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Winter Feeding Tree Choice in Sichuan Snub-Nosed Monkeys (*Rhinopithecus roxellanae*) in Shennongjia Nature Reserve, China

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We investigated patterns of winter feeding tree choice in 4 groups of Sichuan snub-nosed monkeys (Rhinopithecus roxellanae*) in Shennongjia Nature Reserve, China. We collected data during 2 winters from 1998 to 2000. The monkeys used mature forest, young forest and shrub forest, but not grassland. Groups used tree species in a significantly nonrandom pattern. There was a similar composition of preferred tree species between different habitats for each group and among the same habitat types for different groups. They preferred* Abies fargesii, Pinus armandii *and* Salix walliciana *for foraging. The 3 species occur in varying degrees of abundance in different habitats and were used differently by the 4 groups. The difference is probably due to interhabitat differences in availability of tree species, in addition to microclimate. The mean circumference of a tree had little effect on its preference score, but preferred species tend to be larger. A Wilcoxon signed-rank test indicated that the percentage of trees used and average number of feeding bites per tree is significantly greater for larger trees. For all trees in a given habitat, the percentage of trees used and average number of bites per tree have a significant positive correlation with average tree circumference. Our results indicate that* Rhinopithecus roxellanae *prefer to feed in large trees more than small trees in a given habitat, thereby preferring mature forest habitat. There is also a group-size effect; larger groups used higher-quality habitats than those*

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of smaller groups. Both tree species and size are the major determinants of feeding choice, but tree species is more important than tree size. Our results have at least three implications for winter habitat conservation of Sichuan snub-nosed monkeys. Conservation efforts should be focused on mature forest because it is better habitat at Rhinopithecus *than young forest, as long as the same tree species are present. Secondly,* Pinus armandii, Abies fargesii *and* Salix walliciana *should be conserved as top priority in forest communities. Third, the largest trees in each habitat should be given greatest possible protection.*

KEY WORDS: feeding tree choice; Sichuan snub-nosed monkey; *Rhinopithecus roxellanae*; preferred species; tree size selection; selection index; winter habitat; conservation.

INTRODUCTION

Most primates live in tropical or subtropical habitats, and seasonal variation in food supply is due to phenological aspects of the site, which are largely determined by rainfall patterns. In extremely seasonal habitats, the characteristics of the habitat may exert a profound influence on all aspects of a specific ecology. Some evolutionary theorists even surmise that natural selection exerts its influence primarily during lean periods (Wiens, 1989). For example, Marsh (1986) suggested that Tana red colobus (*Piliocolobus rufromitratus*) populations were food-limited only during the dry season. Hladik (1975) documented similar results for, *Hapalemur mustelinus*. Stanford (1991) showed that in highly seasonal habitat *Trachypithecus pileatus* experienced behavioral changes, including dramatic decreases in infant play, when food became scarce. Curtin (1975) showed that Hanuman langurs (*Semnopithecus entellus*) in montane Nepal changed their ranging patterns to include lower elevation habitat and more widely available plant foods during the harsh mountain winter.

Sichuan snub-nosed monkeys (*Rhinopithecus roxellanae*) are an endangered arboreal endemic primate in Sichuan, Shaanxi, Gansu and Hubei provinces of China (Hu, 1998). In the past half-century, they have suffered greatly from habitat loss and fragmentation because of timber felling, forest reclamation and human population growth (Hu, 1998). Although many reserves have been established, illegal deforestation and selected woodcutting in the reserves often occur, and continue to threaten the long-term survival of *Rhinopithecus roxellanae*. Relatively little is known about wintertime behavioral ecology in the species, though it is presumably an ecologically stressful season due to low temperatures and often snowy conditions (Kirkpatrick *et al.*, 1999; Li, 2001). In Shennongjia Nature Reserve, Hubei, China, winter lasts *ca.* 6 mo from complete defoliation in November to leaf flush in early April (Li, 2001). The number of tree species eaten by *Rhinopithecus roxellanae* decreases greatly during this period (Kirkpatrick *et al.*, 1999; Li, 2001; Li and Shi, 1986; Shi *et al.*, 1983). They eat mainly fruits of *Pinus armandii* and lichens growing on trees (Li, 2001), and they also eat bark and insects under bark. Throughout this period the entire habitat is covered with snow, further limiting their use of local food resources. Winter tree selection may influence the survival of the monkeys in winter and breeding in April to May.

We aimed to establish the key habitat variables that affect the winter ecology of *Rhinopithecus roxellanae*. We (1) assessed the preferred tree species of the monkeys in winter; (2) determined the preferred size of trees used by the monkeys; (3) studied the relationship between habitat availability and group size; and (4) formulated recommendations on habitat conservation of *Rhinopithecus roxellanae*.

