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ORIGINAL ARTICLE

Terrestriality and tree stratum use in a group of Sichuan snub-nosed monkeys

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Abstract Morphological characters allow the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) to use multiple tree levels, but very few studies have quantified the terrestriality and tree stratum use of the species. I investigated the terrestriality and tree stratum use in a group of the monkeys from July 2003 to September 2004 (except February) in the Qianjiaping area of Shennongjia Nature Reserve, China. I collected data on the vertical position of individual monkeys in forest in relation to behavior types, diet, age/sex classes, vegetation types, tree height, and distribution of predators. The monkeys were much more arboreal than they were thought to be. They spent 97.1% of their time in trees (n = 21,234 records) and 2.9% on the ground, and mainly used the middle (74.4%) and upper strata (17.4%). The monkeys displayed all behavioral types except searching in the middle and upper strata. The percentage of use of a stratum (except the low stratum) varied among months, and there was a difference in the percentage of use of a stratum among age/sex classes and between vegetation types. Approximately 94.2% of trees used by the monkeys were >6 m tall. They mainly fed on lichens, young leaves, mature leaves, flowers, fruits or seeds, and buds in the middle and upper strata, bark in the low and middle strata and herbs on the ground. Wolf (*Canis lupus*), leopard (*Panthera pardus*), and golden eagle (*Aquila chrysaetos*) are predators threatening the survival of individual monkeys in the study site. The results suggested that the seasonal vertical distribution of food items eaten in forest, predators, and vegetation types had important effects on the terrestriality and tree stratum use of the monkeys.

Keywords Sichuan snub-nosed monkey · Terrestriality · Tree stratum use · Vertical distribution of food items eaten · Predation risk · Behavioral types · Age/sex classes · Vegetation types

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Introduction

Understanding terrestriality and tree stratum use in primates is important to elucidate their pattern of habitat use. Factors influencing the terrestriality and tree stratum use can be divided into ecological factors and morphological characteristics. The ecological factors are predator pressure (Gebo et al. 1994; Gebo and Chapman 1995; McGraw and Bshary 2002; Campbell et al. 2005), sympatric primate species competing for resources (Fleagle and Mittermeier 1980; Cant 1992; Campbell et al. 2005), resource distribution and habitat structure (Cant 1992; Youlatos 2002; Campbell et al. 2005), while the morphological characteristics include body size, tail length, limbs (Napier and Napier 1967; Cant 1992; Fleagle 1998; Nowak 1999; Dunbar and Badam 2000).

Although typical colobine monkeys are arboreal quadrupeds and live in the canopy of moist tropical forests, there are a number of exceptions (Fleagle 1992; Oates and Davies 1994). The most striking example is genus *Rhinopithecus*, which includes four species. This genus is unusual among colobines in having forelimbs

almost as long as their hind limbs and ischial callosities separated in males and females (Napier 1985), and being scattered on the fringes of the Asian colobine geographical range (Napier 1985; Bennett and Davies 1994). The Sichuan snub-nosed monkey (*R. roxellana*), the Yunnan snub-nosed monkey (*R. bieti*), and the Guizhou snub-nosed monkey (*R. brelichi*) inhabit the subtropical and temperate montane forests of China, while the highly arboreal Tonkin snub-nosed monkey (*R. avunculus*) is scattered in the mountains of northern Vietnam. The Sichuan snub-nosed monkey is commonly found between 1,500 and 3,300 m elevation in highly seasonal deciduous coniferous mixed forests in Hubei, Shaanxi, Gansu and Sichuan, where the monkeys experience severe winters with snow cover for 4 months and the lowest average temperature of any non-human primate in the world (Happel and Cheek 1986; Li 2001). Terrestriality and tree stratum use in the species have rarely been quantified (Kirkpatrick 1998; Ren et al. 2001). The Yunnan snub-nosed monkey is partly terrestrial and found in fir-larch forests between 3,000 and 4,300 m elevation in Yunnan and Xizhang (Kirkpatrick and Long 1994; Kirkpatrick 1998), while the Guizhou snub-nosed monkey is arboreal and lives in evergreen-deciduous broadleaf forests of Fan Jing mountain, Guizhou province, but can frequently cross open areas on the ground (Bleisch and Xie 1998). Unlike most colobine monkeys, which are leaf-eaters, the Sichuan snub-nosed monkey and the Yunnan snub-nosed monkey are primarily lichen-eaters (Kirkpatrick et al. 1998; Li 2006). The Sichuan snub-nosed monkey also feeds on leaves, fruits or seeds, buds, bark, flowers, and herbs, and shows a complicated seasonal variation of the diet. The monthly diet varies from primarily lichen eater between November and April, to a mixture of folivore and lichen eater from May to July, and to a mixture of frugivore (or seed eater) and lichen eater or primarily lichen eater between August and October (Li 2006). This primate prefers to forage in larger trees of a tree species, and spends most of the time using primary forest and young forest, rarely uses shrub forest and does not use grassland (Li et al. 2002; Li 2004). Both mammal predators, such as red dog (*Cuon alpinus*), wolf (*Canis lupus*), asiatic golden cat (*Catopuma temmincki*), and leopard (*Panthera pardus*), and eagle predators, like golden eagle (*Aquila chrysaetos*) and goshawk (*Accipiter gentilis*), can threaten the Sichuan snub-nosed monkey (Hu 1980, 1998; Zhang et al. 1999; Li et al. 2002).

