghai-Tibet Plateau, where *R. bieti* resides (Peng, Pan and Jablonski 1993). Thus, this species is unique in colobines and the world’s primates due to its specific adaptation to the harsh ecology surrounded by low temperature and hypoxia, besides scarce food resources (Grueter et al. 2009b). It is one of the critically endangered primate species on the Red List of IUCN (Long, Bleisch and Richardson 2020).

Thus, the frigid climate has made *R.bieti* require tremendous energy to maintain body temperature (Guo et al. 2018, Hou et al. 2020), especially during energy-hungry periods, in which food resources are scarce and variable due to seasonal climate changes, especially prolonged winter (Huang et al. 2012, Kirkpatrick 1996, van Schaik and Brockman 2005). Thus, understanding how this primate species copes with such an environment and ecology through dietary selection and recording its nutritional and chemical components will provide valuable information and evidence for their conservation and captivity feeding for the programs of releasing them into the wild.

Therefore, the primary purposes of this study include 1) elucidate what kind of FBF type the lichens consumed by *R. bieti* belong to; 2) understand how *R. bieti* is unique in evolutionary dietary selection compared with other Asian colobines; 3) understand the selective strategy of the lichen groups in terms of the nutritional and chemical components; and 4) provide scientific information in amending or making conservation strategies and guidelines for dietary management for the creatures in captivity feeding programs.

## Fieldwork and Material

The study site is in Mt. Lasha (26°20′ N, 99°15′ E), Yunling Provincial Nature Reserve, Lanping County, Yunan Province, with a range of altitude from 2,450m to 3,600m. Its vegetation consists of deciduous broad-leaved forest, coniferous broad-leaved mixed forest, and alpine dark coniferous forest from lower to higher altitudes. Food types of the *R. bieti* include two lichen species (*Bryoria* spp. and *Usnea longissimi*), three bamboo species (*Fargesia* *strigosa*, *Fargesia* *edulis* and *Fargesia solida*), one species of mushroom (*Morchella esculenta*), and 29 other plant species (Appendix Table. 1) (Huang et al. 2012). The targeted group comprised more than 100 individuals, with 11 one-male and multi-female units (OMUs) and two all-male units (AMUs). The average annual rainfall is 910 mm, 85% of which occurs from May to October, and the whole year can be divided into dry (November-April) and wet (May-October) seasons (Huang et al. 2012). The annual average temperature is 11.7℃, with the highest (17.4℃) in July and the lowest (-5.6℃) in February (Huang et al. 2012, Huang et al. 2017).

The feeding habits of the monkeys were observed and recorded using a Leica 77 telescope (Solms, Germany) with instantaneous scanning sampling at 10-minute intervals. From May 2008 to April 2009 and from September 2015 to August 2016, we tracked the monkeys every morning from the time leaving the sleeping site to when they entered the sleeping place in the afternoon. We followed each individual for at least 5s to record which dietary items – fruits, seeds, insects, flows, and which lichen species – were consumed by the monkeys: 1) lichens (*Bryoria* spp. and *U. longissima*), which are significantly morphologically distinguishable (Fig. 1) – *Bryoria* spp. mainly covers tree trunk, with black colors, while *U. longissima* principally intertwined among tree branches with suspending thread-like white fibers; 2) dicotyledonous leaves and buds; 3) mature leaves (including bamboo leaves); 4) flowers; 5) fruits and seeds; 6) insects; 7) others, with discriminating methods described by (Huang et al. 2017), at least five days or 50 hours of eating data were recorded every month.

Monthly lichen consumption is compared between five *R. bieti* groups from the southernmost to northernmost of the monkey’s distribution range. Which are Mt. Lasha (26°20′ N, 99°15′ E), Samage (27°34′ N, 99°17′ E), Tachen (27°36′ N, 99°18′ E), Wuyapiya (28°29′ N, 99°06′ E), and Xiaochangdu (29°15′ N, 98°37′ E).

森林里的照片

中度可信度描述已自动生成

Fig. 1 *Bryoria* spp. (left) and *U. longissima* (right).

**Laboratory work**

From July 2015 to November 2015, 11 and 16 samples of *Bryoria* spp. and *U. longissima* were collected randomly at different altitudes (2,450m - 3,450m) without repetitions; each sample was classified and analyzed for their nutrient and chemical contents, including crude protein (CP), fat, all fiber fractions [neutral detergent fiber (NDF), acid detergent fiber (ADF), acid detergent lignin (ADL)], ash, water-soluble carbohydrate (WSC), and starch (Hou et al. 2018).

We first determined the physical differentiation between the two lichen species consumed, then gauged each nutritional (CP, fat, all fiber fractions, ash, WSC, starch) or chemical (tannin) component (percentage) contained in each species. All components were measured with dry lichens. The chemical component, tannin, was determined in the Folin-Ciocalteau phenol reagent (Box 1983). The average of all samples was used in the calculation.

### Data analysis

The following procedures were used to determine the amount of each component consumed by the monkeys from FBF, either from *U. longissima* or *Bryoria* spp.: total non-structural carbohydrates (TNC) and Energy were calculated (Hou et al. 2018). The energy value of NDF was estimated using a previously published NDF digestibility coefficient of 91% (Kirkpatrick et al. 2001).

