



Effects of Seasonal Folivory and Frugivory on Ranging Patterns in *Rhinopithecus roxellana*

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Received: 21 April 2009 / Accepted: 26 November 2009 /
Published online: 11 June 2010
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Abstract The distribution of food resources in time and space may affect the diet, ranging pattern, and social organization of primates. We studied variation in ranging patterns in a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) over winter and summer in response to variation in their diet in the Qingmichuan Nature Reserve, China. There was a clear diet shift from highly folivorous in winter to highly frugivorous in summer. The home range was 8.09 km² in summer and 7.43 km² in winter, calculated via the 95% kernel method. Corresponding to the diet shift, the focal group traveled significantly longer distances in summer (mean 1020±69 m/d) than in winter (mean 676±53 m/d); the daily range was also significantly greater in summer (mean 0.27±0.02 km²/d) than in winter (mean 0.21±0.01 km²/d). There was no significant variation in home range size between winter and summer, and the monkeys did not use geographically distinct ranges in summer and winter. However, overlap in the actual activity area and core range between winter and summer was only 0.13 km², representing 4.4% of the summer core area and 5.3% of the winter core area. Differences were apparent between summer and winter ranging patterns: In summer, the group traveled repeatedly and uninterruptedly across its home range and made 3 circles of movement along a fixed route in 31 d; in winter, the activity area was composed of 3 disconnected patches, and the focal group stayed in each patch for an average of 8 successive days without traveling among patches. Winter range use was concentrated on mixed evergreen and deciduous forest patches where leaves and fruits were available, whereas the summer range

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pattern correlates significantly positively with the distribution of giant dogwood (*Cornus controversa*) fruits. Thus it appears that the diet shift of Sichuan snub-nosed monkeys between winter and summer caused the monkeys to use their home range in different ways, supporting the hypothesis that food resources determine primate ranging patterns.

Keywords frugivory · range size · ranging pattern · *Rhinopithecus roxellana* · Sichuan snub-nosed monkey

Introduction

Knowledge of ranging patterns and spatial needs contributes significantly to an understanding of a species' socioecology (Nkurunungi and Stanford 2006; Singleton and van Schaik 2001). Primates exhibit wide interspecific and intraspecific variation in home range size and ranging patterns. This variation has been attributed to variation in diet (Boonratana 2000; O'Brien and Kinnaird 1997), abundance and distribution of food resources (Basabose 2005; Curtis and Zaramody 1998; Robbins and McNeilage 2003), water availability (Scholz and Kappeler 2004), topographic factors (Furuichi and Hashimoto 2004), group size and population density (Strier 1987), intergroup encounters and availability of sleep sites (Buchanan-Smith 1991), as well as human disturbance (Glessner and Britt 2005). Among these, the spatial and temporal distribution and abundance of food resources are suggested to be the most important environmental determinants of primate range use (Basabose 2005; Clutton-Brock 1975; Harrison 1983; Isbell 1983; Newton 1992). In particular, temporal variation in the availability and distribution of preferred or major food resources shapes primate ranging patterns, and ultimately affects the size and shape of home range (Wallace 2006; Watts 1998). For example, many cercopithecines shift their diets and ranging patterns to include higher proportions of fallback foods when preferred high-quality foods are seasonally scarce, which may be especially significant for those remaining together as cohesive units (Strier 2003).

The rapid increase in human density and consequential deterioration of the environment, accelerated deforestation, and hunting of Sichuan snub-nosed monkeys for food or medicinal purposes during the last 400 yr, and particularly during the past half-century, have pushed this species to the brink of extinction (Hu 1998; Li *et al.* 2002). It is now mainly distributed in several geographic isolated mountainous areas in Sichuan, Shaanxi, Gansu, and Hubei provinces of China, with *ca.* 22,000–23,000 individuals in the wild (Hu 1998; Long *et al.* 1994; Wang and Xie 2004). Although some nature reserves have been established for protecting the monkeys, habitat destruction and illegal hunting still threaten their survival (Li 2004); the species has been listed as Vulnerable by IUCN and Endangered by the Chinese government.

Sichuan snub-nosed monkeys live in large, cohesive groups of 50–600 individuals (Kirkpatrick 1998; Ren 2002), comprising one-male, multifemale units (OMUs) and all-male units (AMUs; Lu 2007). They range at altitudes of 1400–3400 m in 3 vegetation types: mixed evergreen and deciduous broadleaf forests, deciduous broadleaf forests, and mixed deciduous and conifer forests, characterized

by a distinct seasonality of the temperate zone where the monkeys are confronted with food scarcity in cold winters (Hu 1998; Li 2006; Long *et al.* 1994). Early studies suggested that Sichuan snub-nosed monkeys are primarily folivorous, but that they also consume buds, fruit, bark, lichens and insects (Hu *et al.* 1980). However, subsequent research revealed that they eat a wide variety of foods and their diet fluctuates widely across seasons and sites (Guo *et al.* 2007; Li 2006). They prefer fruit, and there is a significant increase in fruit consumption during the fruiting season (Li and Liu 1994; Li 2006; Ma 2003).

Sichuan snub-nosed monkeys usually occupy an extensive home range (Kirkpatrick 1998). However, home range estimates vary greatly in the literature. For example, one group occupied a home range of 51 km² in the Wolong Nature Reserve, while another group in the Zhouzhi Nature Reserve only used a home range of 18.3 km² (Hu *et al.* 1980; Tan *et al.* 2007). So far, except for home range size, little is known about the ranging pattern of this species and its determinants. We studied the ranging pattern of a group of Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve, located at the most western point of the Shaanxi Province, in relation to their seasonal diet shift, focusing on whether this species changed its ranging pattern in response to seasonal changes in their degree of frugivory.

