

Fallback Foods of Temperate-Living Primates: A Case Study on Snub-Nosed Monkeys

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ABSTRACT Only a few primate species thrive in temperate regions characterized by relatively low temperature, low rainfall, low species diversity, high elevation, and especially an extended season of food scarcity during which they suffer from dietary stress. We present data of a case study of dietary strategies and fallback foods in snub-nosed monkeys (*Rhinopithecus bieti*) in the Samage Forest, Northwest Yunnan, PRC. The snub-nosed monkeys adjusted intake of plant food items corresponding with changes in the phenology of deciduous trees in the forest and specifically showed a strong preference for young leaves in spring. A non-plant food, lichens (Parmeliaceae), featured prominently in the diet throughout the year (annual representation in the diet was about 67%) and became the dominant food item in winter when palatable plant resources were scarce. Additional highly sought winter foods were frost-resistant fruits and winter buds of deciduous hardwoods. The snub-nosed monkeys' choice of lichens as a staple fallback food is likely because of their spatiotemporal consistency in occurrence, nutritional and energetic properties, and the ease with which they can be harvested. Using lichens is a way to mediate

effects of seasonal dearth in palatable plant foods and ultimately a key survival strategy. The snub-nosed monkeys' fallback strategy affects various aspects of their biology, e.g., two- and three-dimensional range use and social organization. The higher abundance of lichens at higher altitudes explains the monkeys' tendency to occupy relatively high altitudes in winter despite the prevailing cold. As to social organization, the wide temporal and spatial availability of lichens strongly reduces the ecological costs of grouping, thus allowing for the formation of "super-groups." *Usnea* lichens, the snub-nosed monkeys' primary dietary component, are known to be highly susceptible to human-induced environmental changes such as air pollution, and a decline of this critical resource base could have devastating effects on the last remaining populations. Within the order Primates, lichenivory is a rare strategy and only found in a few species or populations inhabiting montane areas, i.e., *Macaca sylvanus*, *Colobus angolensis*, and *Rhinopithecus roxellana*. Other temperate-dwelling primates rely mainly on buds and bark as winter fallback foods. *Am J Phys Anthropol* 140:700–715, 2009. © 2009 Wiley-Liss, Inc.

Various strategies exist in primates to deal with times of resource scarcity. Among the adaptations are: seasonal movements, seasonal breeding, altitudinal migration, nomadism, hibernation and dietary switching (reviewed in van Schaik et al., 1993; see also Brockman and van Schaik 2005). The phenomenon of fallback foods (foods that are relied upon when preferred items are unavailable (e.g., Altmann 1974; Marshall and Wrangham, 2007) has been particularly well studied in the tropical great apes whose fallback foods include leaves, pith, THV (terrestrial herbaceous vegetation), bark, insects and figs (Knott, 2005). Other tropical primate taxa resort to palm nuts (*Cebus apella*: Struhsaker and Leland, 1977 or nectar *Saguinus fuscicollis*: Terborgh and Goldizen, 1985).

Seasonal resource shortage characterizes primate populations in both the tropics and in the temperate zone, but the duration and harshness of the period during which fallback foods are essential may differ between them. Temperate habitats are characterized by relatively lower productivity and diversity (Latham and Ricklefs, 1993; Cramer et al., 1999). Temperate biomes thus

impose different challenges on the primate consumer and entail specialized dietary adaptations.

The term "temperate primates" refers to species that share the zoogeographic peculiarity of living mainly or