Morphological characteristics allow the Sichuan snub-nosed monkey to use multiple forest strata. This primate is similar to terrestrial cercopithecines in limb proportions, locomotion, sexual dimorphism, and perineal coloring (Napier and Napier 1967; Davison 1982), but remains plantigrade and has a long tail, which are adaptations to life in trees (Fleagle 1992; Oates and Davies 1994; Bennett and Davies 1994). Body size differs between males and females (Nowak 1999). Head–body length and tail length of adult females are about 465–526 and 484–790 mm respectively, and adult males 585–780 and 590–880 mm (Wang et al. 1998).

Captive observation of 2 days indicated that the Sichuan snub-nosed monkey is mainly terrestrial in that males and females spend 82.7 and 74.4% of daylight hours on the ground respectively (Davison 1982). Behavior in the wild may be different. In Sichuan the species is typically arboreal (Hu et al. 1980; Hu 1998), while in Hubei (at Shennongjia Nature Reserve) it is semi-arboreal (Su et al. 1998). In Shaaxi, the species spends 15.3% of daytime on the ground in winter (Ren et al. 2001), and adult males are semi-terrestrial, spending as much as 46.5% of daytime on the floor of forests. Such differences may suggest that ecological factors play important roles in influencing ground and tree stratum use of the species. However, these field studies are usually based on occasional observations or very small sample sizes due to the high elevation and rugged topography of study sites. Long-term field data are needed for understanding relationships between the terrestriality, tree stratum use, and ecological factors.

This study presents detailed information on the terrestriality and tree stratum use of the primate in the Shennongjia Nature Reserve, Hubei. The aims of the study are:

1. To investigate the terrestriality and tree stratum use of the monkeys and their temporal variation
2. To determine differences in the terrestriality and tree stratum use between age/sex classes, behavioral types, and vegetation types
3. To investigate the effects of the distribution of food items eaten and effects of predators on the terrestriality and tree stratum use

Study area and methods

Study site

The study was carried out in the Qianjiaping area of Shennongjia Nature Reserve (31°22′–31°37′N and 110°03′ –110°34′E; Fig. 1), Hubei province. The Qianjiaping area, about 40 km^2, is located in the southern part of the reserve. The area has a rugged

Fig. 1 Location of the study site in the Shennongjia Nature Reserve in Hubei Province, China

topography with elevational range from 1,500 to 2,600 m. The site's climate is highly seasonal (Li 2002). Average temperature is 17.8°C in July and –2.8°C in January at 1,700 m elevation. Annual precipitation is about 1,800 mm. Spring with moderate temperature and a considerable rainfall runs from the growth of new buds to the formation of mature leaves (April to May). Summer is hot (June to the middle of August). Autumn begins with the leaves becoming yellow and the ends of the leaves being totally lost from deciduous trees (middle of August to October). Winter lasts from November to March approximately (stable snow cover between December and March).

The vegetation is temperate deciduous broadleaf coniferous forest (Li 2006), consisting of Farges fir (*Abies fargesii*, 3% of tree number) and Armand pine (*Pinus armandii*, 12%), and a number of deciduous broadleaf tree species, such as birch (*Betula* spp., 19%), David poplar (*Populus davidiana*, 13%), Hupeh mountain ash (*Sorbus hupehensis*, 6%), Japanese spicebush (*Lindera obtusiloba*, 6%), hawthorn (*Crataegus hupehensis*, 5%), Szechuan cherry (*Cerasus discadenia*, 4%), Yichang litsea (*Litsea ichangensis*, 4%), Wallich willow (*Salix wallichiana*, 4%), and rhododendron (*Rhododendron* spp., 4%). The proportion of coniferous trees increases with elevation. A large part of the area was clear-cut from 1950 to 1987 (Zhu 1992). Four types of vegetation cover the area: primary forest, young forest, shrub forest, and grassland. Young forest accounts for the main body of the area. The oldest trees in the forest are 30–50 years old, and a large number of trees are above 6 m in height. Primary forest comprises a number of patches scattered in young forest. Most trees in primary forest are above 9 m. Young forest and primary forest are mainly composed of all the tree types listed above except hawthorn. Shrub forest and grassland mainly occur in plains and tops of some peaks, occupying a small part of the area. Shrub forest is mainly composed of Haus crabapple (*Malus halliana*) and hawthorn (*Crataegus hupehensis)*. A large number of trees in the shrub forest are less than 6 m tall. The grassland is scattered with small trees.