A ratio was created for each lichen species in FBF:

R(*U. longissima*) = Ua/(Ua+Ba)

R(*Bryoria* spp.) = Ba/(Ua+Ba)

Where, **a**: the physical proportion of *U. longissima* or *Bryoria* spp. in FBF, recorded from the wild; **Ua**: the physical proportion of *U. longissima*; and **Ba**: the same proportion of *Bryoria* spp..

The actual amount of a given component consumed from each of the lichen species from FBF was calculated with the following formula:

AU= R(*U. longissima)* × U%, from *U. longissima.*

AB= R(*Bryoria* spp.) × B%, from *Bryoria* spp..

Where, **U%**: component percentage contained in *U. longissima*; **B%**: component percentage included in *Bryoria* spp. They were assessed in the laboratory.

Thus, the total amount regarding a specific component from both lichen groups is:

SUM=AU+AB.

For example, if FBF consists of 67% of *U. longissima*, and 25% of *Bryoria* spp., recorded from the field, R(*U. longissima)* = Ua/(Ua+Ba) = 67/(67+25) = 0.73; R(*Bryoria* spp.) = Ub/(Ua+Ba) = 25/(67+25) = 0.27. If component tannin in *U. longissima* is 4.5% and 6.5% in *Bryoria* spp., separately, from the laboratory records, the actual amount of tannin in FBF from *U. longissima* = 0.045 × 0.73 = 3.29%; and that from *Bryoria* spp. = 0.065 × 0.27 = 1.76%.

Separately, *R. bieti* consumes 3.29% and 1.76% of tannin from *U. longissima* and *Bryoria* spp., with a total of 5.05% from the lichens.

To assess the relative abundance of two lichen groups, we calculated the food availability index (FAI) from June 2008 to September 2009 (Huang et al. 2012). We used Mann-Whitney U-test to compare the time difference of feeding on *Bryoria* spp. to that on *U*. *longissimi*, and analyze the differences in components. Data were processed by SPSS 21.0, and the significance level was set to *p*<0.05. All the results are shown as mean ± SD.

## Results

The first result of the study indicates *R. bieti* feeds 78.9% of lichens, 4.0% of bud and young leaves, 5.1% of mature leaves, 7.3% of fruits, 1.5% of flowers, 1.9% of insects, and 1.3% of others. As for the lichen amounts consumed from different lichen species, three is a significant difference between each other (Mann-Whitney U < 0.001, n1 = n2 = 24, *p* < 0.001, two-tailed) – a higher proportion of *Bryoria* spp. (64.63% ± 13.28%, and 69.86% ± 10.93%) than *U. longissima* (14.48% ± 12.12%, and 17.11% ± 11.56%). However, regarding the amount consumed between the two years for each of the lichen species, there is a variation that does not research a significant level (Mann-Whitney U = 42, n1 = n2 = 12, *p* = 0.089, two-tailed), implying the variation and supply of the two lichen species in the region were stable (Table 1).

**Table 1. Time spent on two lichen species by *R. bieti*.**

|  |  |  |
| --- | --- | --- |
| Period | Time percent spent on Lichens (%) | |
| *Bryoria* spp. (n) | *U. longissima* (n) |
| 2008 – May | 63.2 (382) | 1.0 (6) |
| 2008 – June | 56.6 (179) | 13.6 (43) |
| 2008 – July | 76.0 (336) | 7.9 (35) |
| 2008 – August | 62.0 (631) | 10.2 (104) |
| 2009 – September | 61.4 (766) | 5.2 (65) |
| 2008 – October | 47.0 (316) | 35.8 (241) |
| 2008 – November | 54.5 (1397) | 33.7 (865) |
| 2008 – December | 87.3 (1442) | 9.6 (159) |
| 2009 – January | 91.0 (1676) | 3.1 (57) |
| 2009 – February | 60.5 (1049) | 27.8(482) |
| 2009 – March | 57.7 (1823) | 20.8 (658) |
| 2009 – April | 58.4 (884) | 5.0 (72) |
| 2008 - 2009 Mean ± SD | 64.63±13.28 | 14.48 ± 12.12 |
| 2015 – September | 56.0 (981) | 27.5 (481) |
| 2015 – October | 50.3 (971) | 38.5 (743) |
| 2015 – November | 74.2 (1888) | 15.8 (402) |
| 2015 – December | 67.8 (1938) | 28.8 (823) |
| 2016 – January | 88.6 (2650) | 9.0 (268) |
| 2016 – February | 77.5 (1677) | 2.6 (58) |
| 2016 – March | 79.1 (1619) | 10.4 (213) |
| 2016 – April | 64.9 (2643) | 11.3 (459) |
| 2016 – May | 73.2 (1425) | 3.2 (63) |
| 2016 – June | 70.3 (1116) | 11.7 (186) |
| 2016 – July | 77.7 (243) | 15.7 (69) |
| 2016 – August | 58.7 (269) | 30.8 (141) |
| 2015 - 2016 Mean ± SD | 69.86 ± 10.93 | 17.11 ± 11.56 |

Concerning the food availability index (FAI), both lichen species show a stable supply all year round, except for a lower *Bryoria* spp. in January. Leaves present a remarkable seasonal variation and extreme scarcity from December to April (dry season, Fig. 2).