When food resources occur in small quantities and are widely dispersed within the habitat, primates living in large groups are expected to travel extensively (Chapman 1990; Tan *et al.* 2007). We therefore predicted that 1) the monkeys would exhibit an increase in daily travel distance, daily range, and range size, as their degree of frugivory increased; 2) they would use different parts of its home range depending on their diet, to obtain food efficiently. We also examined whether the water resource distribution and topographic factors—altitude and aspect—affected ranging patterns.

Methods

Study Site and Subjects

We studied Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve on the southern slope of the western part of the Qinling Mountains in Shaanxi Province, China (105°28′–105°40′E, 32°50′–32°56′N, Fig. 1). The Qingmichuan Nature Reserve was established in 2001 to protect the habitat of giant pandas and broadleaf forest ecosystem and was approved by the State Nature Reserve Commission as a national nature reserve in 2008. The altitude of the study area ranges 800–2054 m above sea level. The site has a humid temperate climate with a distinct seasonal shift. In areas above 1200 m, spring lasts from mid-March to May, summer from June to August, autumn from September to October, and winter from November to mid-March. Monthly variation in temperature and precipitation is high (Fig. 2). The vegetation is classified into 3 types: mixed evergreen and deciduous broadleaf forest between 720 m and 1600 m, deciduous broadleaf forest between 1300 m and 1,900 m, and mixed deciduous and conifer forest between 1800 m and 2054 m (Jiang 2005; Liu *et al.* 2006).

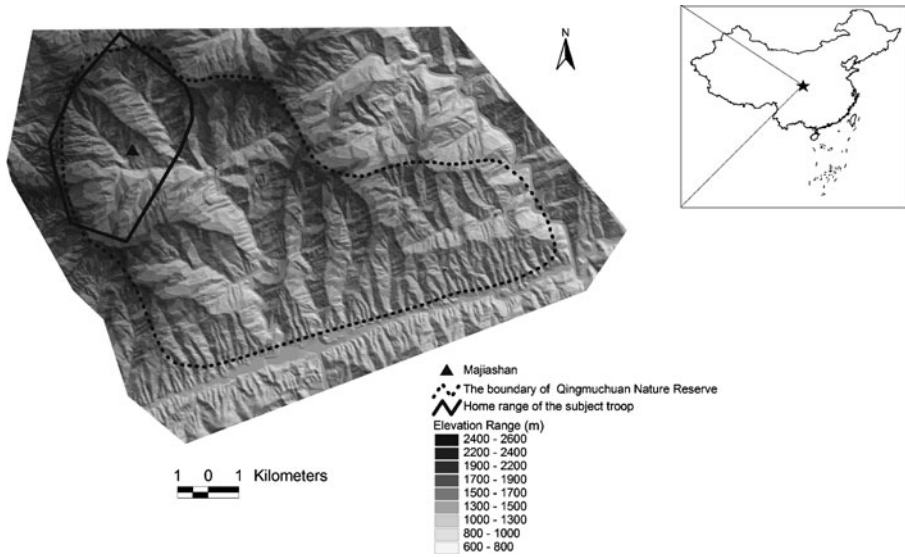


Fig. 1 Map of the study site: Majiashan area, Qingmichuan Nature Reserve, Shaanxi Province, China. The polygon represents the total home range of the focal Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group estimated via the 100% minimum convex polygon method.

We followed 1 group of Sichuan snub-nosed monkeys in the Majiashan area in the Core Protected Zone of the Qingmichuan Nature Reserve. The largest number of individuals we observed when the group traveled through an open habitat was 92, and we estimated that there were *ca.* 100–120 individuals in the group.

Data Collection and Analysis

We determined the general location of the focal group and conducted initial habituation in November and December 2005 and April to June 2006. Once we

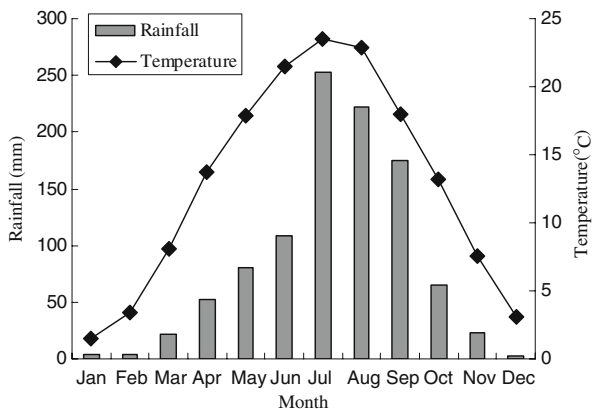


Fig. 2 Monthly changes in average rainfall and temperature recorded by the nearest meteorological station in Guangping, which is located 10 km away from Qingmichuan Nature Reserve.

followed the monkey group, apart from days of heavy fog and rain in winter, we were able to observe them every day throughout the area and we collected data on the animals' ranging and diet systematically in winter (14 d in November 2006, 17 d in December 2006, 11 d in March 2008) and summer (12 d in June 2007, 19 d in July 2007). We conducted full-day observations on the troop and used instantaneous scan sampling to record their behavior from 0830 to 1800 h in winter and from 0830 to 1900 h in summer. We scanned all visible members of the group every 10 min with a pair of 8×30 binoculars and recorded the number of individuals that were feeding and the food types consumed, such as fruits, flowers, leaves, bark, buds, or other.