Data collection

Within the study area, I habituated one group of the monkeys (120–140 individuals) to human observers for 6 months before sampling (Li 2006). I was able to approach the group to within 20–30 m, and observed it consecutively from July 2003 to September 2004, except February 2004. Every morning, the monkeys stay at a sleeping site for about half-hour after waking up, then they travel. There are two travel peaks (morning and afternoon) and a rest period (about 1.5 h) at noon during a day (Li 2002). They stop traveling to sleep at dusk. Each month, I observed the group for 15 days (5 days in January and 14 days in March 2004), each day usually from 10 a.m. to dusk when the group reached a sleeping site. I also made ad libitum observations of behavior when possible besides the observation period of 15 days each month. I did not observe the behavior of the monkeys at night, so the observation only covered behavior during the daytime.

I collected behavioral data via instantaneous scan samples (Altmann 1974) at 15-min intervals. For each scan, I looked at each visible individual for 5 s to determine its behavioral type, age/sex class, vertical position, vegetation type, and height of the tree the monkey was in. To avoid sampling the same individuals twice within a single scan, I scanned from one side of the group to the other without backtracking.

I recognized six types of behavior during the daytime:

1. Inactive: resting, standing or sitting motionless, or sleeping at noon
2. Traveling: locomotion, including walking, running, climbing and jumping
3. Searching: movement associated with looking for insects, such as stripping bark and turning over stones on the ground
4. Feeding: procuring and/or handling food items with the hands or mouth, chewing, or other obvious signs of ingestion
5. Social behavior: behavior between two monkeys, such as allogrooming, play, noncopulatory mounting, copulations, fights or chases

6. Other behavior: grooming oneself, calling, and sentry

The type of food being eaten was noted when it could be discerned. Food items were divided into nine categories:

1. Buds
2. Young leaves
3. Mature leaves
4. Flowers
5. Fruit or seeds
6. Bark
7. Insects
8. Lichens
9. Herbs

Specimens of plants eaten by the monkeys were preserved for identification. I also roughly assessed the height of each tree the monkeys used by the range estimation. The tree height was classed into six categories: ≤3 m, >3 to ≤6 m, >6 to ≤9 m, >9 to ≤12 m, >12 to ≤15 m, and >15 m. I only estimated the height of a tree once when more than one monkey had simultaneously used the tree. I calculated the proportion of each category in vegetation types.

I systematically collected data for four age/sex classes: adult females, adult males, juveniles, and infants. Adult females are brownish black on their head and upper parts, with elongated nipples. Adult males are larger than adult females. They are grayish black on the top of the head, nape, shoulders, upper parts of the arms, back and tail, overlaid with long silvery hairs. They have two especially tumescent warts on the upper lip on both sides of the corners of their mouths. Juveniles are smaller than the adult females, but with a proportionately larger head, are paler and fluffier, and without elongated nipples. Infants are less than 1 year old, with the palest, the fluffiest and smallest body sizes. They often suckle and their mothers or other members often hold them. During the study period, the group was composed of about 10% infants and 90% juveniles and adults. The sex ratio was about 1:1.3 (male:female).

I assigned the height of each visible monkey in the trees to one of four categories: ground, low stratum, middle stratum, and upper stratum. The low, middle, and upper strata are above the ground to one third of the height of a tree, the middle third of the tree and the top third of the tree respectively. I calculated the monthly percentages of use of a stratum for behavioral types, age/sex classes, and vegetation types. The average monthly percentage for stratum use is the sum of the monthly percentages divided by the number of months sampled.

I reviewed the distribution of the predators of the monkeys in the Qianjiaping area from published data (Chui 1996). The group in Qianjiaping was occasionally habituated before 1998 (Li et al. 2002), but regularly observed from 1999 to 2003. During this period, the group was studied for 15 seasons, 1 month each season, which included four springs (1999, 2001–2003), four summers (1999–2002), three autumns (1999, 2001–2002), and four winters (1999–2002). I summarized the events of predators attacking the monkeys in different periods including the present study period of July 2003 to September 2004.

I applied a Chi-squared test to test:

1. If the monkeys were randomly distributed in tree strata with an expected frequency of one in three in each of the tree strata
2. If six types of behavior were evenly distributed in each of the vertical levels with a frequency of one in six for each type
3. If distribution of tree height differs among vegetation types
4. If there were differences in the vertical distribution among food items eaten

I used a one-way ANOVA to examine differences in the average monthly percentages of ground and tree stratum use among behavioral types, age/sex classes, and vegetation types, and then performed multiple comparisons using the Tukey HSD test. I excluded the infant class from the age/sex classes when analyzing the difference in tree stratum use among age–sex classes because the behavior of this class is usually associated with adult females. I implemented single variable regressions to determine the relationships among monthly percentages of different forest strata used and monthly percentages of different food items and their combinations in the monkeys' diet (Li 2006). The level is 0.05 for all comparisons.