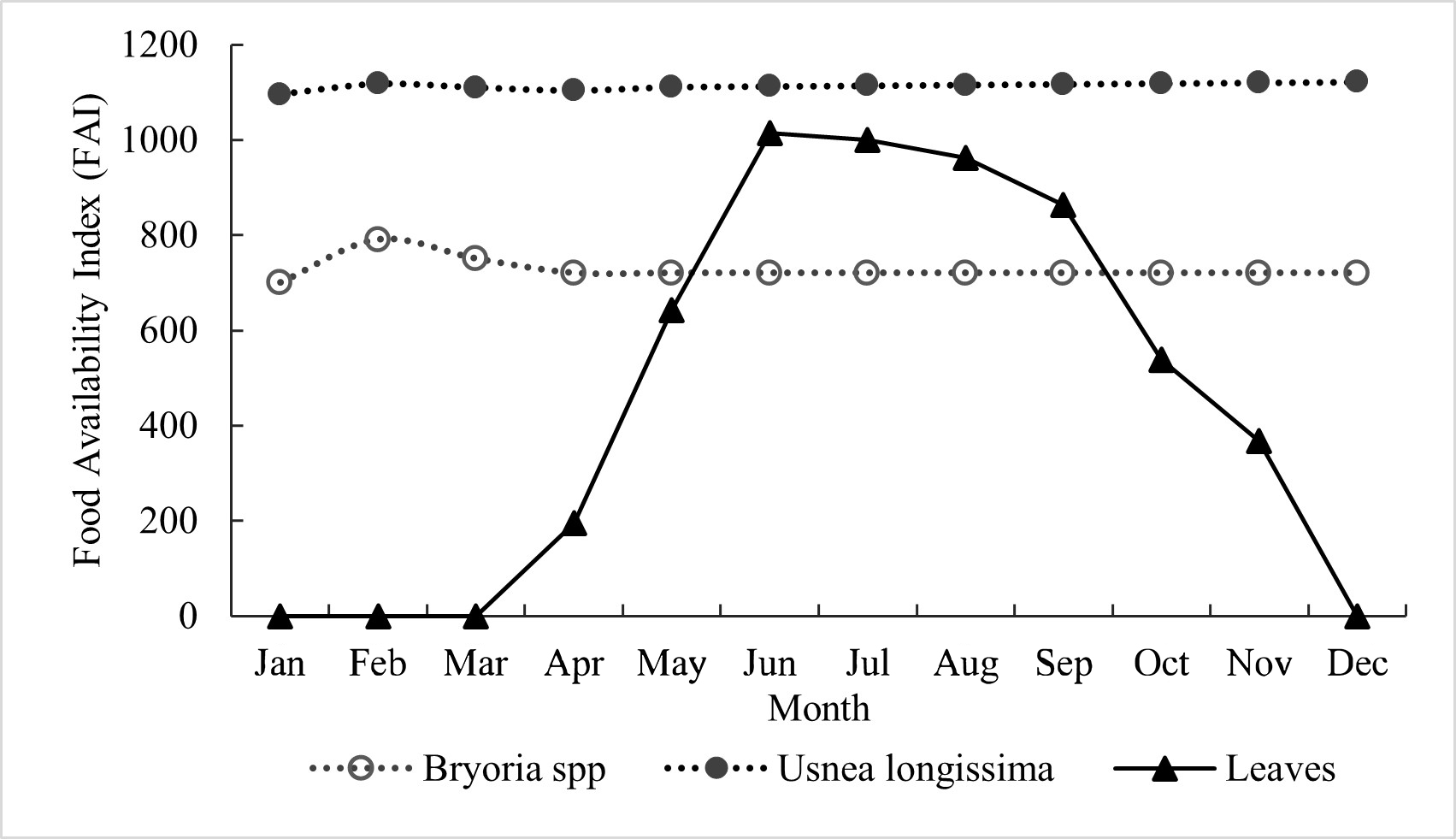
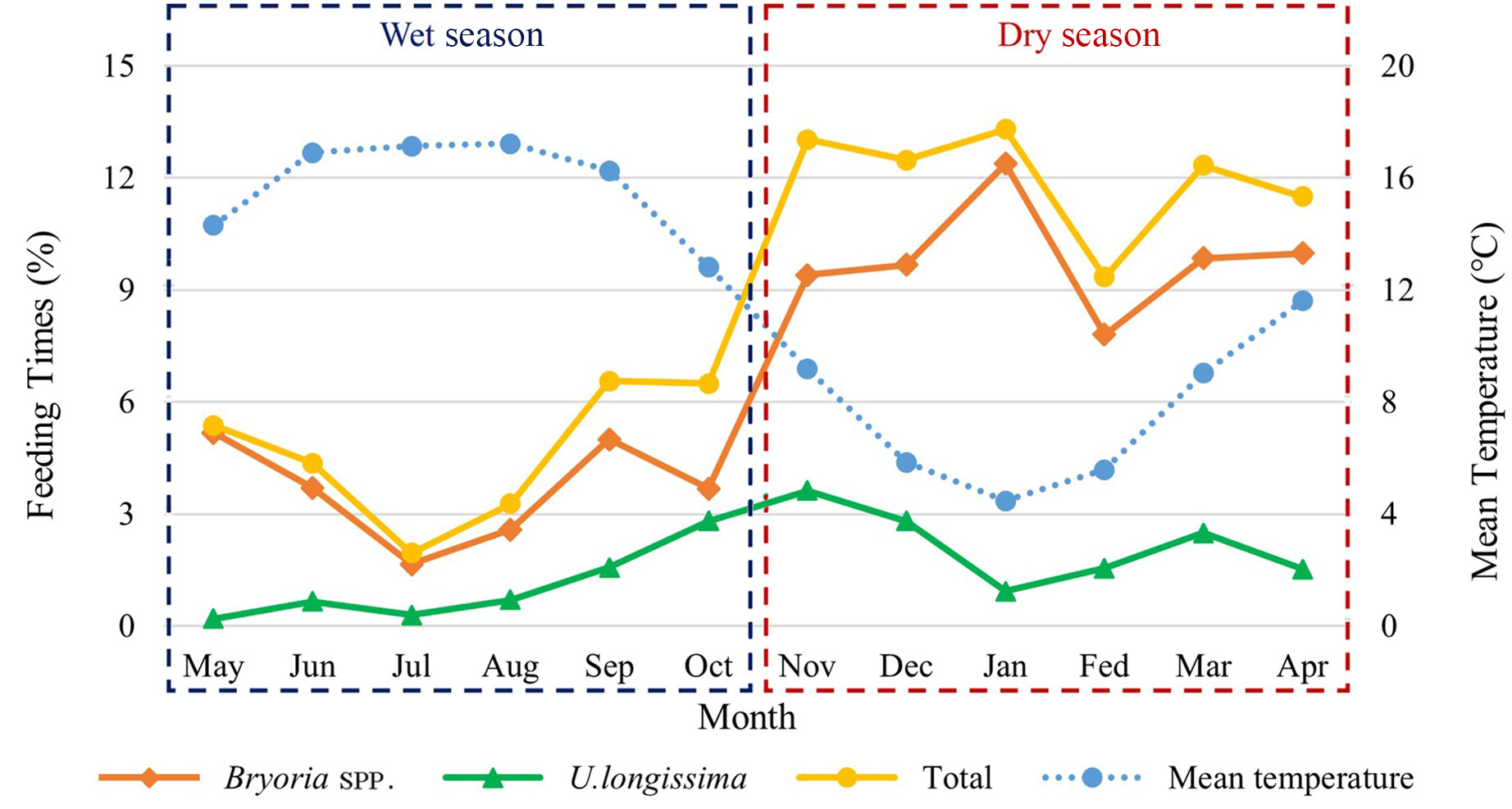
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Fig. 2 FAI index of the two lichen groups and leaves.