We paralleled our movement to the movement of the monkeys, chose optimal location to observe them, and recorded the grid coordinates of locations where we observed the monkey group. We used a compass and a telemeter (Yardage pro 400, Bushnell Performance Optics, Richmond Hill, Ontario) to measure the distance and bearing from our observation location to the center of the monkey group, which we called the activity center of the monkeys. When we changed observation location or the activity center of the monkeys moved >100 m, we recorded the new observation location, distance, and bearing. We also recorded the times the group entered and left each activity center and then calculated the time it spent in this specific area.

We entered the GPS coordinates of each observation location and the relative bearing and distance to the monkey group into ArcView3.2 (ESRI Inc.) to calculate the corresponding location of the focal group for each activity center at a specific time. Choice of analytical method significantly affects primate home range estimates (Grueter *et al.* 2009), particularly in studies where few data are available (Glessner and Britt 2005; Singleton and van Schaik 2001; Sterling *et al.* 2000), so we calculated the home range size and overlap between summer and winter with both the 100% minimum convex polygon (MCP) method and the 95% kernel method in Biotas 1.03a (Ecological Software Solutions). We calculated daily path lengths as the distance between all the activity centres from morning to the dusk in time sequence.

To analyze home range use patterns, we superimposed a grid of 250 × 250 m quadrats over the daily ranging maps of the group, and expressed the intensity of quadrat use as the total number of minutes of all occupancy records per quadrat. We calculated daily range by multiplying the number of quadrats used by the group each day by the size of the quadrat (6.25 hm²). We defined core areas by selecting quadrats that contained the highest use intensity until 80% of the total use intensity was included (Basabose 2005; Harris and Chapman 2007).

To quantify the use intensity at different elevation ranges by the monkeys, we grouped elevation into 100-m intervals, and calculated the time the monkey group spent at a given 100-m interval by summing the stay times of the monkeys in those activity centres located in the given elevation interval.

To calculate the correlation between ranging patterns and food distribution, we mapped the vegetation distribution on a 1:50,000 topographic map based on a vegetation survey along 20 transects, and digitized the distribution and size of mixed ever-green and deciduous broadleaf forests, deciduous broadleaf forests, mixed deciduous, and conifer forests via ArcView 3.2. To quantify the abundance of fruits, we established 10 1200–2000 m×50 m transects perpendicular to elevation contour lines in the summer range, with no 2 transects lying within 500 m of each other.

Along each transect, we recorded the number of trees with fruit consumed by the monkeys in summer. We extracted a digital elevation model from a vector contours in a 1:50,000 topographic map acquired from the Qingmichuan Nature Reserve Administration. Using ArcView3.2, we extracted the corresponding forest type, aspect, elevation, and distance to water sources of each quadrat, and used Spearman correlations to determine the correlation between quadrat use intensity and fruit abundance, aspect, elevation, and distance to water source. Most ecological data exhibited some degree of spatial autocorrelation, which may inflate the degrees of freedom in significance tests (Diniz-Filho *et al.* 2003). To correct for spatial autocorrelation, we used Dutilleul's method (1993) to calculate the p -value of correlation coefficients using the program Mod- t -test (Legendre 2000). We refer to corrected p -values for Spearman correlation analysis as P_{adj} .

We then compared the difference in ranging parameters between winter and summer using independent samples t -tests. When the data did not meet the assumptions of parametric statistical tests (even after transformation), we used nonparametric Mann-Whitney U -tests. We also used a Mann-Whitney U -test to test for a difference in elevation between winter and summer. We performed all statistical analyses in SPSS 11. All tests are 2-tailed with a significance level of $p < 0.05$.

Results

Diet Shift

The monkeys consumed totally 40 plant species: 24 in winter and 20 in summer (Table I). They consumed only 4 plant species in both winter and summer. Limited visibility in summer due to dense leaves prevented us from observing a large number of individuals in any scan. Even when we stayed in the center of the focal group, we could observe only 1–10 individuals feeding (mean 3 individuals per scan). Nevertheless, we documented a diet shift from highly folivorous in winter to highly frugivorous in summer. Fruit consumption increased from 5.6% in winter (24 of 426 records) to 72.2% in summer (135 of 187 records). In summer, giant dogwood (*Cornus controversa*) fruits were the major food resource and the monkeys were not seen to consume any other fruit. Most feeding events occurred in giant dogwood trees, and the loud sound associated with chewing fruits provides further evidence that giant dogwood is a major summer food for Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve. Leaves accounted for 25.0% of the summer diet, but were the main food of the monkeys in winter, accounting for 73.0% of the feeding records (311 of 426 records). Buds and barks together accounted for 21.3% of the winter diet, not eaten in summer.

Home Range Size and Habitat Use

We recorded a total of 160 activity centers for the focal group in winter (mean stay time: 107.8 ± 6.6 min) and 190 in summer (mean stay time: 98.6 ± 5.3 min). Estimates of home range size using MCP method, kernel method, and grid-cell analysis varied greatly (Table II), and 95% kernel analysis fitted the area actually visited by the

Table 1 Tree species consumed in winter and summer by the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qingmichuan Nature Reserve