Results

Use of tree stratum and ground

I scanned the group 6,025 times in the study period, obtaining 21,234 records of ground and tree stratum use for individual monkeys. The number of monkeys per scan ranged from 1 to 19 individuals, on average 3.5 individuals (± 1.7) per scan. Vertical distribution of the monkeys per scan ranged from ground or one tree stratum to ground and all tree strata.

The monkeys used tree strata non-randomly ($\chi^2 = 17{,}878.72$, $df = 2$, $P < 0.001$). They were highly

arboreal, spending 97.1% of the time in trees and 2.9% on the ground. They mainly used the middle (74.4%) and upper strata (17.4%), and rarely used the low stratum (5.3%) and the ground.

The monkeys displayed six behavioral types in each of the tree strata and on the ground non-randomly (e.g., low stratum: $\chi^2 = 1921.77$, $df = 5$, $P < 0.001$). They mainly traveled, searched and ate on the ground and in the low stratum (Fig. 2). These three behavioral types accounted for 99.4% of the time on the ground and 91.0% in the low stratum. They rarely displayed social and other behavior, and inactive behavior in these two strata. The monkeys displayed all behavioral types in the middle stratum and the upper stratum.

The monthly percentages of ground use varied between 0.7 and 13.5% (Fig. 3). The monkeys spent 66.1–80.5% of the time in the middle stratum monthly, 12.7–25.0% in the upper stratum, and 3.8–7.0% in the low stratum. There were differences in stratum (except low stratum) use among some months. For example, the percentage of ground use in July 2003 was higher than that in other months (e.g., $\chi^2 = 119.45$, $df = 1$, $P < 0.0001$ between July and August 2003; $\chi^2 = 151.45$, $P < 0.001$ between July 2003 and 2004). Furthermore, the percentages of upper stratum use from May to October were lower than from November to April ($t = 2.373$, $df = 12$, $P = 0.035$). The monthly percentages of middle stratum use were negatively correlated with the monthly percentages of ground use and upper stratum use ($r = -0.607$, $n = 14$, $P = 0.021$ for ground use; $r = -0.65$, $n = 14$, $P = 0.012$ for upper stratum use).

One-way ANOVA showed that there was a difference in the average monthly percentages (AMP) of records among different strata ($F = 1383.507$, $df = 3$, $P < 0.001$). The AMP of middle stratum use (74.3 ± 4.5%) was higher than that of other stratum uses (e.g., Tukey HSD test, mean difference MD = 56.93, $P < 0.001$ for comparison between middle stratum use and upper stratum use). Furthermore, the AMP of upper stratum use (17.3 ± 3.7%) was higher than that of low stratum use (5.2 ± 0.9%) and ground use (3.2 ± 3.2%; e.g., MD = 14.204, $P < 0.001$ for comparison between upper stratum use and ground use).

All behavioral types except searching mainly occurred in the middle and upper strata. Nearly 99.8% of resting, 92.2% of feeding, 96.9% of social, 94.0% of traveling, and 99.6% of other types of behavior occurred in the middle and upper strata (Table 1). When searching, the monkeys monthly spent 10.8% of the time on the ground, 43.5% in the low stratum, 31.1% in the middle stratum, and 14.5% in the upper stratum.

The monthly percentages of ground use and tree stratum use differed among behavioral types by the ANOVA (e.g., $F = 15.764$, $df = 5$, $P < 0.001$ for comparison of percentage of ground use among behavioral types). The AMP of ground use or low stratum use in searching was higher than that of other types of behavior (e.g., MD = 10.839 between searching and inactive on the ground, $P < 0.001$; Table 2). But the AMP of middle stratum use in searching was lower than other types of behavior (e.g., MD = 26.559 between feeding and searching, $P < 0.001$). The AMP of middle stratum use in feeding was lower than for other types of behavior except searching. However, the

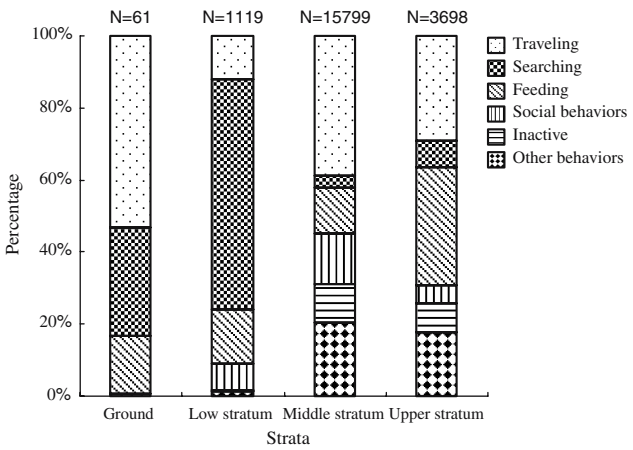

Fig. 2 The composition of behavioral types on the ground and in the tree strata for the monkeys