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exclusively within the temperate zone. The northern-hemisphere temperate zone extends from the Tropic of Cancer (at 23.5° north geographical latitude) to the Arctic Circle (at 66.5° north latitude.) The southern-hemisphere temperate zone extends from the Tropic of Capricorn (at 23.5° south latitude) to the Antarctic Circle (at 66.5° south latitude). The main difficulties associated with inhabiting the northern temperate zone include "... the lower biological productivity of the land, the greater seasonality and reduced vegetation season, the great extremes in temperature, and the greater expenditures of energy required to maintain homeostasis and reproduce" (Geist, 1978, p 271). Only a small number of extant primate species are temperate-dwelling; e.g., the Chinese snub-nosed monkeys (*Rhinopithecus* spp.) and Japanese macaques (*Macaca fuscata*) are typical representatives of the North temperate zone and chacma baboons (*Papio hamadryas ursinus*) are inhabitants of the South temperate zone. Some local environments inhabited by North-temperate species are extreme by primate standards, with lowest recorded temperatures of -30°C *Rhinopithecus roxellana* (Su et al., 1998), -25°C *R. bieti* (Li et al., 1982), -20°C *Macaca mulatta* (Qu et al., 1993), and -19.5°C *M. fuscata* (Suzuki, 1965). However, even within the temperate zone, there are habitats that are warmer and more subtropical in nature; this applies especially to lower lying habitats in areas with strong vertical vegetative zonation, e.g., Samage in China (Li et al., 2008) and Yakushima in Japan (Hanya et al., 2003).

Black-and-white snub-nosed monkeys (*Rhinopithecus bieti*), alternatively referred to as Yunnan snub-nosed monkeys, are among the few non-human primates able to cope with hostile environmental conditions associated with living in cold temperate montane forests. These heavy, stocky primates of the subfamily Colobinae are highly endangered (total population size about 2,000) and have an extremely restricted geographic distribution in the Hengduan Mountains which border the Himalaya Range (Long et al., 1994). They primarily inhabit temperate alpine forest ecosystems and occasionally venture into very high elevations, reaching 4,700 m (Long et al., 1996). Yunnan snub-nosed monkeys live in very large super-groups or bands which are composed of single-male core families or harems (Kirkpatrick et al., 1998; Grueter et al., 2008a). They move as cohesive groups inside vast nondefended home ranges (Kirkpatrick et al., 1998; Grueter et al., 2008b).

Pronounced seasonality in their climatologically extreme natural habitat produces temporal fluctuations in plant food availability and a prolonged winter season characterized by scarcity of edible plant resources. Unlike many tropical-living primates which have the option of turning to young leaves in times of fruit shortage (van Schaik and Brockman, 2005), the temperate-living snub-nosed monkeys face a lean season for both fruit and flush at the same time and experience seasonally pronounced dietary stress. The vegetation at the study site (Samage) is dominated by evergreen trees such as conifers, oaks and azaleas (Grueter et al., in prep.) whose foliage is known for low palatability (Kirkpatrick, 1996). All deciduous trees are bare by early winter, and this natural abscission further enhances the severity of the "dietary dilemma" confronting the monkeys. In this article, we elucidate how this cumulative absence of palatable plant parts in winter is dealt with by the snub-nosed monkeys and how they allocate their feeding time

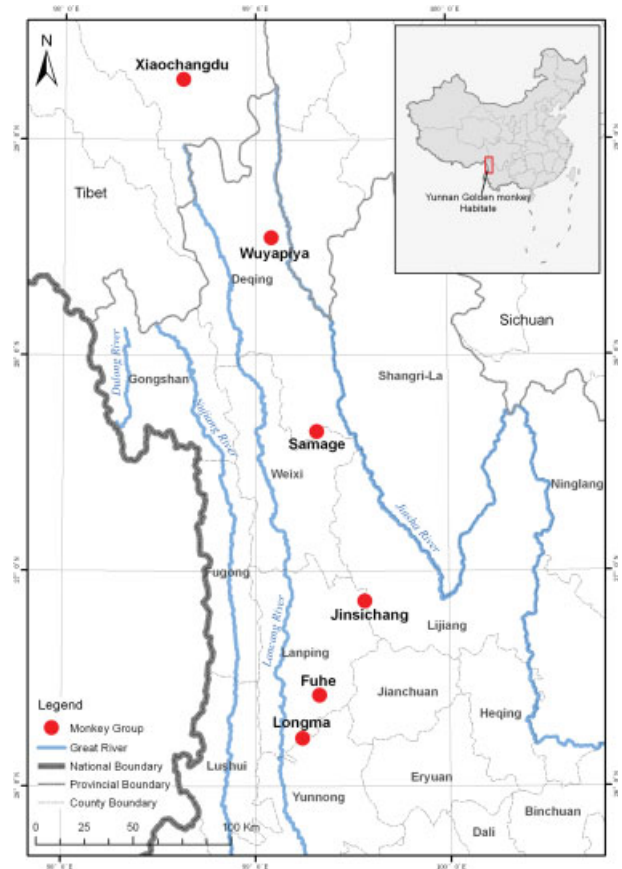


Fig. 1. Map of Northwest Yunnan indicating the locations of all investigated groups of *Rhinopithecus bieti* including the one at the Samage Forest that is the focus of this study. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