STUDY AREA AND METHODS

Study Area

The study site is in the Shennongjia Nature Reserve (31°22′–31°37′N and 110°03′ 110°34′E), Hubei province of China. The Shennongjia Nature Reserve is a mountainous area of *ca*. 800 km^2 with an elevational range from 398 m to 3105.4 m (Chui, 1996). The vertical distribution of vegetation >1700 m elevation (within the distribution of *Rhinopithecus roxellanae*) can be classed into 2 types: temperate deciduous broadleaf coniferous forest between 1700 m and 2600 m, and temperate evergreen coniferous forest >2600 m. The study area is approximately 100 km^2, ranging between 1700 and 2950 m elevation. The climate was typical of the subtropical humidity monsoon zone. At 1700 m, the mean temperature is 17.5°C in July and 3.0°C in January (Chui, 1996). Snow cover appears by mid December and lasts until mid March. We considered that a habitat is composed of a several communities dominated by one or several species. Habitats in Shennongjia Nature Reserve are of 4 types: young forest, mature forest, shrub forest and grassland:

1) Young forest is *ca*. 25–45 years old with most trees 10–15 m in height. It accounts for most of Shennongjia Nature Reserve. The young forest zone emerged during 1955–1975, after mature forest was cleared (Chui, 1996).
2) Mature forest is >80 years old and 15–20 m in height. It consists of many remnant patches, scattered throughout the young forest. The young forest and mature forest communities consist mainly of *Pinus*

armandii, *Abies fargesii*, *Betula utilis*, *Betula albo-sinensis*, *Populus davidiana*, *Fagus engleriana*, *Rhus verniciflua*, *Tetracentron sinensise* and several mixed communities (Wuhan Institute of Botany, 1980). Each community usually consists of one to several coniferous species, plus deciduous broadleaf species.

3) Shrub tree forest occurs in some dry areas, such as peaks and hillsides, and is composed mainly of *Crataegus hepehensis*, *Malus halliana* and other shrub-tree species. The zone is also scattered with *Pinus armandii*, *Betula utilis*, *Betula albo-sinensis*, *Populus davidiana* and *Salix walliciana* <6 m in height.
4) Grassland comprises of *Triisetum clarkei* and *Festuca rubra*, and is scattered with *Malus halliana*, *Crataegus hepehensis* and other shrub species.

Study Groups

We studied 4 groups of the snub-nosed monkeys (Li, 2001). Group 1 had 104 individuals in 1999, and their home range was in the Qianjiaping area (Fig. 1), at elevations between 1700 m and 2585 m (Li, 2001). Group 2 had 140–150 individuals in 1998 and lived in Jinghouling area, at elevations between 2000 m and 2900 m. Group 3 comprised 40–50 monkeys in 1999 and was distributed in Qingnianpao area, at elevations between 1700 m and 1900 m. Group 4 had seven individuals in 1999, which lived on the south-western side of the Hongshiguo River between Xiaolongtan conservation station and Yazikou conservation station, at elevations between 1800 m and 2000 m (Fig. 1). Habitats for Groups 1 and 2 included all habitat types. We observed each of them ≤30 days in winter. We observed group 2 from 27 December 1998 to 25 January 1999 and Group 1 between 16 December 1999 and 14 January 2000. Because habitat for Group 3 and 4 included only one habitat type—young forest—we followed them for 14 days each between 1 and 14 January 1999.

Groups 1 and 2 have occupied their current ranges since >1973 (Zhu, 1992). The habitats for Groups 2, 3, and 4 are in a larger area, that was fragmented by human interference into its present size in the 1970s. However, Group 2 occasionally used the home range of group 4 in autumn of 1999 and Group 3 occasionally used the edges of the home range of Group 2 in winter 2000 when they were far away. Group 4 was formed after 1995. We do not know when Group 3 formed because they had not been monitored before our study. The habitats of Group 1 bordered those of Group 2, but were far away from those of Groups 3 and 4.