Species	Plant type	Parts consumed	Season	
			Winter	Summer
<i>Sorbus tsinglingensis</i>	D	Leaves		√
<i>Sorbus hemsleyi</i>	D	Leaves		√
<i>Padus obtusata</i>	D	Bark	√	
<i>Cerasus</i> spp.	D	Bark	√	
<i>Rosa brunonii</i>	CS	Bark	√	
<i>Sorbus folgneri</i>	D	Leaves		√
<i>Stranvaesia davidiana</i>	D	Leaves		√
<i>Fagus hayatae</i>	D	Bark	√	
<i>Quercus lanceolata</i>	E	Bark	√	
<i>Cyclobalanopsis gracilis</i>	E	Leaves		√
<i>Qurrus aliena</i>	D	Leaves		√
<i>Castanea henryi</i>	D	Leaves		√
<i>Dendrobenthamia japonica</i>	D	Bark, flowers, buds	√	√
<i>Swida macrophylla</i>	D	Buds, barks	√	
<i>Cornus controversa</i>	D	Fruits, flowers		√
<i>Betula luminifera</i>	D	Leaves, bark	√	√
<i>Betula insignis</i>	D	Leaves, carpospores		√
<i>Betula albosinensis</i>	D	Leaves		√
<i>Zelkova serrata</i>	D	Leaves, bark	√	√
<i>Ulmus bergmanniana</i>	D	Leaves	√	
<i>Rhus punjahensis</i> var. <i>sinica</i>	D	Petiole, bark	√	
<i>Rhus chinensis</i> var. <i>chinensis</i>	D	Petiole	√	
<i>Meliosma veitchiorum</i>	D	Petiole	√	
<i>Meliosma oldhamii</i>	D	Leaves		√
<i>Lyonia ovalifolia</i>	D	Bark, leaves	√	√
<i>Litsea pungens</i>	D	Buds	√	
<i>Dalbergia mimosoides</i>	D	Bark	√	
<i>Ilex pedunculosa</i>	E	Inflorescence, leaves	√	
<i>Idesia polycarpa</i>	D	Leaves		√
<i>Acer tsinglingense</i>	D	Bark	√	
<i>Holboellia grandiflora</i>	ES	Bark	√	
<i>Berchemia sinica</i>	LS	Leaves		√
<i>Aesculus chinensis</i>	D	Leaves, fruits		√
<i>Tilia tuan</i>	D	Leaves		√
<i>Taxus wallichiana</i>	EC	Bark	√	
<i>Symplocos botryantha</i>	E	Leaves	√	
<i>Elaeagnus umbellata</i>	DS	Fruits	√	
<i>Actinidia chinensis</i>	DC	Bark	√	
<i>Aralia chinensis</i>	DS	Petiole	√	
<i>Broussonetia papyrifera</i>	D	Leaves		√

D deciduous tree; E evergreen broadleaf tree; CS climber shrub; ES evergreen shrub; DS deciduous shrub; DC deciduous climber; LS liana shrub.

Table II Home range size, core area size, and range overlap for a Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group at Qingmuchuan in winter and summer, generated via the minimum convex polygon method, kernel method, and grid-cell method

Season	Home range 100% MCP (km ²)	Home range 95% kernel (km ²)	Home range 250-m grid (km ²)	Core area (km ²)
Summer	12.71	8.09	5.56	2.94
Winter	17.21	7.43	5.13	2.44
Overlap	10.53	1.80	0.63	0.13

group best (Fig. 3). Core areas of the home ranges were 2.94 km² in summer and 2.44 km² in winter.

Although the monkey group used all vegetation types within its home range, the proportion of use differed among habitat types (Table III). A comparison between the proportion of different habitat types within the home range and their use by the group showed a clear preference for mixed evergreen and deciduous forests in both summer and winter (Table III). In winter, the focal group used deciduous broadleaf forests and mixed deciduous and conifer forests less often than expected (Table III). In summer, they also selectively used mixed deciduous and conifer forests, but avoided deciduous broadleaf forests (Table III).

Home Range Use

The focal group did not use geographically distinct summer and winter ranges. According to the 95% kernel method, overlap between winter and summer home ranges was 1.80 km², comprising 24.2% of the winter range and 22.3% of the summer range. However, there was little overlap in the actual activity centers between summer and winter home range because core area overlap was only 0.13 km², which represented 4.4% of the summer core area and 5.3% of the winter core area of the focal group.

The movement and home range use patterns of the focal group showed distinct seasonal variations. The daily travel distance in summer (mean 1020±69 m/d, $n=24$) was significantly longer than in winter (mean 676±53 m/d, $n=27$; $t=3.98$, $df=49$, $p<0.001$), and the daily range was significantly larger in summer (mean 0.27±0.02 km²/d; range: 0.13–0.50 km²/d) than in winter (mean 0.21±0.01 km²/d; range: 0.06–0.38 km²/day; $t=-2.76$, $df=49$, $p<0.01$). In winter, the home range of the focal group was characterized by 3 discontinuous patches; the group used each food patch successively for a mean of 8 d without movement among patches (Figs. 3a and 4a). Specifically, in winter 2006, the group first used patch A for 12 successive days, then moved to patch B and stayed there for 14 d, and finally moved to patch C and

Fig. 3 Home range of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group at Qingmuchuan, Shaanxi, China. **(a)** Winter home range of the Sichuan snub-nosed monkey group, generated with 95% kernel method and 100% minimum convex polygon (MCP) method. Coordinates represent user-defined local coordinates in the form of a user grid. **(b)** Summer home range of the Sichuan snub-nosed monkey group, generated with the 95% kernel method and 100% minimum convex polygon method.