to various food items throughout the annual cycle in relation to plant phenology. We compare the results obtained at two different sites showing different levels of productivity. We discuss possible implications of their fallback strategy on various aspects of their biology, including range use, sociality, masticatory morphology, and conservation. We also put our findings within a comparative context by offering a preliminary review of fallback strategies in other temperate primates.

METHODS

Study location

We conducted the present study in the predominantly temperate Samage Forest (27°34'N, 99°17'E) in Yunnan's Baimaxueshan National Nature Reserve (see Fig. 1). Narrow valleys and steep hillsides characterize the topography at Samage. Land cover at the research area is a mosaic of various vegetation types. Along an ascending altitudinal gradient, the forest grades from evergreen broadleaf forest at 2,500–3,000 m (mostly subtropical oaks of the genus *Cyclobalanopsis*) and *Pinus yunnanensis* forest at 2,500–3,100 m forest to predominantly mixed coniferous and deciduous-broadleaf forest at 2,900–3,600 m to mostly *Abies georgei* forest at 3,500–4,000 m. Parts of the Samage Forest have been selectively logged, and herdsmen let cattle graze on spacious

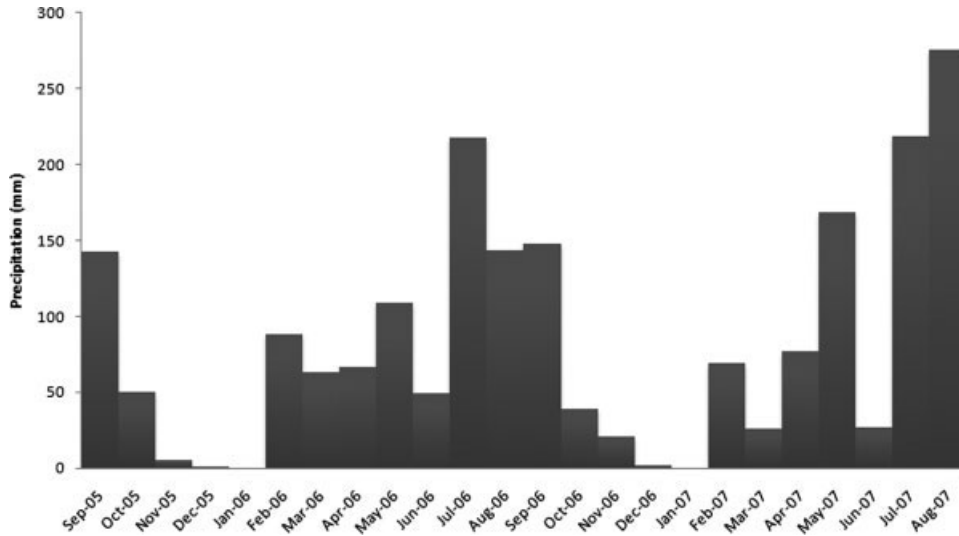


Fig. 2. Monthly precipitation [mm] in the Samage Forest from September 2005 to August 2007. Precipitation in February was mainly in the form of snow.