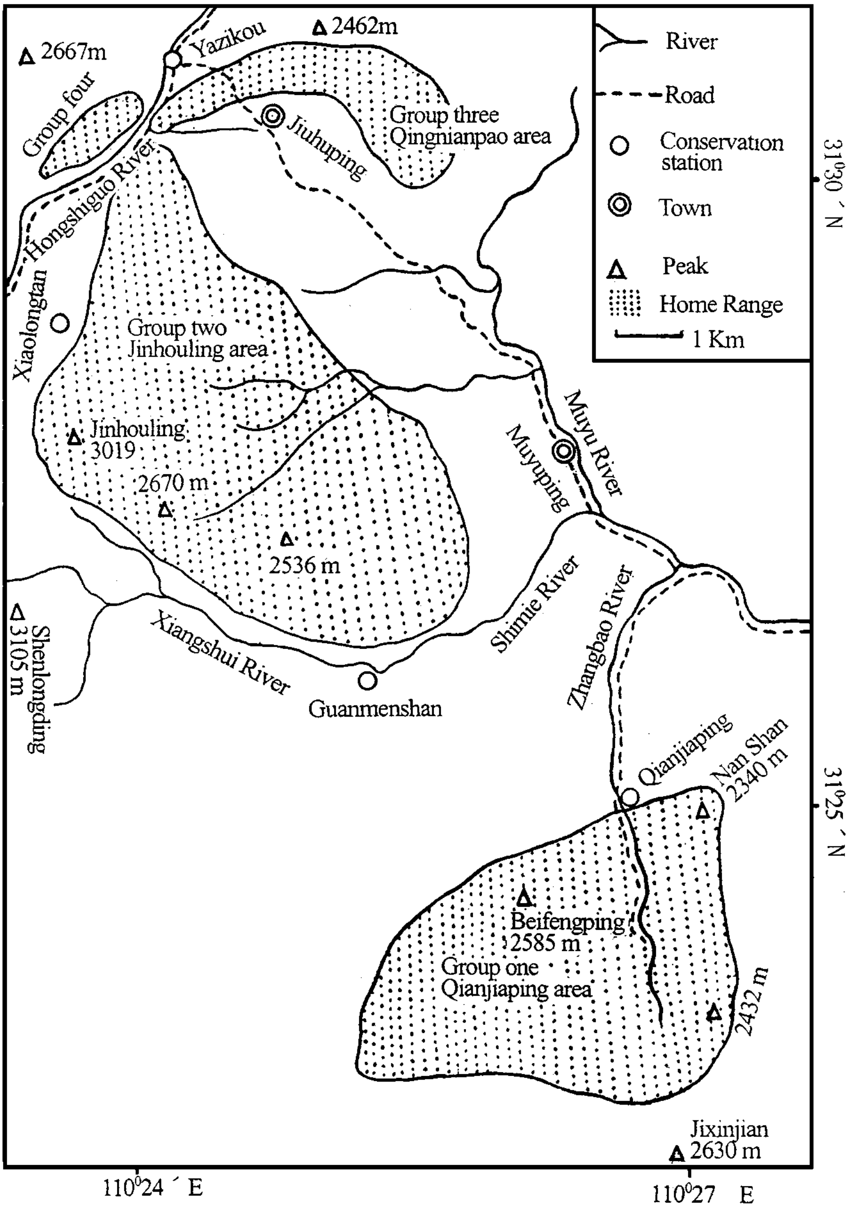

Fig. 1. Home ranges of 4 groups of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China.

Sampling

We sampled habitats via 20 × 20-m plots, semirandomly located to represent all vegetation types, but intended to sample the actual daily foraging path of a focal group. We established the plots within a half-day following the group's movement through the sampled area. Each day we established 0–3 plots, depending on a group's daily path length. When daily path length was short, as when heavy snow fell, it was not always possible to establish a plot. The number of plots in the foraging path of Groups 3 and 4 is relative fewer than those of Groups 1 and 2 because Groups 3 and 4 traveled very slowly. We sampled a total of 119 plots and 6191 trees. The distribution of plots and numbers of trees of each species are in Table I. To ensure that plots were located in the foraging path, we inspected trees ≤3 m of the plot borders. The foraging path was easily identified in the field; it was usually 30–80 m wide, depending on the size of the group. In winter snub-nosed monkeys use their hands to break branches of food trees and then eat seeds and lichens on them. They sometimes strip bark from trees and eat both the bark and insects under it. The bite marks and strip bark are obvious evidence of their foraging. New bites and newly stripped bark on the trees and on the ground evidenced that a group had used a tree (Li *et al.*, 1999).

We determined food trees by inspecting trees for new bite marks and stripped bark. We used the percentage of trees used and number of bites per tree as measures of tree use. When evidence of use was obscure, we climbed up the trees to determine if the trees had been foraged by the monkeys. According to our data, evidence of tree use by other animals was very rare in the study site, usually below one bite mark recorded per 1000 trees,

Table I. The distribution of sample plots and numbers of trees and species measured in winter habitats of 4 groups of *Rhinopithecus roxellanae*

Habitats	Group 1	Group 2	Group 3	Group 4
Mature forest				
Number of plots	40	20	—	—
Number of trees	1692	859	—	—
Number of species	29	16	—	—
Young forest				
Number of plots	12	9	4	10
Number of trees	757	919	300	725
Number of species	19	16	18	17
Shrub forest				
Number of plots	16	8	—	—
Number of trees	415	524	—	—
Number of species	21	20	—	—

compared with 1500–2000 bites per 1000 trees used by snub-nosed monkeys. We therefore assume that all tree evidence to be the result of use by monkeys. We recorded tree damage inflicted by monkeys both on the ground and in the tree itself. Most new bites are >10 cm long and most newly striped bark weighed >10 g. Some new bites <10 cm long and newly striped bark <10 g were not eaten by monkeys or were caused by their movements in the trees. The monkey rarely used the trees <10 cm circumference at breast height (cbh). We counted bites only if they were >10 cm in length and new bark strips if they weighed >10 g. We identified all tree species >10 cm cbh according to Wuhan Institute of Botany (1980), Huo (1992) and Qi (1994). We collected tree specimens for identification whenever possible. We measured the circumference of each tree >10 cm cbh in the plots.

Statistical Analysis

To measure tree specific preference we tested whether groups used tree species in habitats significantly differently from their abundance. We used a selection index to represent tree specific preference (Krebs, 1999; Manly *et al.*, 1993; Savage, 1931; Williams and Marshall, 1938). The availability of a species in a habitat is the number of trees of the species in the habitat. The formula for the selection index (Krebs, 1999; Manly *et al.*, 1993) is:

$$\mathrm{Wi} = \mathrm{Oi}/\mathrm{Pi}$$

in which Wi is the selection index for tree species *i* in a habitat, and Oi is the percentage of trees of species *i* used in the habitat. Pi is the percentage of species *i* available in the habitat. Via a G-test we tested the null hypothesis that groups randomly selected tree species in the habitat (Krebs, 1999; Manly *et al.*, 1993):

$$X^2 = 2\sum_{i=1}^{n}[u_i \ln(u_i/Up_i)]$$

Where in ui = number of trees of species *i* used in the habitat

U = total number of trees of all species used in the habitat $U = \sum u_i$

X^2 = Chi-squared value with (n − 1) degrees of freedom (H_0: random selection)

n = Number of species in the habitat

We calculated the standard error for a single selection index via the formula (Krebs, 1999; Manly *et al.*, 1993):

$$SE = \sqrt{\left(o_i(1 - o_i)\big/Up_i^2\right)}$$

Where in SE = standard error of selection index for species *i* in the habitat
Oi = proportion of trees of species *i* used in the habitat
Pi = proportion of trees of species *i* among all trees in the habitat