When the two lichen species are combined, the difference between dry and wet seasons is illustrated in Fig. 3. The dry season shows a significantly higher amount than the wet season. When they are analyzed separately, *Bryoria* spp. presents a significantly higher amount in the dry season than the wet one, but not *U. longissima*.

Fig. 3 The monthly contributing proportion of two lichen species in different seasons.

### Lichen consumption among five monkey groups

Lichens are consumed all year around and account for 72.99±11.30% (range from 56.27% - 82.70%) among five monkey groups, including the southernmost (82% for Mt. Lasha), midland (67% for Samage, 56% for Tachen, 77% for Wuyapiya) and northernmost (83% for Xiaochangdu) of the whole home range (Table 2). The average monthly consumption is 72.44±18.40% (range from 29%-98%).

**Table 2. Seasonal and regional lichen variations in the diet of *R. bieti* \*.**

|  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| Location | Feeding times (%) | | | | | | | | | | | | Reference |
| J | F | M | A | M | J | J | A | S | O | N | D |
| Mt. Lasha | 96 | 84 | 84 | 70 | 70 | 76 | 89 | 81 | 75 | 86 | 89 | 97 | Our study |
| Samage | 83 | 90 | 83 | 42 | 29 | 68 | 96 | 46 | 64 | 54 | 79 | 97 | Grueter et al., 2009b |
| Tachen | 74 | 82 | 48 | 40 | 44 | 59 | 54 | 48 | 54 | 55 | 61 | 69 | Ding & Zhao, 2004 |
| Wuyapiya | - | - | - | - | 53 | 64 | 92 | 94 | 60 | 93 | 86 | 95 | Kirkpatrick, 1996 |
| Xiaochangdu | 96 | 98 | 88 | 81 | 53 | 56 | 83 | 84 | - | 91 | 97 | 97 | Xiang et al., 2007 |

\*: From J to D: January, February, March, April, May, June, July, August, September, October, November, and December.

### Nutritional and chemical components of the lichens

*Bryoria* spp. comprises significantly higher percentages of ash than *U. longissima*; the latter, however, includes significantly higher portions of ADF, fat, tannin, and energy than the former. After being adjusted, except for fat, monkeys consume a substantially more significant amount of *Bryoria* spp. (AB) than from *U. longissima* (AU, Table 3).