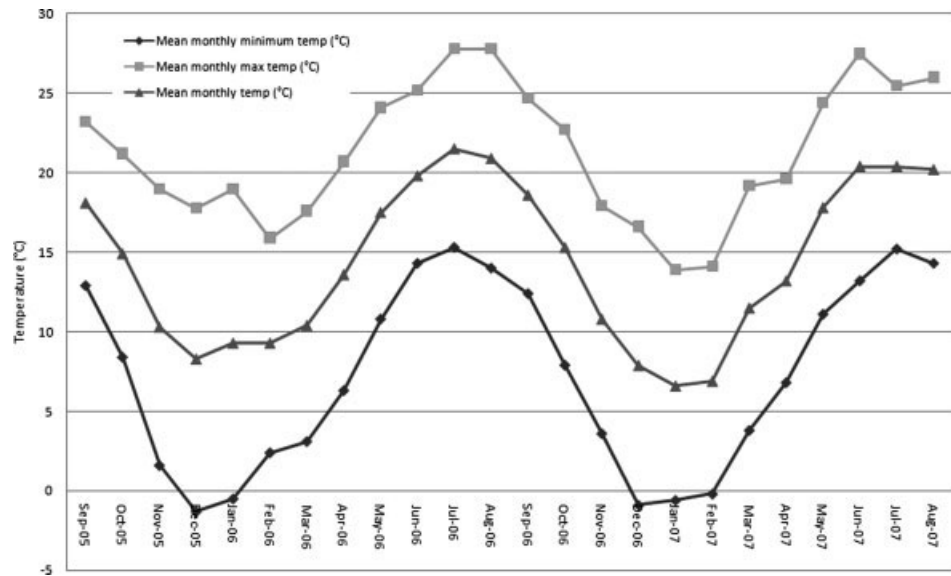


Fig. 3. Mean monthly temperature and mean monthly minimum and maximum temperatures in the Samage Forest from September 2005 to August 2007.

alpine meadows in the summer. Collection of mushrooms and herbal plants by villagers is widespread.

The snub-nosed monkeys' habitat at this locality ranges from 2,500 m to 4,000 m and includes all major vegetation types, of which the monkeys clearly prefer mixed forest (Li et al., 2008). The focal group is composed of at least 410 members. For more details on the study site and study group, see (Grueter et al., 2008b).

The climate data presented here are based on 2 years whereas the data in Li et al., (2008) are based on 1 year. Climate data were gathered at the research station at an altitude of 2,448 m (800 m below the most frequently used altitude of the study group). Mean annual rainfall was 1,004 mm (mean of two measurements with two different rain gauges). Distribution of precipitation was highly irregular. The highest monthly rainfall was 275 mm in August 2007, the lowest 0 mm in January 2006 and January 2007 (see Fig. 2). There was a steep increase in rainfall from spring onwards and a prolonged dry season with minimal precipitation from November to

February (in both years) and high irradiance during which the vegetation became desiccated. Most snowfall occurred in February (in both years) during which snow accumulated up to 80 cm in depth at an elevation of 3,100 m. Higher areas were temporarily off limits due to even greater snow depth.

Mean annual temperature was 14.3°C. Temperature varied strikingly with seasons: Temperatures fell between two extremes of -3.8°C in January 2007 and 35.4°C in July 2006. The two winters covered during this study were relatively mild compared with previous winters and the subsequent one, e.g., the lowest recorded temperature in winter 2007/2008 was -7.9°C. The month with the highest average temperature was July 2006 (21.5°C), the month with the lowest average temperature was January 2007 (6.6°C) (see Fig. 3). There were considerable day-night fluctuations in temperature, especially in winter. Greatest daily temperature range was 26.4°C. For more details on the area's climate, see (Li et al., 2008).

Data collection

Feeding observations. We established contact with the focal group on an average of 12 days per month throughout the 20-month study period (Sep. 2005–May 2006; Aug. 2006–Nov. 2006; Jan. 2007–Jul. 2007). We usually located the group based upon its position during previous observation days and information about the animals' whereabouts gained from local rangers. Using a high-performance spotting scope (Kowa[®] TSN 820, 20–60x Zoom), behavioral observations were usually conducted from rocky outcrops, ridges or hillsides at a distance of 50–1,200 m to the location of the monkey group. These distance observations (>100 m) ensured that the group was not perturbed and allowed us to obtain a better overview of the spatial configuration of the group members and see into forest patches that were difficult to reach on foot. However, group members now and then accepted the main researcher (CCG) to stay within 10–30 m (flight distance) to them (close observations, <100 m).