Some species in a habitat are very rare and their standard errors are very large due to small samples. We considered that only selection index values >1.0 and significantly >0 by the Chi-square test indicate preference and values <1.0 indicate avoidance. We applied a simplified formula that compares the difference between two selection ratios as following (Krebs, 1999; Manly *et al.*, 1993):

$$X^2 = (w_i)^2/\left(o_i(1 - o_i)/UP_i^2\right)$$

in which X^2 = the Chi-square value with 1 degree of freedom (H0: $w_i = 0$) w_i = selection index of species i which is >1.0 in the habitat.

We analyzed selection of tree sizes via a Wilcoxon rank-sum test (Steel and Torrie, 1960). The null hypothesis is that the monkeys selected the sizes of trees in a species randomly. We ranked all trees in a species or a habitat from the smallest to largest cbh. We divided the rank into 2 samples by the median: a subsample with larger trees in the rank and a subsample with smaller trees in the rank. When the number of the trees in a rank was an odd number, the number of the trees in larger tree subsample is (n/2) + 1 and the number of trees in smaller tree subsample is n/2. If the number of trees is an even number, the number of trees in both subsamples have same number, n/2. In each subsample the availability of a species is the number of trees of the species in the sample. We calculated the percentage of trees used and the average number of bites per tree in each subsample for a species. We paired the percentage of trees used and the average of bites per tree between two subsamples in a species. Then we performed a Wilcoxon signed-rank test for all species in each habitat and for preferred and avoided species in all habitats for each group to discern whether the percentage of trees used and the average number of bites per tree differed significantly between the two subsamples of a species. The steps of the test are (Steel and Torrie, 1960, pp. 400–403):

1. Rank the differences (the value in the larger tree subsample—that in smaller tree subsample) between paired values from smallest to largest without regard to sign;
2. Assign to the ranks the signs of the original difference;
3. Compute the sum (T) of negative ranks, which is smaller
4. Compare the sum obtained at step 3 with the critical value

The probability of T can be calculated by the formula:

$$z = (T - u_T)/\sigma_T$$

where in $u_T = n(n+1)/4$

$$\sigma_T = \sqrt{(n(n+0.5)(n+1)/12)};$$

n = number of species in a habitat or number of preferred species (or avoiding species) in habitats for each group. The significant value is $p < 0.05$. The probability table of a random value of z can be used to test significance (Steel and Torrie, 1960).

In a second test, we ranked all trees in a habitat from smallest to largest cbh. We arbitrarily divided rank into 10 subsamples with equal numbers of trees. If the sample of trees was not exactly divisible by 10, we added the remainder to the subsample with the largest mean cbh. In each subsample, tree availability is the number of trees in it. We calculated the percentage of trees used, the average number of bites per tree and the average circumference of trees. We conducted a linear regression between percentage of trees used, average number of bites per tree, and average cbh of trees in each habitat for all groups with SAS 6.12 (SAS Inc., 1993).

RESULTS

Preferred Tree Species

There are ≥48 tree species in areas where monkeys foraged in winter. Groups 1 and 2 used mature forest, young forest and shrub forest, but not grassland. There a differences in specific composition between habitats used by different groups (Table II). In Group 1's range, *Pinus armandii* dominated mature forest (32.3%) and young forest (49.4%). In Group 2's range, the mature forest and young forest were dominated by *Abies fargesii* (49.1% in young forest and 57.3% in mature forest). The young forest of Groups 3 and 4 was dominated by *Populus davidiana* and *Pinus armandii* (18.0% and 13.3%, respectively, for Group 3; 33.5% and 21.2%, respectively, for Group 4).

Monkey groups used only 32 tree species. Table III shows the selection indices of preferred species in the several habitats. Groups used tree species significantly nonrandomly (G-test; $p < .001$) (Table III). There is similar composition of preferred species in similar habitats of different groups and between different habitats for each group. For example, Groups 3 and 4 used *Betula albo-sinensis* and *Pinus armandii*. Group 1 preferred *Pinus armandii* and *Salix walliciana* in both young and mature forest, and preferred *Salix walliciana* in shrub forest. All groups preferred *Pinus armandii* and *Salix walliciana* in most habitats. Groups 1, 2, and 3 preferred *Abies fargesii* in some habitats. Other preferred tree species were only preferred in one or two habitats by one or two groups.