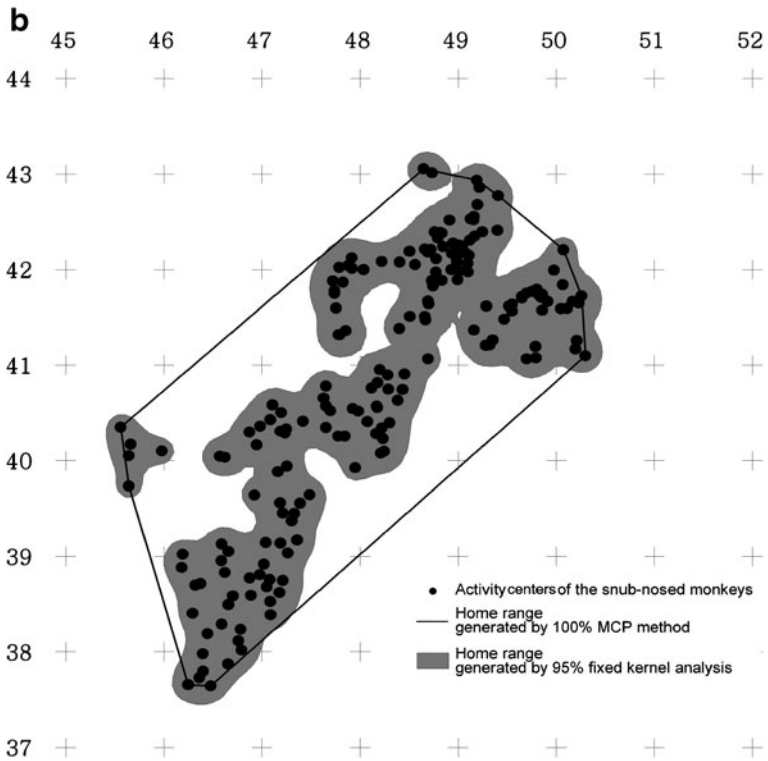
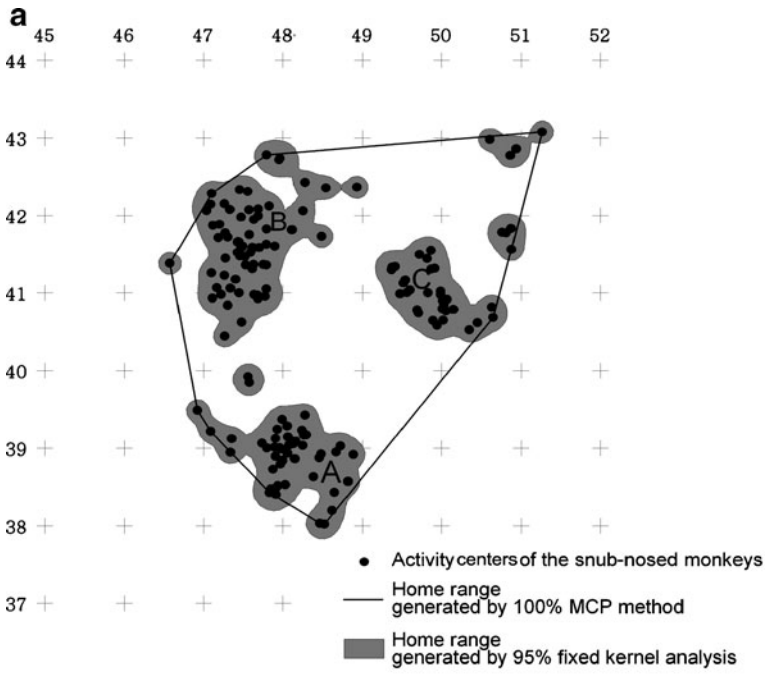


Table III Habitat type use by the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group at Qingmichuan in comparison to expected values based on the area of vegetation types within the home range in winter and summer

Habitat types	Proportion (%) of home range area		Observed use in minutes (%)		Expected use (minutes) ^a		χ^2 (df=1)		<i>p</i>	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
Deciduous / conifer forests	5.3	9.4	205 (1.2)	2134 (11.4)	914	1768	550.37	75.95	< 0.001	< 0.001
Deciduous broadleaf forests	67.8	73.7	9281 (53.8)	12,136 (64.8)	11,698	13,811	499.22	203.03	< 0.001	< 0.001
Evergreen / deciduous broadleaf forests	26.8	16.9	7767 (45.0)	4470 (23.9)	4624	3162	2136.70	541.18	< 0.001	< 0.001

^a We calculated expected use by multiplying the proportion (%) of each vegetation type within the home range area with the total observed use (minutes).

stayed for 3 d. In winter 2007, the group used patch C for 6 d and then moved to patch B. In contrast, summer ranging was characterized by repeated travel across the group's home range. In 31 successive days, the group traveled 3 circles across its summer range (Figs. 3b and 4b).