Systematic data on diet were collected via scan sampling (Altmann 1974; Morrison et al., 1998) of the focal group. Scans of all visible animals were taken at 15 or 30 min intervals ($n_{15\text{-min scans}} = 1,372$, $n_{30\text{-min scans}} = 225$). The decision of choosing 15 vs. 30 min intervals depended on the number of animals in view. If a large number of monkeys (usually >25) was in view, 30-min scans were made; if only a small fraction (usually <20) was visible, 15-min scans. As a rule of thumb, intervals were usually 15 min during close observations and 30 min during distance observations, but not exclusively. The main criterion for choosing a scan interval was that a scan had to be completed at least 5 min before the beginning of the next scan. Every scan included information on date and time and weather conditions. For every subject being scanned, we recorded age, sex, activity, and distance to nearest neighbor. The individual was recorded as 'unknown' if age/sex class could not be recognized because of low visibility or only some fur or tail parts being visible.

Group members were often spread out over large distances (>100 m) in the forest and across forest strata, precluding data collection on all members of the group during a single scan. Because animals on the ground were frequently overlooked during scans due to poor visibility, there is some bias towards feeding on arboreal food items. We occasionally changed our location between scans to sample different portions of the group. Sampling was discontinued during periods of heavy rain/snow and dense fog. We strove to get scan data from mornings, evenings, and afternoons.

Activities were grouped into mutually exclusive categories, following the definitions of Grueter (in prep.). Feeding is the only activity considered here and is defined as inspecting and picking food with hand or mouth, manipulating food, putting food into the mouth, and chewing. Although feeding does not include inactivity during feeding sessions, it includes obvious search for food.

Observation conditions permitting, scan records of feeding behavior also included the food item, plant part and its age as well as plant species. The following foods were distinguished: lichens (fruticose vs. foliose), young leaves (including spring buds/shoots), mature leaves, buds (dormant leaf and flower buds), flowers, bark, pith, herbs, fruit (both ripe and unripe), invertebrates, snow,

fungi, water, bamboo shoots, and tuber. Flower buds were often hard to distinguish from leaf buds when observing via telescope, so we included them in 'buds'. It was difficult to see whether the small fruits were eaten wholly or whether the flesh was discarded, so we did not distinguish between seeds and pulp/rind. Moreover, both leaf blades and petioles were treated as 'leaves'. Limited visibility made it difficult to consistently recognize the item ingested, and for the following analyses feeding records lacking information on the nature of the food item were omitted. For analyses, the following categories were lumped into 'other': bark, snow, tuber, water, fungi, and invertebrates. We also recorded whether the animals fed in a broadleaf, conifer or dead tree and noted the tree species and genus whenever possible.

During forest walks outside the scan sessions, we recorded all partially consumed and discarded foods on the forest floor with tooth marks or other signs of having been handled. We used evidence from such feeding sign as a complementary measure to estimate seasonal variance in diet composition, and used their diameter to roughly divide them into large, small and medium sized ones to allow for quantification.

Tree and lichen survey. Using a stratified random sampling design (Mueller-Dombois and Ellenberg, 1974) and taking into account the proportional availability of distinct habitat types and altitudinal stratification, we established a total of 67 20 m × 20 m plots. For details on plot design, see (Li et al., 2008). We recorded various physical dimensions for all trees (girth >40 cm) in the plots (Li et al., 2008) and identified individual trees ($n = 1,851$) to species or genus level using reference books (Raven and Wu, 1994–2005; Unknown, 1972) and via collection of vouchers.

Each of the marked trees was given a lichen-load category, ranging from 0 for 'None' to 4 for 'Heavy', following (Kirkpatrick, 1996) and (MacLennan, 1999 (Snub-nosed monkey research and conservation project: preliminary report. Unpublished report)) and representing a simple and effective method of evaluating the biomass of arboreal lichens available to snub-nosed monkeys as potential forage.

To estimate the regeneration time of lichen, a one-year growth experiment was conducted. Fifteen trees (oaks and conifers) within the core zone of the group's home range were selected. In each tree, one live branch over 10 cm in circumference was designated, and circumference was recorded. All fruticose lichens were then stripped from these branches. After 1 year, we stripped all lichens from the same branches and dried them to constant weight. Lichen growth, i.e., replacement rate (percent per year) was calculated by dividing the weight of lichen collected from the "stripped" stem at year's end by the weight collected at the year's beginning (Kirkpatrick, 1996).