Table II. Composition (%) of tree species in winter habitats of 4 groups of *Rhinopithecus roxellanae*. All species that are >5% in a habitat are listed

Tree species	Group 1			Group 2			Group 3	Group 4
	MF	YF	SF	MF	YF	SF	YF	YF
Abies fargesii	5.76	0.00	0.00	57.28	49.08	1.72	0.00	0.28
Betula albo-sinensis	5.79	7.79	0.00	2.33	6.20	7.63	11.00	12.00
B. utilis	13.36	8.05	0.48	20.14	4.79	3.63	0.00	0.00
Buxus microphylla	10.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cerasus discadenia	0.65	0.92	0.00	1.98	3.26	2.67	5.67	2.62
Corylus ferox	0.53	1.06	0.00	3.38	5.33	0.00	0.00	0.00
Crataegus hepehensis	0.00	6.07	26.27	0.00	5.22	0.57	4.00	3.03
Fagus engleriana	4.37	2.64	0.00	1.51	0.00	0.95	16.37	0.00
Lindera obtusiloba	1.18	0.00	0.00	2.44	0.00	5.15	0.00	0.00
Litsea ichangensis	0.59	1.06	0.00	0.00	0.00	0.00	0.00	0.00
Malus halliana	0.00	0.00	28.97	0.00	0.00	0.00	1.33	0.00
Phyllanthus flexuosus	0.00	1.59	10.84	2.33	0.22	5.92	0.00	0.00
Pinus armandii	32.27	49.41	0.00	0.00	1.51	2.48	13.33	21.24
Populus davidiana	6.56	11.76	1.45	0.00	13.06	6.22	18.00	33.52
P. wilsonii	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.76
Rhododendron spp[a]	2.78	0.00	0.00	2.79	0.00	7.25	0.00	0.00
Rhus verniciflua	3.55	1.45	0.00	0.00	0.00	0.57	17.00	7.31
Salix walliciana	1.83	4.76	13.98	0.00	2.83	18.70	6.00	10.34
Sorbus hupehensis	0.19	0.00	0.00	0.00	0.00	25.38	0.00	0.00
Other species	9.60	3.44	18.01	5.82	8.50	11.16	7.30	2.90

Note. MF: mature forest; YF: young forest; Sh: shrub forest. The number of trees and species sampled in each habitat are listed in the Table I.
[a] Including several species.

Tree Size Selection

The average size for a given tree species had only a modest effect on foraging preference (Table IV). For example, *Salix walliciana* is a medium-sized tree in all habitats, but the monkeys preferred it in almost all habitats, except by Group 4 in young forest. *Litsea ichangensis* is a smaller tree (32.0 ± 5.8 cm cbh), but it was preferred by Group 1 in mature forest. Distribution of preferred species is not uniform. The preferred species tend to be larger. In mature forest (Table IV), 2 of the 5 largest tree species in Group 1's range were preferred species. Among 10 other species, the monkeys preferred only *Litsea ichangensis*. Group 2 preferred 4 species in young forest, all of which were among the 5 largest tree species.

For a given species, the percentage of trees used and number of bites in the larger subsample usually were larger than those in the smaller subsample. The average cbh of trees in the larger subsample is 1.43–4.34 times that in smaller subsample. A Wilcoxon signed-rank test shows that the percentage of trees used and the number of bites per tree in the larger subsample a significantly greater than those in the smaller subsample ($p < .05$; Table V).

Table III. Selection indices of preferred tree species in habitats for Groups 1–4

Tree species	Group 1 MF	Group 1 YF	Group 1 SF	Group 2 MF	Group 2 YF	Group 2 SF	Group 3 YF	Group 4 YF
Abies fargesii	1.821 ± 0.205[a]	—	—	1.399 ± 0.035[a]	1.356 ± 0.062[a]	1.917 ± 0.666[a]	—	0
Betula albo-sinensis	0.686 ± 0.129	0.491 ± 0.160	0	0.757 ± 0.284	0.666 ± 0.206	1.024 ± 0.225[a]	1.604 ± 0.376[a]	1.065 ± 0.157[a]
B. utilis	0.529 ± 0.073	0.211 ± 0.105	0	0.550 ± 0.078	0.691 ± 0.240	1.135 ± 0.351[a]	—	—
Cerasus discadenia	0	0.460 ± 0.459	0	0.636 ± 0.283	0.760 ± 0.306	1.540 ± 0.477[a]	0	0
Coriaria nepalensis	—	—	0	0.361 ± 0.126	0	1.318 ± 0.388[a]	—	—
Fagus engleriana	0.639 ± 0.145	1.448 ± 0.473[a]	—	0.666 ± 0.331	—	0	0.504 ± 0.183	—
Litsea ichangensis	1.991 ± 0.700[a]	0.402 ± 0.401	—	—	—	—	—	—
Malus halliana	0	—	1.586 ± 0.128[a]	—	—	0.568 ± 0.251	0	0
Pinus armandii	1.886 ± 0.058[a]	1.385 ± 0.061[a]	0	—	1.628 ± 0.656[a]	0.664 ± 0.329	2.294 ± 0.375[a]	1.564 ± 0.125[a]
Populus davidiana	0.471 ± 0.101	0.470 ± 0.127	0.687 ± 0.483	—	1.108 ± 0.173[a]	1.483 ± 0.301[a]	0.980 ± 0.230	0.963 ± 0.079
R. verniciflua	0.622 ± 0.159	0.878 ± 0.503	0.687 ± 0.685	—	—	2.156 ± 1.237	0.900 ± 0.230	1.093 ± 0.210[a]
Salix. walliciana	2.007 ± 0.394[a]	2.592 ± 0.451[a]	1.953 ± 0.224[a]	—	1.169 ± 0.406[a]	1.496 ± 0.154[a]	1.765 ± 0.556[a]	0.998 ± 0.166
χ^2	475.435	105.039	99.611	112.198	73.919	51.427	54.651	75.719
Degree of freedom	17	12	10	10	11	16	6	8
Probability	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Note. MF: mature forest; YF: young forest; Sh: shrub forest. Dash indicates data not available.
[a]Preferred species.