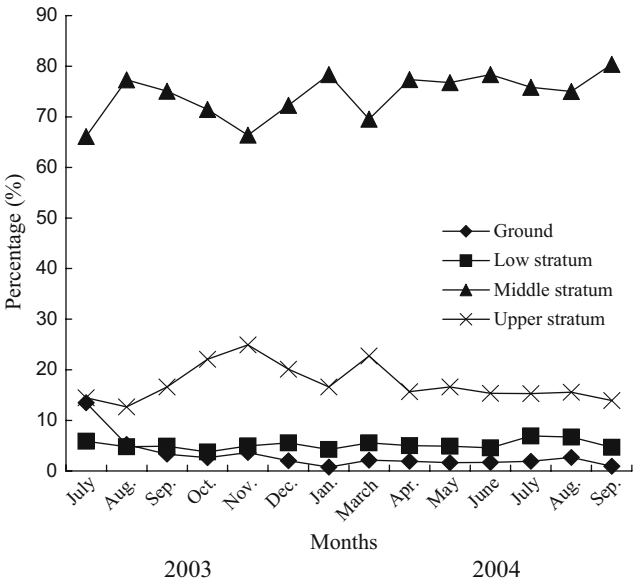

Fig. 3 The monthly percentages of scan records for individual monkeys on the ground and in the tree strata

AMP of upper stratum use in feeding was higher than that of other types of behavior (e.g., MD = 18.316 between feeding and other behavioral types, $P < 0.001$).

A difference in the AMP of different strata except the middle stratum used by the monkeys was detected among adult males, adult females, and juveniles (e.g., $F = 8.767$, $P = 0.001$ for the upper stratum). Adult males used ground and the low stratum more than the other two classes monthly (e.g., MD = 3.950, $P = 0.014$ between adult males and adult females on the ground) (Table 3). Juveniles spent more time in the upper

Table 1 The average and standard deviation (SD) of monthly percentages of ground and tree stratum use of the monkeys

Terms (number of records)	Ground	Low stratum	Middle stratum	Upper stratum
Total percent (21,234)	2.9	5.3	74.4	17.5
Behavioral types				
Inactive (1,981)	0 ± 0	0.2 ± 0.4	84.7 ± 3.3	15.2 ± 3.2
Feeding (3,485)	3.0 ± 3.8	4.5 ± 3.1	57.6 ± 9.5	34.8 ± 11.4
Social behavior (2,503)	0.2 ± 0.8	2.9 ± 2.1	89.7 ± 3.1	7.2 ± 2.7
Searching (1,682)	10.8 ± 8.0	43.5 ± 6.0	31.1 ± 7.8	14.5 ± 7.4
Traveling (7,693)	4.4 ± 4.0	1.7 ± 0.8	79.8 ± 8.1	14.2 ± 5.6
Others (3,890)	0 ± 0	0.4 ± 0.5	83.1 ± 7.0	16.5 ± 6.7
Sex/age groups				
Adult males (10,877)	5.4 ± 5.8	7.4 ± 1.6	72.6 ± 5.3	14.6 ± 3.7
Adult females (3,979)	1.4 ± 1.7	3.3 ± 1.4	77.6 ± 5.1	17.7 ± 5.7
Juveniles (5,970)	0.6 ± 0.8	2.5 ± 1.3	74.4 ± 6.2	22.6 ± 5.5
Infants (436)	0.3 ± 1.1	4.5 ± 4.8	87.3 ± 11.1	7.9 ± 9.7
Forest types				
Primary forest (1,923)	2.7 ± 4.5	3.7 ± 2.4	78.7 ± 5.7	14.9 ± 4.8
Young forest (19,232)	3.1 ± 3.1	6.1 ± 2.6	73.5 ± 4.3	17.3 ± 3.6
Shrub forest[a] (128)	21.9	4.7	30.5	43.0
Grassland	0	0	0	0

[a] The monkeys used shrub forest in March 2004

Table 2 Multiple comparisons of the average monthly percentages of ground and tree stratum use among behavioral types of the monkeys

Behavioral types	Feeding	Other behavior	Social behavior	Searching	Traveling
Ground					
Inactive	–3.033 (0.342)	0.000 (1.000)	–0.222 (1.000)	–10.839 (<0.001)	–4.379 (0.051)
Feeding		3.033 (0.342)	2.811 (0.428)	–7.806 (<0.001)	–1.346 (0.946)
Other behavior			–0.222 (1.000)	–10.839 (<0.001)	–4.379 (0.051)
Social behavior				–10.617 (<0.001)	–4.157 (0.074)
Searching					6.460 (0.001)
Low stratum					
Inactive	–4.324 (0.003)	–0.203 (1.000)	–2.740 (0.142)	–43.370 (<0.001)	–1.496 (0.753)
Feeding		4.121 (0.005)	1.584 (0.753)	–39.046 (<0.001)	2.828 (0.119)
Other behavior			–2.537 (0.207)	–43.168 (<0.001)	–1.293 (0.849)
Social behavior				–40.630 (<0.001)	1.244 (0.868)
Searching					41.874 (<0.001)
Middle stratum					
Inactive	27.032 (<0.001)	1.561 (0.991)	–5.032 (0.394)	53.591 (<0.001)	4.901 (0.424)
Feeding		–25.470 (<0.001)	–32.064 (<0.001)	26.559 (<0.001)	–22.131 (<0.001)
Other behavior			–6.593 (0.130)	52.030 (<0.0001)	3.340 (0.796)
Social behavior				58.623 (<0.001)	9.933 (0.004)
Searching					–48.690 (<0.001)
Upper stratum					
Inactive	–19.675 (<0.001)	–1.359 (0.995)	7.993 (0.030)	0.618 (1.000)	0.974 (0.999)
Feeding		18.316 (<0.001)	27.668 (<0.001)	20.293 (<0.001)	20.649 (0.001)
Other behavior			9.352 (0.006)	1.977 (0.972)	2.333 (0.943)
Social behavior				–7.376 (0.057)	–7.020 (0.080)
Searching					0.356 (1.000)