Of the 1,851 enumerated trees, 307 trees were selected for monthly phenological monitoring, and another subset of 157 deciduous monoecious trees from 21 genera known to contribute significantly to the diet (Grueter et al., in prep.) was then selected for the analyses presented in this article. These latter phenological records were intended to characterize seasonal changes in the availability of *Rhinopithecus bieti* food resources. Trees chosen for phenological monitoring were mature individuals with girth over 40 cm that offered a good view of their crowns. We conducted phenological sampling at

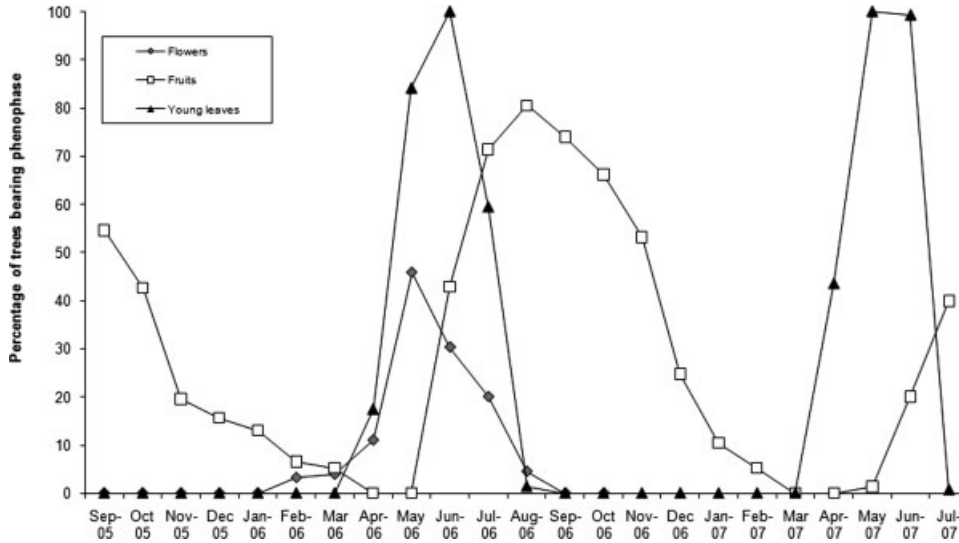


Fig. 4. Availability of fruits, young leaves, and flowers of *Rhinopithecus bieti* food trees at the Samage Forest, in 2005/2006/2007. Data obtained from 157 sampled tree specimens.

monthly intervals between the sixth and thirteenth of each month, when we visually inspected each marked tree, and recorded the presence of fruits and open flowers (reproductive parts) as well as young leaves and senescent leaves (vegetative parts). Mature and immature fruits were noted simply as fruits because of difficulties in determining the maturity of many fruits based on a visual assessment through binoculars.

Temporal availability of bamboo shoots (*Fargesia cf. melanostachys*) was investigated in five specifically designed bamboo plots (two at 3,650 m and three at 3,400 m) by recording the density of bamboo culms vs. shoots at monthly intervals in spring and summer (April to July 2007). Young shoots were easily identifiable from older stems/culms based on softness, color, and height.

Data analysis

The behavior of every animal scanned was intended to be an instantaneous sample. The practice of alternating between 15- and 30-min scan intervals yielded two data sets (DS15 and DS30). We compared the two data sets and found significant differences in proportional representation of both major age/sex classes ($\chi^2 = 9.78$, $df = 3$, $P = 0.021$) and specific food items ($\chi^2 = 59.4$, $df = 4$, $P < 0.001$). We therefore analyzed the two data sets separately. Proportions of the different food items in the diet were calculated for each month and each season.

For the main phenological analyses, we calculated the proportion of monitored trees bearing each of the phenophases every month (presence vs. absence). For the analysis of leaf senescence (as evidenced by obvious changes in color), deciduous angiosperm trees were ranked on a scale reflecting percent of senescent leaves of all present leaves (0 = 0%, 2.5 = <5%, 15 = <25%, 37.5 = <50%, 87.5 = <75%, 100 = 100%). The period of leaf fall was monitored by noting whether a tree was bare, had full foliage or was partly defoliated. For the analysis of bamboo shoot availability, the number of shoots/the number of culms $\times 100$ (% of ground shoots) was used to estimate monthly availability of shoots relative to the availability of culms in the forest (Tan, 2000).