Table IV. Mean cbh of species in winter habitats of Groups 1–4

Tree species	Group 1			Group 2		Group 3	Group 4	
	MF	YF	SF	MF	YF	SF	YF	YF
Abies fargesii	151.5 ± 51.4[a]	—	—	87.2 ± 21.3[a]	39.7 ± 30.5[a]	60.2 ± 28.9[a]	—	12.0 ± 0
Betula albo-sinensis	106.8 ± 46.8	42.0 ± 23.1	—	42.5 ± 22.0	35.3 ± 23.7	38.2 ± 18.7[a]	32.7 ± 13.1[a]	32.4 ± 11.8[a]
B. utilis	111.9 ± 47.4	31.4 ± 16.8	15.0 ± 1.4	68.1 ± 38.7	46.5 ± 20.1	38.9 ± 20.6[a]	—	—
Buxus microphylla	22.3 ± 5.8	—	—	—	—	—	—	—
Cerasus discadenia	47.5 ± 21.7	26.9 ± 12.2	—	29.0 ± 18.7	35.6 ± 20.3	19.8 ± 10.2[a]	19.3 ± 7.1	20.1 ± 8.1
Corylus ferox	48.9 ± 11.2	40.8 ± 20.4	—	27.7 ± 15.3	25.2 ± 12.8	—	—	—
Crataegus hepehensis	—	22.9 ± 6.4	22.3 ± 7.1	—	18.8 ± 7.6	18.7 ± 7.1	12.7 ± 1.3	15.2 ± 4.1
Fagus engleriana	99.8 ± 41.1	42.5 ± 21.0[a]	—	46.5 ± 15.6	—	20.3 ± 11.3	—	—
Lindera obtusiloba	50.3 ± 17.4	—	—	51.38 ± 29.9	—	27.3 ± 8.9	—	—
Litsea ichangensis	32.0 ± 15.8[a]	21.5 ± 3.7	—	—	—	—	—	—
Malus halliana	—	—	37.5 ± 11.5[a]	—	—	—	14.0 ± 2.0	—
Phyllanthus flexuosus	—	13.9 ± 3.0	12.4 ± 1.5	16.7 ± 4.3	13.0 ± 0	22.5 ± 15.6	—	—
Pinus armandii	102.4 ± 40.0[a]	48.5 ± 22.2[a]	—	—	52.7 ± 33.3[a]	41.5 ± 22.4	47.5 ± 21.4[a]	42.2 ± 17.5[a]
Populus davidiana	83.0 ± 31.5	41.7 ± 20.9	45.3 ± 17.4	—	40.76 ± 17.8[a]	36.7 ± 13.0[a]	25.4 ± 8.8	33.24 ± 13.2
P. wilsonii	—	—	—	—	—	—	—	37.3 ± 3.6
Rhododendron spp[b]	35.6 ± 9.2	—	—	59.3 ± 27.6	—	21.2 ± 7.1	—	—
Rhus verniciflua	74.3 ± 17.6	37.5 ± 21.0	—	—	—	60.33 ± 6.5	27.9 ± 13.6	34.0 ± 16.7[a]
Salix walliciana	50.5 ± 14.6[a]	34.6 ± 11.0[a]	32.2 ± 10.9[a]	—	49.6 ± 28.1[a]	26.7 ± 12.1[a]	26.7 ± 6.9[a]	34.8 ± 18.7
Sorbus hupehensis	70	14.3 ± 2.3	—	—	—	14.0 ± 3.4	—	—

Note. All species that are >5% in a habitat are listed. MF: mature forest; YF: young forest; Sh: shrub forest. Unite: cm. The number of trees and species sampled in each habitat are listed in Table I. Dash indicates data not available.
[a]Preferred species.
[b]Including several species.

Table V. Wilcoxon signed-rank tests comparing larger trees and smaller trees in habitats of 4 groups

Habitats and species	Comparison of percent of trees used between two samples				Comparison of average number of bites between two samples			
	Group 1	Group 2	Group 3	Group 4	Group 1	Group 2	Group 3	Group 4
Mature forest								
N	11	10	—	—	15	10	—	—
T	7	7.5	—	—	5	8	—	—
Probability	<0.01	<0.0212	—	—	<0.0009	<0.0239	—	—
Young forest								
N	9	10	6	7	11	9	6	7
T	5	3	0	2	7	3	0	3
Probability	<0.0192	<0.0064	<0.0139	<0.0217	<0.0104	<0.0104	<0.0139	<0.0322
Shrub forest								
N	8	13	—	—	8	16	—	—
T	4	14	—	—	3	9	—	—
Probability	<0.025	<0.0139	—	—	<0.0179	<0.0011	—	—
Preferred species								
N	7	11	—	—	9	12	—	—
T	0	0	—	—	0	0	—	—
Probability	<0.0091	<0.0017	—	—	<0.0039	<0.0011	—	—
Avoided species								
N	20	21	—	—	25	23	—	—
T	41	54	—	—	40	54	—	—
Probability	<0.0087	<0.0166	—	—	<0.0005	<0.0054	—	—

Note. N: number of species in the test; T: sum of negative ranks (see context).