**Table 3.** **Nutritional and chemical components contained in the two lichen groups and the amount consumed by *R. bieti* through FBF.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Nutrition type | Contained in lichens | | | AB and AU | | |
| *Bryoria* spp. | *U.* *longissima* | P | *Bryoria* spp. | *U. longissima* | P |
| Crude protein | 5.36% | 6.37% | *NS.* | 4.34% | 1.22% | \*\* |
| Fat | 1.02% | 3.84% | \*\* | 0.83% | 0.74% | *NS.* |
| Neutral detergent fiber | 40.64% | 34.58% | \* | 32.85% | 6.62% | \*\* |
| Acid detergent fiber | 4.02% | 5.90% | \* | 3.25% | 1.13% | \*\* |
| Acid detergent lignin | 0.54% | 0.42% | *NS.* | 0.43% | 0.08% | \* |
| Ash | 2.41% | 1.78% | \* | 1.95% | 0.34% | \*\* |
| Water-soluble carbohydrate | 3.68% | 4.05% | *NS.* | 2.97% | 0.78% | \*\* |
| Starch | 21.31% | 19.78% | *NS.* | 17.23% | 3.78% | \*\* |
| Tannin | 0.26% | 0.45% | \*\* | 0.21% | 0.09% | \*\* |
| Total non-structural carbohydrates | 50.56% | 53.43% | *NS.* | 40.88% | 10.23% | \*\* |
| Energy | 13.85 | 14.86 | \*\* | 11.20 | 2.85 | \*\* |

U-text is used in Table 3, and \* for *p* < 0.05, \*\* for *p* < 0.001. AB= R(*Bryoria* spp.) × B%, from *Bryoria* spp.; AU= R(*U. longissima)* × U%, from *U. longissima.* R(*U. longissima*) = Ua/(Ua+Ba); R(*Bryoria* spp.) = Ba/(Ua+Ba). **Ua**: the physical proportion of *U. longissima*; **Ba**: the same proportion of *Bryoria* spp.

### Nutritional and chemical components between the dry and wet seasons

### Lichens provide more significant components in the dry season than in the wet one (Fig. 4.). A general decreasing trend of nutritional and mechanical components was found: TNC > NDF > starch > CP > ADF > WSC > ash > fat > ADL > tannin.

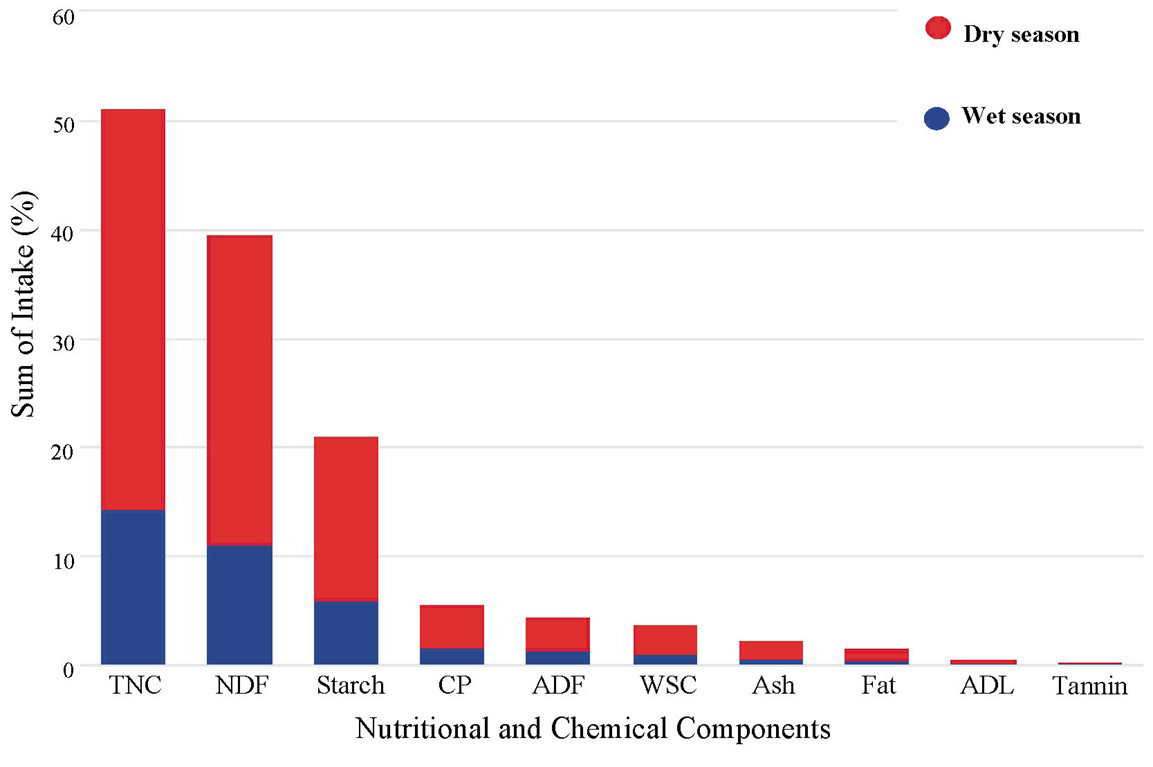
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Fig. 4 The nutritional and chemical components consumed by *R. bieti*, between dry and wet seasons, based on SUM values.

## Discussion

This study exposes the uniqueness of the dietary selection of *R. bieti,* which considerably depends on lichens as staple fallback food and for their nutritional and chemical components. As expected, it provides valuable evidence and information to understand *R. bieti’*s unique ecological selection, environmental adaptation, and evolutionary development, shaped by the most frigid habitats at the highest altitude of nonhuman primates.

**Unique dietary selection and evolutionary development**

The results explored in this study now allow us to figure out the unique dietary selection of *R. bieti,* developed during the Quatery, andcompared with the other Asian colobines based on a broader literature review (Fig. 5).