Statistical analyses (Spearman rank correlations, chi square tests and one-way analysis of variance) were performed in SPSS 16 for Windows.

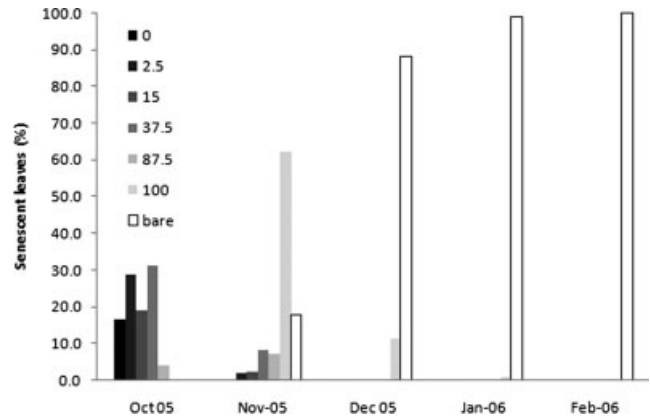


Fig. 5. Temporal patterns of leaf shedding of deciduous angiosperms at Samage. The numbers denote the percentage of senescent leaves. For details, see text.

RESULTS

Phenological patterns

Fruit production peaked in August, and the majority of species fruited at some stage during the rainy season or during the transition between the rainy and dry season (see Fig. 4). Deciduous trees produced new leaves in big bursts, and this leaf flush coincided with the onset of the monsoon season, as evidenced by a positive correlation between rainfall and young leaf availability ($r_s = 0.462$, $P = 0.026$, $n = 23$). Deciduous leaves started becoming senescent in October and were mainly shed in November and December (see Fig. 5). All deciduous trees were bare by January as a result of this natural abscission. None of the phenophases showed a peak in availability in winter.

Seasonality in food use

The results are founded on a total of 2,674 feeding records (1,784 in DS15, 890 in DS30) that included information on the identity of the ingested food item. By averaging monthly proportional representations of particular food items, we obtained an annual percentage for each food type (the first number refers to DS1, the sec-

TABLE 1. Monthly variation in the percent of feeding records as a function of food type

	<i>n</i>	Lichens	Buds	Fruits	Mature leaves	Young leaves	Flowers	Herbs	Other
(a) DS15									
Sep 05	32	62.5	3.13	34.38	0	0	0	0	0
Oct 05	151	80.79	0	3.31	14.57	0	0	0	1.32
Nov 05	99	98.99	1.01	0	0	0	0	0	0
Dec 05	93	96.77	3.23	0	0	0	0	0	0
Jan 06	38	100	0	0	0	0	0	0	0
Feb 06	16	93.75	0	0	0	0	0	0	6.25
Mar 06	137	89.78	8.03	0	2.19	0	0	0	0
Apr 06	203	36.45	0	0	2.46	60.1	0.49	0.49	0
May 06	157	20.38	0.64	0	0	71.34	7.64	0	0
Aug 06	134	27.61	0	66.42	5.22	0	0	0.75	0
Sep 06	159	60.38	0	32.7	6.92	0	0	0	0
Oct 06	98	51.02	0	25.51	19.39	0	0	0	4.08
Nov 06	165	62.42	0	26.06	11.52	0	0	0	0
Jan 07	145	80.69	8.28	10.34	0.69	0	0	0	0
Feb 07	122	86.89	10.66	0.82	0.82	0	0	0.82	0
Mar 07	102	90.2	4.9	4.9	0	0	0	0	0
Apr 07	276	40.94	0	0	0.72	53.98	2.54	1.45	0.36
May 07	149	44.97	0	0	0	55.04	0	0	0
Jun 07	181	54.7	0	0	0	45.3	0	0	0
Jul 07	160	95.63	0	0	2.5	0	0	0	1.88
(b) DS30									
Sep 05	34	79.41	0	11.76	8.82	0	0	0	0
Oct 05	24	83.33	0	4.17	12.5	0	0	0	0
Nov 05	104	94.23	0.96	0	4.81	0	0	0	0
Dec 05	102	98.04	0	0	1.96	0	0	0	0
Jan 06	9	100	0	0	0	0	0	0	0
Feb 06	29	93.1	0	0	6.9	0	0	0	0
Mar 06	101	84.16	3.96	0	7.92	0	0.99	0	2.97
Apr 06	48	62.5	0	0	0	37.5	0	0	0
May 06	40	7.5	0	0	0	92.5	0	0	0
Aug 06	23	65.22	0	26.09	8.7	0	0	0	0
Sep 06	108	55.56	0	31.48	12.04	0	0	0	0.93
Oct 06	0								
Nov 06	177	59.32	0	29.94	10.73	0	0	0	0
Jan 07	156	50	12.82	14.1	0	0	0	23.08	0
Feb 07	62	85.48	11.29	0	0	0	0	0	3.22
Mar 07	9	66.67	33.33	0	0	0	0	0	0
Apr 07	17	29.41	0	0	0	70.59	0	0	0
May 07	75	41.33	0	0	1.33	53.33	1.33	1.33	1.33
Jun 07	32	81.25	0	0	0	18.75	0	0	0
Jul 07	105	97.14	0	0	2.86	0	0	0	0