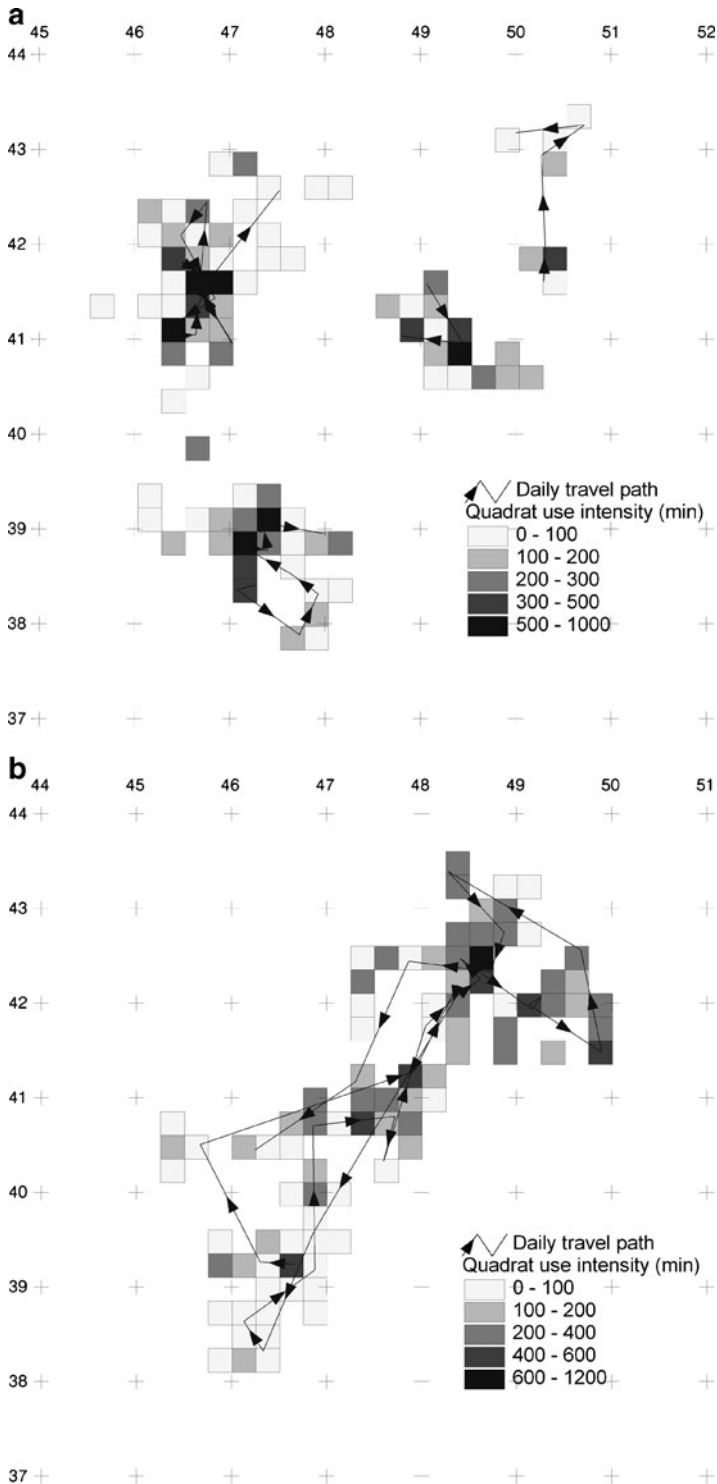
The focal group used their range unevenly and concentrated their activities in particular quadrats in both summer and winter (Fig. 4). 63.2% of the activity time in winter and 56.9% of the activity time in summer were spent in 30.0% of quadrats. There was no significant difference in the intensity of quadrat use between summer (mean 2,113±18 min; range: 30–1,211 min; *n*=89) and winter (mean 210±22 min; range: 20–1,012 min; *n*=82) (Mann-Whitney *U*-test: *U*=3409.0, *p*=0.458).

The focal group ranged between 1,000 and 2,020 m, with a mean elevation of 1,493±10 m (*n*=350 activity centers; Fig. 5). There was no significant seasonal difference in elevation (Mann-Whitney *U*-test: *U*=17.0, *p*=0.872). In winter, the monkeys ranged between 1,000 m and 1,900 m, with a mean elevation of 1,456±15 m (*n*=160), and spent 1.5% of their activity time at ≥1,800 m and 8.5% at ≤1200 m. In summer, they ranged between 1176 m and 2020 m, with a mean elevation of 1524±14 m (*n*=190), and they spent 11.7% of their activity time at ≥1800 m and 0.8% at ≤1200 m.

Determinants of Ranging Patterns

Variation in ranging pattern over winter and summer correlates significantly with the spatial distribution of food resources. The giant dogwood occurs in discrete clumps

Fig. 4 Intensity of quadrat use by the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group at Qingmichuan, Shaanxi, China, expressed as the total minutes of all occupancy records per quadrat. (a) Winter range. (b) Summer range.



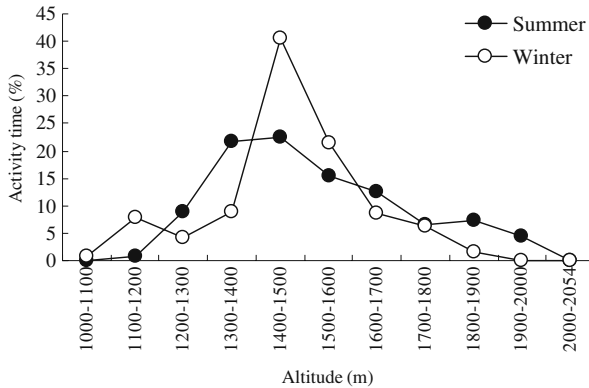


Fig. 5 Altitudinal distributions of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) group at Qingmichuan in summer and winter.

across the home range of the monkeys and the linear distance among giant dogwood clumps ranged from 117.9 m to 718.8 m, with mean 255.2 m. The spatial distribution of giant dogwood fruits correlates significantly positively with the distribution of use intensity within the summer home range of the monkeys ($r=0.524$, $n=37$, $P_{adj}=0.022$). There is also a significant positive correlation between summer quadrat use intensity and aspect ($r=0.291$, $n=89$, $P_{adj}=0.042$), but no significant correlations between the intensity of summer quadrat use and distance to the next water source ($r=-0.134$, $n=89$, $P_{adj}=0.380$), or elevation ($r=-0.221$, $n=89$, $P_{adj}=0.271$).

In winter, topographic factors and distance to water showed no significant impact on the ranging use within home range; there is no significant correlation between the intensity of quadrat use and elevation ($r=-0.095$, $n=80$, $P_{adj}=0.496$), aspect ($r=0.046$, $n=80$, $P_{adj}=0.682$), or distance to the next water source ($r=-0.172$, $n=80$, $P_{adj}=0.258$). However, forest type was an important determinant of home range use because among 3 types of forest habitat, the monkeys showed significant preference for the mixed evergreen and deciduous forests in winter ($r=0.295$, $n=80$, $P_{adj}=0.021$).