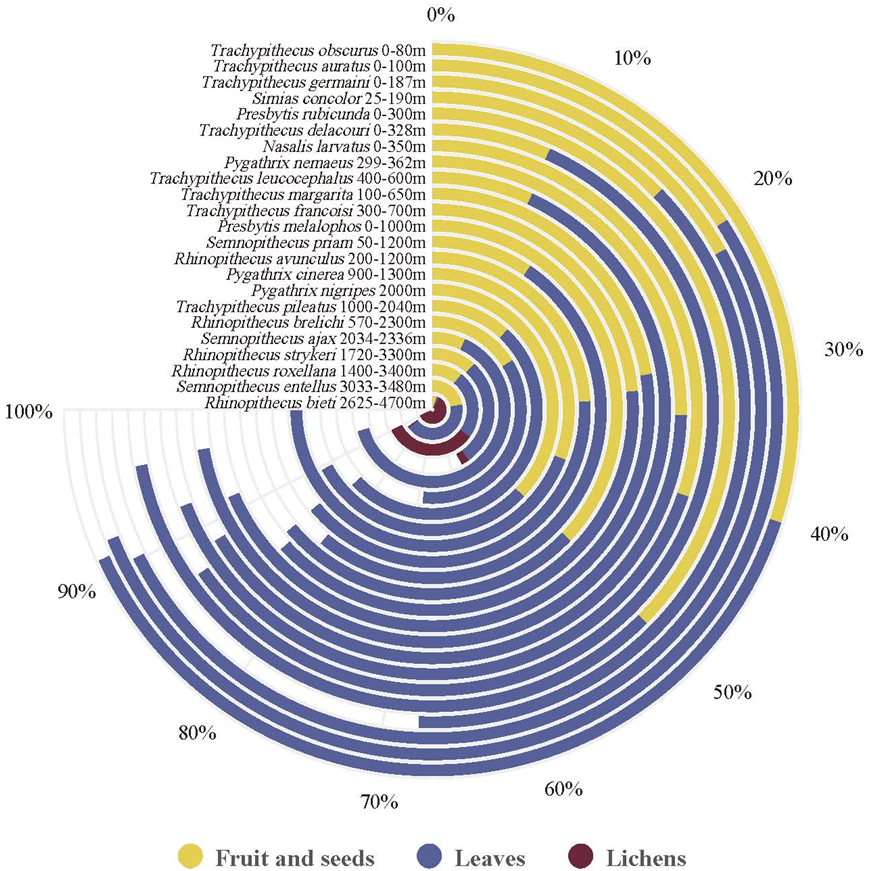


Fig. 5 Dietary selection among Asian colobines. Database resources: Appendix Table. A2

Clearing, *R. bieti* is singled out for its unique dietary selection - the highest lichen and the lowest leaves, fruit, and seeds proportions compared to other Asian colobines. That can be regarded as a specific evolutionary development and the solution of environmental adaptation and ecological selection in the highest habitat elevation and harshest survival condition than any other nonhuman primates in this globe (Kirkpatrick 1996). Such scenarios imply that lichens must have been a dietary choice for the ancestors of the Asian colobines before they dispersed to the places where they dwell (Roos et al. 2011), especially regarding the odd-nosed group (*Rhinopithecus*, *Nasalis,* and *Pygathrix*), based on the profile of the *R. bieti* (Figs. 2-3, and 5).

*Rhinopithecus bieti* and other Asian colobines originated from Africa in the Middle Miocene and migrated into Eurasia through the gateway of North Africa, possibly in the Late Miocene, about 10 mya ago (Davies 1994, Roos et al. 2011). They arrived at a Convergency-Divergency Centre where *R. bieti* is located (Zhang et al. 2022). The oldest colobine fossil species associated with Europe and Asian taxa, *Mesopithecus,* unearthed in the Late Miocene (Davies 1994, Heintz, Brunet and Battait 1981), was discovered recently in Zhaotong, Yunnan, in the deposit of Late Miocene or Early Pliocene. It has been reckoned to be closely related to the taxa in *Rhinopithecus*, possibly *R. bieti* (Ji et al. 2020)*.*

In other words, *R. bieti* is the only Asian colobine species in the Qinghai-Tibet Plateaus and Mt. Hengduan, which have been significantly uplifted due to the accelerated tectonic movement of the plateaus and mountains (Sun et al. 2011). Other colobines, however, were dispersed to the other parts and are widely distributed in East Asia and South East Asia, reaching oceans (Peng et al. 1993, Zhang et al. 2022). Thus, *R. bieti*, different from other primate species in other parts of the world, can be regarded as a species facing severe challenges year-round, divided into dry and wet seasons. It keeps the original dietary selection of the Asian colobines – lichens, especially from *Bryoria* spp. (Fig. 3). This also implies that, following decreasing temperature in the dry seaosn, *R. bieti* consumes more food and energy to maintain body temperature (Bissell 2014). Such mechanisms is the adoptation of going through the period with the scarcest resources in the high altitudinal region.