The number of preferred and avoided species for Groups 3 and 4 is too small to permit us to investigate the effect of tree size selection. For a preferred species or an avoided species in habitats of Groups 1 and 2, the percentage of trees used and the number of bites per tree in the larger subsample is significantly greater than those in the smaller subsample ($p < .05$). These results suggested that the monkeys preferred the larger trees of a species.

Table VI has correlation coefficients between the percentage of trees used, number of bites per tree and the mean cbh of trees in each habitat. The percentage of trees used and number of bites per tree are significantly positively correlated with the mean cbh of trees, which indicates that the percentage of trees used and number of bites increased with increasing mean cbh of trees in each habitat. The relationship between percentage of trees used and average cbh have correlation coefficients ranging from 0.89 in shrub forest habitat of Group 1 to 0.98 in young forest habitat of Group 2 (Table VI). The variance of mean cbh of trees explained 77.9% of the variation in percentage of trees used by Group 1 in shrub forest, and 94% of the variation in percentage of trees used by them in mature forest. For the relationship between average number of bites per tree and mean cbh of trees, the

Table VI. Correlation coefficients and probability of linear regression models between percent of trees used or average number of bites per tree and mean circumference of trees each part in a habitat

Items	Percent of trees used in a part		Average number of bites per tree in a art	
	R^2	P	R^2	P
Group 1				
Mature forest	0.9397	<0.0001	0.9253	<0.0001
Second forest	0.9244	<0.0001	0.8638	<0.0001
Shrub forest	0.7786	<0.0007	0.8929	<0.0001
Group 2				
Mature forest	0.8194	<0.0003	0.9562	<0.0001
Second forest	0.9553	<0.0001	0.9145	<0.0001
Shrub forest	0.8417	<0.0002	0.9037	<0.0001
Group 3				
Second forest	0.9314	<0.0001	0.9219	<0.0001
Group 4				
Second forest	0.9092	<0.0001	0.9597	<0.0001

correlation coefficients range from 0.96 in young forest used by Group 2 to 0.98 in young forest used by Group 4. The variance of the mean cbh accounts for 86.4% of variation in number of bites in young forest used by Group 2 and 95.8% of variation in number of bites in young forest used by Group 4.

DISCUSSION

Preferred Species in Winter

Other primates studies have demonstrated feeding tree patterns similar to our results (Brown and Zunino, 1990; Chapman, 1987; Dietz *et al.*, 1997; Norton *et al.*, 1987; Overdorff, 1996; Remis, 1997; Stevenson *et al.*, 1994; Strier, 1991; Watts, 1991). Three factors affected the differences among groups in feeding tree selection. The primary factor is the difference in availability of tree species in various habitats. There were differences in composition of tree species among habitats used by a group and among different groups in same type of habitat. For example, there were 23 species in the mature forest habitat of Group 1 and 13 species in that of Group 2. Fifteen species in the mature forest habitat of Group 1 did not occur in the mature forest habitat of Group 2, and 5 species in mature forest habitat of Group 2 did not occur in mature forest habitat of Group 1. *Litsea ichangensis, Pinus armandii* and *Salix walliciana*, which occur in mature forests, were not preferred by Group 2 simply because they did not occur in their habitat. There were 15 young forest species, 2 of which did not exist in the young forest habitat of group 2. Four species in young the forest habitat of Group 2 were not in their mature forest range.

A second factor influencing intergroup differences is the tendency for a group to feed on fallback foods when preferred food species were unavailable or were too rare (Lock, 1972; Norton *et al.*, 1987). For example, both *Pinus armandii* and *Abies fargesii* are evergreen coniferous tree species preferred by snub-nosed monkeys. When the deciduous tree species were bare in winter, *Pinus armandii* and *Abies fargesii* became important food sources and refuges for monkeys. In mature forest in the range of Group 2, where *Pinus armandii* was not available, they used *Abies fargesii*. *Abies fargesii* was rare in young forest habitat of Group 4, and they used *Pinus armandii*.

Thirdly, microclimate will affect group feeding ecology. In winter, the monkeys mainly ate seeds of *Pinus armandii* and lichens that grew on trees. Accordingly, the abundance of lichens on the bark of a given tree species affected its selection index value. The abundance of lichens on trees is determined by microclimate; wet and warm microclimate facilitates lichen growth: the monkeys preferred them. However, microclimate varies greatly due to the complicated mountain landscape of Shennongjia Nature Reserve; different elevations and different slopes at the same elevation have very different microclimates.