Figures in the table represent mean differences (probabilities). The Tukey HSD test was used

Table 3 Multiple comparisons of the average monthly percentages of ground and tree stratum use among age/sex classes for the monkeys

Age/sex classes	Adult females	Juveniles
Ground		
Adult males	3.950 (0.014)	4.752 (0.003)
Adult females		0.802 (0.829)
Low stratum		
Adult males	4.075 (<0.001)	4.937 (<0.001)
Adult females		0.862 (0.266)
Middle stratum		
Adult males	–4.954 (0.059)	–1.743 (0.686)
Adult females		3.211 (0.288)
Upper stratum		
Adult males	–3.072 (0.256)	–7.946 (<0.001)
Adult females		–4.874 (0.039)

Infants were not included in the analysis. Figures in the table represent mean differences (probabilities). The Tukey HSD test was used

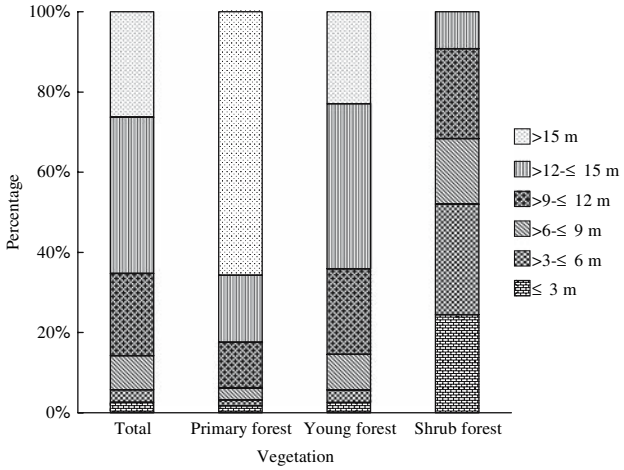

Fig. 4 The distribution of the height of trees used by the monkeys among the different vegetation types

stratum than adult males and females (e.g., MD = 7.946, $P < 0.001$ between juveniles and adult males in the upper stratum).

The monkeys used the middle stratum more and the low stratum less in primary forest than those in young forest monthly ($t = 2.632$, $P = 0.015$ for the middle stratum; $t = 2.417$, $P = 0.024$ for the low stratum).

Distribution of tree height used by the monkeys, food items eaten in different tree strata, and predators

I estimated the heights of 15,523 trees used by the monkeys for 20,923 records (98.5% of total records, the heights of trees for the other 311 records were not assessed), including 14,158 trees in young forest, 98 trees in shrub forest, and 1,267 trees in primary forest. The number of trees ≤3 m tall only accounted for 2.6% of trees assessed (Fig. 4). Approximately 94.2% of trees were >6 m tall. The distribution of tree height differed among vegetation types (e.g., $\chi^2 = 1{,}311.34$, $df = 5$, $P < 0.001$ for comparison between primary forest and young forest; $\chi^2 = 691{,}431.2$, $df = 5$, $P < 0.001$ for comparison between primary forest and shrub forest). Approximately 64.0 and 82.0% of trees in young forest and primary forest were >12 m respectively, while only 9.0% of trees in shrub forest were >12 m and 51.0% of trees in this type of vegetation were ≤6 m.

I compiled 3,452 eating records with discerned food items (Li 2006). Lichens accounted for 43.3% of the records, young leaves 28.7%, fruits or seeds 14.6%, buds 5.4%, mature leaves 3.5%, herbs 2.1%, bark 1.4%, and flowers 1.1%. Tree parts and lichens on trees consisted of 97.9% of diet composition. The monkeys fed on these food items in tree strata in a non-random way (e.g., lichens $\chi^2 = 900.65$, $df = 2$, $P < 0.001$). They mainly fed on lichens, young leaves, mature leaves, flowers, fruits or seeds, and buds in the middle and upper strata (Table 4), but they mainly ate bark in the low and middle strata and herbs on the ground. The Chi-squared test showed that they fed on lichens in higher tree strata than mature leaves, bark, and herbs (e.g., $\chi^2 = 11.437$, $df = 3$, $P < 0.01$ for comparison between lichens and mature leaves), but lower than young leaves and fruits or seeds (e.g., $\chi^2 = 8.134$, $df = 3$, $P < 0.043$ for comparison between lichens and fruits or seeds). The monkeys in trees mainly ate tree parts and lichens (99.1% of eating records in tree strata) attached to trees and almost did not feed on herbs (<0.1% of eating records), while on the ground they mainly fed on herbs (71.7% of eating records on the ground). Tree parts and lichens only accounted for a small part (28.3%) of eating records on the ground.