Discussion

Diet Shift

We found that the population of Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve shifted its diet from primarily frugivorous in summer to primarily folivorous in winter. This species uses a wide range of food species, and their predominant food types vary across study sites, but there is also a clear increase in the degree of frugivory during summer-autumn in other populations (Guo *et al.* 2007; Li 2006; Liu *et al.* 2004; Ma 2003). Such a seasonal variation in diet composition is a common feature in primates, both in the tropics (Dasilva 1994; Oates 1987) and in the temperate zone (Hill 1997; Maruhashi 1980), and differences in the temporal availability and spatial distribution of food resources can account for much of the dietary variation observed across populations of 1 species (Strier 2003).

Giant dogwood was a major summer food of Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve. This fruit also occurs in the diet of other *Rhinopithecus* populations (Li 2006; Yang *et al.* 2002). However, we lack an understanding of the nutritional value of this deciduous tree. The high proportion of giant dogwood fruit in the diet of our focal group may largely be due to its high abundance (737 trees/km², mean diameter at breast height [DBH] 82 cm) and the fact that our study period in summer coincided with the fruiting season of giant dogwood (June–August). By the end of August, almost no giant dogwood fruits can be found at the site, which means that our observation period was biased toward the period when giant dogwood dominates its summer diet.

Although lichen (*Usneaceae*) was present in the winter range of the monkey group in the Qingmichuan Nature Reserve, we did not observe the monkeys eating it; instead, they ate mostly leaves, buds, and bark in winter. Lichens have frequently been reported to be a major food of other Sichuan snub-nosed monkey populations in winter (Guo *et al.* 2007; Li 2006), but eating lichens is considered to be a proximate response to a habitat with fewer choices of foods (Ding and Zhao 2004). The home range of Sichuan snub-nosed monkeys in the Qingmichuan Nature Reserve lies at the lowest elevation of the *Rhinopithecus* populations studied, and the extensive evergreen vegetation in the low-lying areas of the reserve may provide substantial food resources to the monkeys and thus reduce their dependence on lichens or bark in winter.

Home Range Size and Core Area

Home range generated using the MCP method included large areas never visited by the monkey group in both winter and summer. In winter the home range was composed mainly of 3 segregated patches. The monkeys used their range erratically and moved between discontinuous range patches rather than using the entire area evenly. Grid-cell analysis performs well in measuring the use intensity of home range by individuals within a grid system, but home ranges calculated via the grid-cell analysis are heavily dependent on the grid size and commonly underestimate range size unless sampling effort is very large (Harris *et al.* 1990; Singleton and van Schaik 2001; Sterling *et al.* 2000). The grid method gave the smallest range size estimates in our study because the quadrats with no records of use were not added to the total number of used quadrats even though those quadrats were located between the used ones. In fact, the interjacent quadrats may have been visited by the monkeys occasionally.

Our focal group occupied a home range of 20.35 km². *Rhinopithecus* species in China have much larger home ranges than do other colobines. A group of Sichuan snub-nosed monkeys with >112 individuals in Zhouzhi Nature Reserve had a home range of 18.3 km² (Tan *et al.* 2007), and another group of *ca.* 90 individuals in the same reserve occupied a home range of 22.5 km² (Li *et al.* 2000). Considering the strong positive relationship between group mass and home range size across primates (Clutton-Brock and Harvey 1977; Milton and May 1976), the large body mass (*ca.* 20 kg) and large group size (usually >100 individuals) of Sichuan snub-nosed monkeys may account for their larger home range. According to the formula given by Milton and May (1976), $\log HR = 1.23 \log BW - 2.86$, where HR is home

range size in square kilometers and BW is group mass of the subject in kilograms, a group of 100–120 individuals of Sichuan snub-nosed monkeys would be expected to occupy a home range of *ca.* 16–20 km², which is approximately what we observed, suggesting that Sichuan snub-nosed monkeys fit the general primate model well.

Variation in Home Range Use

We found no positive relationship between home range size and degree of frugivory, although such a pattern has been found in some primate studies (Robbins and McNeillage 2003). Frequent reuse of a particular area may not lead to an increase in overall home range area, despite an increased daily travel distance. The relationship between a seasonal increase in frugivory and home range size in snub-nosed monkeys varies across different groups. Liu *et al.* (2004) found that the home range size of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) was larger in summer-autumn, when they are frugivorous (8.4 km²), than in winter-spring, when they are folivorous (4.9 km²). In the Zhouzhi Nature Reserve, 1 group of Sichuan snub-nosed monkeys exhibited no significant seasonal changes in home range size (9.5 km² in summer, 12.1 km² in autumn, 12.3 km² in winter, and 14.1 km² in spring; Li *et al.* 2000), but another group's home range shrank from 7.1–11.9 km² in spring-winter, when they were highly folivorous, to 2.9–5.0 km² in summer-autumn, when they were highly frugivorous (Tan *et al.* 2007). Black-and-white snub-nosed monkeys at Samage also experienced a home range reduction in autumn, when fruit abundance reached a peak (Grueter *et al.* 2008). In the Samage Forest, the key fruit species for black-and-white snub-nosed monkeys occurred at relatively high densities within clumps and showed overall synchrony in their fruiting patterns, making it possible for black-and-white snub-nosed monkeys to feed largely on fruit within relatively small areas (Grueter *et al.* 2008). Fruit species and its spatial distribution may account for the variation in home range size of snub-nosed monkey groups.