Tree Size Selection

Wilcoxon signed-rank tests indicate that the percentage of trees used and the average number of bites per tree in the larger subsamples are significantly greater than those in the smaller subsamples. These results suggest that the monkeys prefer larger trees than smaller trees of each species. A few studies have documented that some bird species prefer large trees (Flemming *et al.*, 1999; Zwicker and Walters, 1999). Some arboreal primates also prefer mature forests that are mainly composed of large trees (Lahm, 1986; Stevenson *et al.*, 1994). At least three reasons explain their preference for larger trees.

First, a large tree usually supplied more food than a small tree of same species. The travel cost within trees by individual monkeys is less than that between trees (Chapman, 1990; Nakagawa, 1990). Second, monkeys in larger trees may be be better protected from predators. If a tree was too small to accommodate all members of the group, some would forage on the ground, which may have increased the chance of being captured by predators. Larger trees also had more complicated structure to hide monkeys from aerial predators. Mammalian and avian predators, including red dog (*Cuon alpinus*), wolf (*Canis lupus*), Asiatic golden cat (*Catopuma* *temmincki*), leopard (*Panthera pardus*), golden eagle (*Aquila chrysaetos*), and goshawk (*Accipiter gentilis*) are potential predators on *Rhinopithecus* (Hu, 1998). At least 3 cases of predation on the snub-nosed monkeys are documented. One case occurred in Fuping Nature Reserve in Shaanxi Province, where a juvenile monkey was killed by a goshawk (Zhang *et al.*, 1999). Two cases occurred in our study area (Li, unpublished data). Thirdly, monkeys foraging in larger trees may have higher foraging efficiency due to their ability to see other food sources around them.

Two reasons are responsible for the positive linear relationship between percent of trees used or average number of bites per tree and average cbh of tree species in habitat. First, the preferred species tend to be larger; consequently, large trees should have a higher percent of trees used and a higher average number of bites per tree than the smaller trees in the habitat. Secondly, monkey groups preferred larger trees to smaller trees of a given species.

Habitat Quality and Group Size

Group size in primates can be influenced by two ecological factors: food resource availability, including home range area and habitat quality, and predation (Chapman *et al.*, 1994; Janson and Goldsmith, 1995; Stanford, 1998; Terborgh and Janson, 1986). Large home ranges and higher quality habitat may provide more food or higher quality food. *Rhinopithecus roxellanae* lives in very large groups compared to those of most other colobine monkeys, and they have a complex structure (Kirkpatrick *et al.*, 1999). Focal group size ranged from 7 to ≥100 monkeys. How did habitat quality and the availability of feeding sites influence this wide variation? Larger groups might occupy higher quality habitat and large home ranges due to their ability to compete successfully with smaller groups for preferred feeding sites (Wrangham, 1980). This seemed to be the case for the Sichuan snub-nosed monkeys. The habitat of Group 1 contained 25.5% mature forest. The habitats of Group 2 was even better than that of Group 1 (Li, unpublished data): >30% mature forest. Habitats of Groups 3 and 4 consisted only of young forest. This suggests that larger groups occupied better habitats than smaller group. Large Groups 1 and 2 not only occupied high-quality habitat as measured by the abundance of preferred tree species and size classes, but also had larger home ranges. The home range area for Group 1 is *ca.* 30 km^2 (Li, unpublished data) and the home range size for Group 2 is even larger (Fig. 1). While our home range estimates are approximate, Groups 3 and 4 had home ranges smaller than those of Groups 1 and 2. In all groups, the monkeys preferred larger versus smaller trees. The results of habitat preference analysis for Group 2 in winter supports this conclusion. Group 2 preferred mature forest to young forest and shrub forest in winter (Li, unpublished data). Mature forest typically has larger biomass than the young forest. For example, the timber reserve in mature forest is several times that in young forest (Chui, 1996). This large biomass may contain more food.

Both species and size are major determinants of winter feeding trees. However, tree size has a much smaller effect on monkey preference for tree species. Usually not all larger species are preferred in some habitats, and some smaller species, such as *Litsea ichangensis* in mature forest of Group 1, and some mid-sized tree species, such as *Salix walliciana* in several habitats are preferred by the monkeys (Table IV). Accordingly, specific identity probably affects use of trees more than tree size does. Tree size plays an important role in use of trees of some species because the monkeys preferred larger trees of those species.

Habitat Conservation Implications

Sichuan snub-nosed monkeys are an endangered species; *ca*. 20,000 individuals remain in the wild (Hu, 1998). Habitat loss and decline in habitat quality are the main factors threatening them. Winter is ecologically stressful for the monkeys; the loss of one key food species due to human disturbance might make a forest tract too degraded to support a population of *Rhinopithecus roxellanae*. Therefore, winter habitat conservation plays a key role in conservation of their habitats. Our results show that they prefer larger trees in winter. *Pinus armandii*, *Abies fargesii* and *Salix walliciana* are the main preferred species. Larger groups used habitat with larger trees than smaller groups. Accordingly, there are 3 implications for habitat conservation in Sichuan snub-nosed monkey. First, habitat conservation should be focused on mature forests because they provide more secure monkey habitat than young forest does if other ecological factors are the same. Secondly, communities of *Pinus armandii*, *Abies fargesii* and *Salix walliciana* should be conserved as top priority. Clear-cutting of such tree communities will destroy key winter food habitats for the monkeys. Thirdly, large trees should be preserved especially because the monkeys prefer them.

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