Another interest is the comparison between *R. bieti* and other taxa in the same genus: 1) Not all species of *Rhinopithecus* have FBF; and 2) Not all *Rhinopithecus* species choose lichens as FBF; among five species, FBF has been reported for *R. bieti* (Grueter et al. 2009b, Kirkpatrick 1996), *R. roxellana* (Li 2006, Hou et al. 2018) and *R. brelichi* (Bleisch and Xie 1998, Xiang et al. 2013, Yang et al. 2019), but not for *R. strykeri* and *R.* *avunculus* (Yang et al. 2019). Such a scenario must be associated with their homogeny in the phylogenetic development of the *Rhinpithecus*, in which *R. bieti*, *R. brelichi,* and *R. roxellana* are closely related to one from another due to their separations were most recently in the Late Pleistocene (Peng et al. 1993).

## Staple FBF of *R. bieti*

What is indicated by Table 2 shows that lichens are the most dominant food type of the monkeys analyzed (81.81±8.32% of annual dietary consumption), and there is a stable supply among the five groups. Such a portion in the dry season can reach 100%. That is to say, lichens are the monkeys’ dietary selection year-round, which can be regarded as the staple FBF of the species according to the type definition (Marshall and Wrangham 2007).

### Nutritional character and ecological adaptation

Lichens exhibit a crucial nutritional value for *R. bieti*, considering their dominant high proportion in annual dietary composition, especially in the dry season, regarded as FBF with more than 80.0% of dietary composition (Table 1). Some components, such as fibers, usually indicate the component of NDF, mainly cellulose, and hemicellulose, is indigestible in normal animals (Lewis, Hotchkiss and Ullrey 2005). However, *R. bieti* can hydrolyze them into digestible volatile fatty acids by unique microbial fermentative processes in their multichambered stomach (Li et al. 2023, Xia et al. 2022). Therefore, lichen with high NDF would be a thriving food and nutrients resources for *R. bieti*. Tannin is always avoided in food selection in primates since its difficulty in being absorbed (Chivers 1994, DeGabriel et al. 2009). That may explain why *R. bieti* prefers *Bryoria* spp. over *U. longissimi,* resulting from the low level of tannin and higher NDF.

*U. longissima* contains significantly higher portions of fat, ADF, energy, and tannin than *Bryoria* spp.; the latter includes a considerably higher amount of DNF and ash (Table 3). However, after such numbers have been adjusted, referring to the actual amount consumed by *R. bieti* (SUM, including AB and AU), monkeys eat significantly higher proportions from *Bryoria* spp., rather than from *U. longissima*, simply because the former occupies a much higher physical amount consumed (Table. 3).

The study also reveals that *R. bieti* progressively reduces taking energy from TNC, NDF, starch, CP, ADF, WSC, ash, fat, and ADL, and the minimum amount of chemical element (tannin - Fig. 4). During the dry season the creatures significantly consume more those components from lichens, which, as addressed above, is due to the scarcity of other food resources in the season. That also implies that *R. bieti* receives more components from non-FBF (fruits, seeds, and leaves) during the wet season (Figs. 2-3). Thus, consuming lichens in the dry season, the only available food resource, is vital for *R. bieti* to cope with dual stresses - nutrition requirements and low temperature. Taking lichens, which have high availability and wide distribution in the dry season, is an evolutionary and ecological adaptation – avoiding monkeys consumes unnecessary energy loss due to traveling long distances to seek alternative foods. This energy-conserving strategy is also very critical in other animals in dealing with harsh ecology and unique periods; for instance, *R. roxellana* mainly consumes bark and buds in cold and food shortage periods (Hou et al. 2020, Hou 2018), Arctic fox (*Vulpes lagopus*)consumes stored food in cold winter (Prestrud 1991).

**The implication of conservation**

The rapid growth and activities of the human population triggered significant natural resource exploitation, land conversion, and pasture extension, which have led *R.bieti*, like any other primate taxa, to face prominent conservation pressure (Pan et al. 2016, Xiao et al. 2003), especially being suffered from the fragmentation (Grueter et al. 2009b, Marshall et al. 2009). As found in this study, lichens play a vital food supply for survivability and future development for *R. bieti* – a unique evolutionary development, ecological selection, and environmental adaptation. It has been reported that a renewal cycle of lichens, if damaged, could take as long as 21 years (Kirkpatrick 1996, Seaward 1987). Although the population of *R.bieti* is increasing, lichen product is, unfortunately, rapidly decreasing, further constraining its prosperity (Grueter et al. 2009b). In addition to anthropogenetic activities, the increasing air population must be the cause (Cao 1989). Lichen is very sensitive to the environment and ecology, especially to atmospheric nitrogen (N) deposition that has increased in recent years in China, which can significantly disturb the nutrient balance of the lichens besides constraining their growth and survival. The lichens’ thallus growth and propagule survival can substantially decrease when nitrogen addition changes from 6.25 to 50.0 kg N·ha-1·y-1. Further, lichen biomass could be reduced by 11.2%-70.2% when the deposition addition exceeded 6.25 kg N·ha-1·y-1 (Wang et al. 2020). Thus, increasing the protection attention to the lichens is necessary to mitigate conservation pressures on the *R. bieti*.

The results found in this study can provide a scientific reference to maintaining balanced nutritional and chemical components for the monkeys, which have developed during their evolutionary and phylogenetic development and are the consequence of ecological adaptation. Since this primate species has been categorized as a critically endangered primate species, captivity-feeding programs have been applied in some places (He and You 2015). Alternative food resources have been used in the case of lichens being absent. Thus, it is critical to maintain their nutritional and chemical balances by referring to Fig. 4 to select alternative dietary components and plant species for captivity breeding.