There was no significant spatial separation between the home range of Sichuan snub-nosed monkeys in summer and winter in the Qingmuchuan Nature Reserve. Similar findings have been obtained for a group of the same species in the Zhouzhi Nature Reserve, where the degree of overlap between home range in different seasons ranged 57.7–92.4% (Li *et al.* 2000). However, in our study, the frequently used area and core area have a small degree of overlap, indicating that the major activity area in summer and winter was not consistent. Thus it appears that although there was no significant spatial separation in the summer and winter ranges of the focal monkey group at large spatial scale, the spatial separation did exist at small scale within the home ranges of the focal group.

We found significant increases in daily travel distance and daily range size with the summer increase in frugivory. This is in agreement with cross-site studies of *Rhinopithecus*, which have revealed that the mean daily travel distance increases significantly in summer and autumn when richness and availability of food resources are greatest (Li 2002; Tan *et al.* 2007). It also follows the general rule for primates that both travel requirement for finding fruits and the time and energy available for travelling increase as the proportion of fruits in the diet increases (Strier 2003).

Although there was no significant difference in the altitudinal range use between winter and summer, our focal group used the elevation interval from 1,400 to 1,600 m

more frequently (62.0%) in winter, while in summer the group used each elevation interval relatively evenly. Evidence for seasonal variation in altitudinal distribution of *Rhinopithecus* is varied. Sichuan snub-nosed monkeys at Wolong range low in winter and high in summer (Hu *et al.* 1980), but this is not the case for populations at Shennongjia (Ren *et al.* 2000) and Zhouzhi (Tan *et al.* 2007). Black-and-white snub-nosed monkeys in the Samage Forest use different elevation zones in different seasons (Li *et al.* 2008), but descend in spring, not winter. Differences between populations in the influence of season on altitude may be influenced by the availability of food resources at a particular elevation (Kirkpatrick and Long 1994; Tan *et al.* 2007), but also by security considerations or interruption by human activities, which may determine the lower limit of the altitudinal range (Kirkpatrick 1998): Monkeys at our study site may be unable to descend lower due to the presence of villages.

Determinants of Ranging Pattern

The distribution of giant dogwood appeared to determine the pattern of travel across the monkeys' home range in summer. The giant dogwood occurs in discrete clumps in our study area and was sparsely distributed within the summer range of the subject. A longer daily travel distance and nonrandom movements along a relatively fixed route in summer can be seen as an efficient foraging adaptation allowing the individuals to collect and update quickly information on the location and phenology of feeding sites (*cf.* Oates 1987). Good evidence for the importance of food resources in determining primate home range use comes from a Japanese macaque (*Macaca fuscata*) troop encountering artificial feeding in tourism areas: As a result of provisioning, the home range size of the troop shrank considerably and its ranging patterns altered (Koganezawa and Imaki 1999).

The home range use pattern of the focal group was also influenced by the distribution and availability of food resources in winter. In winter, leaves and fruits existed only in patches of mixed evergreen and deciduous forests in valleys at low altitudes. The group foraged in patches of mixed evergreen and deciduous forest for several successive days without moving long distances, and preferred this forest type in winter. Deciduous broadleaf forests and mixed deciduous and conifer forests make up of the majority of the forest at Qingmichuan, but the subjects used them less than expected; when they did use them, bark was their major food resource. Food shortage is the most frequent cause of bark stripping (Ueda *et al.* 2002), which may explain why subjects used deciduous broadleaf forests and mixed deciduous and conifer forests less than expected in winter.

Li *et al.* (2006) suggested that sunbathing may help snub-nosed monkeys to maintain their temperature in cold winter, resulting in a preference for sunny aspect. However, aspect was not a determinant of winter range use by the monkeys in Qingmichuan. It may be that the monkeys' preference for the valley bottom allowed them to avoid winds in winter, with the same effect as sunbathing. In contrast, aspect was a significant determinant for range use in summer, when the monkeys spent most time (61.3%) in eastern and western aspects. This may match the distribution of the giant dogwood that grows in part shade sun, in addition to temperature considerations.

Winter and spring are the dry season in the Qingmichuan Nature Reserve, but we found no significant correlation between quadrat use intensity and the distance to

water sources. However, the distribution of water sources may have an impact on the range use of Sichuan snub-nosed monkeys at a larger scale, i.e., by determining the location of the home range or core range. The 3 patches of the winter range all have water sources in valley bottoms. In summer, rainfall supplies abundant water to the monkeys in our study area. In addition, the high water content in fruits may reduce water requirement of the snub-nosed monkeys in summer.

Summary and Conservation Implications

We found that Sichuan snub-nosed monkeys traveled quickly and repeatedly across their whole range in summer, without staying in a single food patch for a long time. However, in winter, the monkeys stayed in a single food patch for several days without long travel among food patches. The majority of their summer diet consisted of the giant dogwood fruit, and the spatial distribution of this species significantly affected the monkeys' range use pattern in summer, at least during our study months. This important food resource is also a valuable timber for architecture and sculpture. Due to its importance for Sichuan snub-nosed monkeys, we suggest that illegal logging of this tree species in the Core Protected Zone of the Qingmichuan Nature Reserve should be stopped immediately.

Acknowledgments We thank Dr. Joanna M. Setchell and an anonymous reviewer for suggestions that improved the article. We thank Chenghui Shen, Yihong Zhang, Tao Miao, and Youkui Xu for their help and support during field work. We thank Dengqing Mo, Shuqiang Wei, Xingrong Ma, Kaichun Tu, Shihua Pang for their help in monitoring the monkey group in the mountains and providing logistic support to the field camp. We acknowledge the Knowledge Innovation Project of the Chinese Academy of Sciences (No. CXTDS2005-4) and the Columbus Zoo and Aquarium, USA for financial support. We thank the Shaanxi Provincial Forestry Bureau and Qingmichuan Nature Reserve Administration for permission to conduct this study.

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