There were positive relationships between monthly percentages of ground use and percentages of herbs in monthly diet of the monkeys ($r = 0.896$, $n = 14$, $P < 0.001$) and between monthly percentages of a combination of tree stratum use (summing the use of low, middle, and upper strata) and percentages of lichens and tree parts in the monthly diet ($r = 0.896$, $n = 14$, $P < 0.001$).

Wolf (*Canis lupus*), leopard (*Panthera pardus*), and golden eagle (*Aquila chrysaetos*) are predators of the monkeys in the Qianjiaping area. Three cases of predators attacking the monkeys have occurred in the area since 1988. In one case, a golden eagle was observed to attack an infant monkey, and in two cases, leopards killed two monkeys.

Table 4 The distribution of food items eaten by the monkeys

Stratum	Lichens	Buds	Young leaves	Mature leaves	Flowers	Fruits or seeds	Bark	Herbs	Total
Upper stratum	481 (32.2)	61 (33.0)	430 (43.4)	31 (25.6)	15 (39.5)	194 (38.6)	7 (14.9)	0 (0.0)	1,219 (35.4)
Middle stratum	977 (65.5)	123 (64.5)	447 (45.1)	83 (68.6)	23 (60.5)	302 (60.0)	14 (29.8)	0 (0)	1,969 (57.1)
Low stratum	31 (2.1)	1 (1.6)	92 (9.3)	5 (4.1)	0 (0.0)	7 (1.4)	25 (53.2)	1 (1.4)	162 (4.7)
Ground	3 (0.2)	0 (0.0)	22 (2.2)	2 (1.7)	0 (0.0)	0 (0.0)	1 (2.1)	71 (98.6)	99 (2.9)
Total (records)	1,492 (100)	185 (100)	991 (100)	121 (100)	38 (100)	503 (100)	47 (100)	72 (100)	3,449 (100)

Percentages (%) are shown in parentheses. Out of a total of 3,452 eating records, 3,449 have records of ground use or tree stratum use

Discussion

The Sichuan snub-nosed monkey is highly arboreal. They only occasionally descend to the ground. This result accords with observations in the Sichuan province (Hu et al. 1980; Hu 1998). Based on evidence from physical and locomotor characters, several studies have suggested that the species is at least partly terrestrial (Davison 1982; Tan and Poirier 1988). Their limb proportion, sexual dimorphism, perineal coloring, and behavior reflect a tendency toward terrestriality convergent with cercopithecines such as baboons and macaques. This is supposed to be due to the fact that food sources are mainly located in the middle and low strata of forests, which leads to the combination of arboreal and terrestrial adaptations for the monkeys to move from source to source. This study strikingly differs from the supposition. The monkeys mainly used the middle and upper strata, which accounted for 91.8% of the scanning records.

This study may overestimate the percentage of ground use of the monkeys. Compared with the sex ratio (1:1.3 for males and females), the sample size of adult males was approximately three times that of adult females (Table 1), suggesting that males were more often observed than females. This arose because the females were generally shyer toward an observer than the males. As males used the ground and the low stratum more than the other classes, a large sample size in males would lead to a terrestriality-biased estimation for the monkeys.

A high degree of arboreality of the monkeys in the reserve may be attributed to:

1. Vertical distribution of food resources in the trees and on the ground
2. Predation risk
3. Vegetation types

The vertical distribution of food items in the diet may largely reflect the distribution of food resources in forests. The diet of the monkeys is mainly composed of lichens on trees and tree parts, while herbs on the ground only account for a very small part of the diet. The main food resources for the monkeys in the study area are in the trees, almost all of which (97.4%) range from above 3 m tall. The monkeys on the ground mainly feed on herbs, as they cannot access most of the tree food resources. The high proportion of tree use enables them to consume more food resources. Higher arboreality also reduces the risk of being attacked by the mammal predators. Due to the risk on the ground, the monkeys display fewer behavioral types there than in tree strata, which reduces ground use. Traveling is a main component of ground use for the monkeys. The monkeys usually travel on the ground in open areas. Vegetation with a high proportion of open areas will increase ground use. In the study area, there are few open areas and crowns of forests are connected. Therefore, the monkeys rarely traveled on the ground (4.4% of traveling records).