**AUTHOR CONTRIBUTIONS**

**Hao Pan**: writing – original draft (lead); writing – review and editing (lead); project administration (lead). **Rong Hou**: formal analysis (lead). **He Zhang**: formal analysis (supporting); writing – original (supporting). **Zhi-Pang Huang**: Conceptualization (equal); investigation (equal); funding acquisition (equal); project administration (supporting). **Yan-Peng Li**: Conceptualization (equal); investigation (equal). **Liang-Wei Cui**: project administration (supporting); funding acquisition (equal). **Wen Xiao**: project administration (supporting); funding acquisition (equal).

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**CONFLICT OF INTEREST STATEMENT**

The authors have no conflict of interest to declare.

**DATA AVAILABILITY STATEMENT**

The datasets generated during and/or analyzed during the current study are available in the figshare repository (<https://10.6084/m9.figshare.22785356>).

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Table A1. Food repertoire of *R. bieti* at Mt. Lasha.

|  |  |  |  |
| --- | --- | --- | --- |
| **Families** | **Genus** | **Species** | **Food parts** |
| Actinidiaceae | *Actinidia* | *purpurea* | bud, leaf, flower, fruit |
| Adoxaceae | *Viburnum* | *betulifolium* | fruit |
| Aquifoliaceae | *Ilex* | *delavayi* | leaf |
| Araliaceae | *Acanthopanax* | *evodiaefolius* | bud, leaf, flower, fruit |
| Betulaceae | *Betula* | *albo* | bud, leaf |
| Caprifoliaceae | *Lonicera* | *hispida* | bud, leaf |
| Celastraceae | *Euonymus* | *tingens* | fruit |
| Clethraceae | *Clethra* | *monostachya* | bud, leaf |
|  | *Cornus* | *controversa* | fruit |
| Cornaceae | *Macrocarpium* | *chinense* | flower, fruit |
| Helwingia | *Helwingia* | *japonica* | bud, fruit |
| Lauraceae | *Lindera* | *cubeba* | bud, flower |
| Liliaceae | *smilax* | *menispermoidea* | bud, fruit |
| Magnoliaceae | *Schisandra* | *rubriflora* | bud, leaf, flower, fruit |
| Ranunculaceae | *Clematis* | *Yunnanensis* | bud, leaf, flower |
| Rosaceae | *Prunus* | *conadenia* | bud, leaf, flower, fruit |
|  | *Sorbus* | *rufopilosa* | bud, leaf, flower, fruit |
|  |  | *thibetica* | bud, leaf, flower, fruit |
|  |  | *zahlbruckneri* | bud, flower, fruit |
|  |  | *megalocarpa* | bud, leaf, flower, fruit |
|  |  | *oligodonta* | bud, leaf, flower, fruit |
| Salicaceae | *Populus* | *bonatii* | bud, leaf |
|  |  | *yunnanensis* | bud, leaf, flower |
|  | *Pterocarya* | *delavayi* | bud, leaf, flower, fruit |
|  | *Salix* | *radinostachya* | flower |
| Sapindaceae | *Acer* | *cappadocicum* | bud, leaf |
|  |  | *flabellatum* | bud, leaf |
|  |  | *oliverianum Pax* | bud, leaf |
| symplocaceae | *Symplocoa* | *grandia* | leaf, flower |

Table A2. Data sources of dietary selection among Asian colobines.

|  |  |  |
| --- | --- | --- |
| **Genus** | **Species** | **Reference** |
| *Nasalis* | *larvatus* | Yeager, 1989; Rowe & Myers, 2017 |
| *Presbytis* | *melalophos* | Davies et al., 1988; Nijman et al., 2020 |
|  | *rubicunda* | Hanya & Bernard, 2012 |
| *Pygathrix* | *cinerea* | Long et al., 2022a; Long et al., 2022b |
|  | *nemaeus* | Phiapalath et al., 2011 |
|  | *nigripes* | Rawson, 2009; Rowe & Myers, 2017 |
| *Rhinopithecus* | *avunculus* | Hai, 2011; Rowe & Myers, 2017 |
|  | *bieti* | Present study; Rowe and Myers, 2017 |
|  | *brelichi* | Xiang et al., 2012; Rowe & Myers, 2017 |
|  | *roxellana* | Li, 2007; Rowe and Myers, 2017 |
|  | *strykeri* | Yang et al., 2019; Geissmann et al., 2011 |
| *Semnopithecus* | *ajax* | Thakur et al., 2022 |
|  | *entellus* | Sayers & Norconk, 2008 |
|  | *priam* | Vanara & Pragasan, 2021; Singh et al., 2020 |
| *Simias* | *concolor* | Erb et al., 2012 |
| *Trachypithecus* | *auratus* | Tsuji et al., 2019 |
|  | *delacouri* | Workman, 2010 |
|  | *francoisi* | Zhou et al., 2006 |
|  | *germaini* | Le et al., 2019 |
|  | *leucocephalus* | Zhou et al., 2011 |
|  | *margarita* | Hoang et al., 2022 |
|  | *obscurus* | Ruslin et al., 2018 |
|  | *pileatus* | Solanki et al., 2008 |