Since almost all food resources are located in the trees, why do the monkeys descend to the ground to eat herbs, at a risk of being attacked by predators? They mainly eat one species of herbs—Heracleum (*Heracleum hemsleyanum*)—on the ground (Li 2006), which accounts for 98.6% (71 out of 72) of herbs records (Table 4). The leaves of the herb contain a higher proportion of proteins than the leaves, bark, and buds of most tree species and lichens (Li Yiming, unpublished data). Thus, the monkeys may feed on herbs on the ground possibly because the herb can provide important food proteins. The primates usually prefer higher protein food and not higher fiber or secondary compounds, such as tannin and alkaloids (Milton 1979; Oates et al. 1980; Mckey et al. 1981; Waterman and Choo 1981; Waterman and Kool 1994).

Seasonal availability in food items is partly responsible for the monthly variation of tree stratum and ground use in the monkeys. Leaves, flowers, buds and fruits or seeds of trees and herbs are seasonal food items (Li 2006). Herbs are only available from May to October. The positive relationship between percentages of ground use and percentages of herbs in the monkeys' diet suggests that the monkeys might spend more time on the ground as they increasingly consumed the herbs during this season. The difference in

the percentage of ground use between July 2003 and 2004 indicated that there was an annual variation in ground use for the monkeys. This may be due to the annual change of herbs in the diet (Li 2006). Lichens are in lower tree strata than young leaves and fruits or seeds, but higher than mature leaves and herbs. As the monkeys ate more young leaves and fruits and fewer lichens from May to October than from November to April (Li 2006), it would be expected that the monkeys used the upper stratum from May to October more frequently than from November to April. However, there was less upper stratum use from May to October than from November to April, contrary to this prediction. This may be partly due to the fact that the monkeys also ate mature leaves and herbs in lower tree strata and ground than lichens between May and October, which might have reduced upper stratum use. Another reason is that individual monkeys were less visible between May and October with dense foliage than between November and April (as deciduous trees leaves fall in November and new leaves show at the end of April). Individuals in the tree crown between May and October were especially more difficult to observe than in other forest strata because of dense foliage and the longest distance from the observers on the ground. This may create a small sample size of individuals in the upper stratum between May and October and therefore underestimate upper stratum use.

The monkeys mainly feed in the middle and upper strata because the main food items such as lichens, leaves, fruits or seeds, and buds are distributed in these two strata. Less upper stratum use in types of behavior other than eating is because of the bird predator, which reduces this behavior in this stratum. Low stratum usually has fewer branches and trunks than the middle and upper strata. Therefore, the monkeys use this stratum less often for all behavioral types except searching than other two strata. Some studies documented that the monkeys eat insects (Su et al. 1998; Li 2001). In this study, I did not find insects in the diet, perhaps because insects are simply less visible than the ingestion of plant material and lichens (Li 2006). Searching accounts for a part of a monkey's time, suggesting that the monkeys might have fed on some insects. Low stratum has richer old or dead bark under which insects can hide than the other tree strata. Therefore, searching mainly occurs in this stratum.

Different body size, anti-predator ability and distribution of time budget for the best intake of nutrition may contribute to the difference in stratum use among age/sex classes. Adult males, with the largest body size (Nowak 1999), have the strongest anti-predator ability, and use the ground more often. Adult males and females are heavier than juveniles. Many branches in the upper stratum may not support them, as a result, they use the upper stratum less than juveniles. Adult males use the low stratum more often than the other classes, partly because the males spend more time searching than other classes (Li Yiming, unpublished data), and partly because they use the ground more often, which may increase low stratum use. Individuals that fall to the ground from trees will be wounded (Li et al. 2005). They have to use the low stratum for descending to the ground.

Vegetation types have an effect on tree stratum and ground use. There may be a difference in the distribution of food resources, the proportion of open areas and predation risk for tree strata among vegetation types due to the differences in vegetation height and structure, which results in the monkeys using tree strata differently in different vegetation types.

Ren and colleagues (Ren et al. 2001) compiled 4,938 scanning records of the Sichuan snub-nosed monkey with regard to the vertical distribution of trees at in winter at Qinling Mountains, Shaaxi province, and found that the monkeys spent 15.3, 24.3, 28.2, and 32.2% of daytime on the ground, in the low stratum, middle stratum, and canopy (upper stratum) respectively. Adult males spent 46.7% of the time on the ground, and sub-adult males and sub-adult female and young individuals (similar to the juveniles in this study) used canopy (38.3–38.9%) more than any other strata. The results of this study are different from those of Ren and colleagues. Their study site is drier and colder than the Qianjiaping area. Rainfall in their study site is only about half of that in Qianjiaping (Su et al. 1998). There may be a difference in the proportion of open areas, vertical distribution of food items, and predators for vegetation types between the two sites, which may have contributed to the difference in results. It is commonly found that the degree of terrestriality in a primate species varies widely from place to place (Napier and Napier 1967; Wu et al. 1988; Wu 1993; Kirkpatrick and Long 1994). The variation in terrestriality and tree stratum use for the Sichuan snub-nosed monkey among different sites is in accordance with this generality.

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