ond to DS2: lichens 66.0/67.7%, fruits 13.9/8.8%, young leaves 12.9/11.9%, mature leaves 4.0/4.2%, buds 2.3/4.8%, flowers 0.2/0.1%, herbs 0.3/2.0%, and other 0.5/0.5%.

The relative representation of food items in the diet varied widely among months (Table 1). Fruit consumption showed a sharp peak in August. Using of lichens dropped precipitously as new foliage became available in spring. Amount of young leaves in the diet correlates with phenological availability (DS15: $r_s = 0.863$, $P > 0.001$, $n = 20$; DS30: $r_s = 0.867$, $P > 0.001$, $n = 19$; Fig. 6). The amount of fruit in the diet also showed a positive correlation with availability (DS15: $r_s = 0.636$, $P = 0.003$, $n = 20$; DS30: $r_s = 0.714$, $P = 0.001$, $n = 19$). The proportion of flowers in the diet correlates with availability in DS15 ($r_s = 0.725$, $P = 0.008$, $n = 12$), but not DS30 ($r_s = 0.218$, $P = 0.519$, $n = 11$). Flowers were available only during a short temporal window in spring during which they were consumed occasionally. Overall, they did not form a noticeable portion of the diet.

The first bamboo shoots appeared in May at mid-elevations. Bamboo shoot availability in plots (at high elevations) was 0 in April and May. The relative availability of bamboo shoots was 30.5% in June and 36.4% in July.

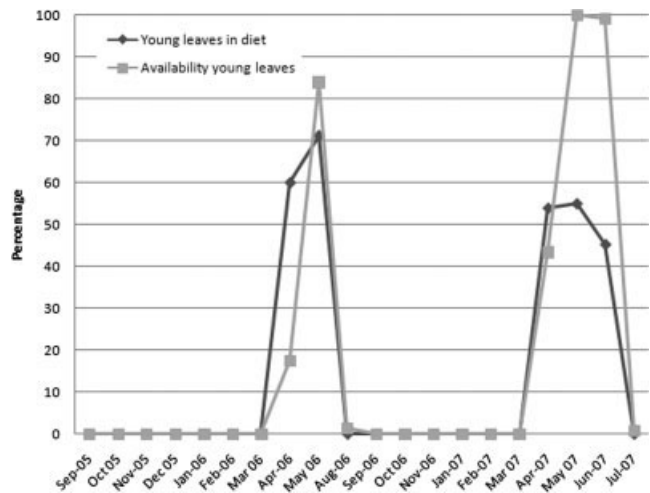


Fig. 6. Comparison of how young leaf consumption varies with young leaf availability. 'Young leaf in diet' refers to the percentage of feeding time on young leaves, 'availability of young leaves' refers to the percentage of trees bearing young leaves.

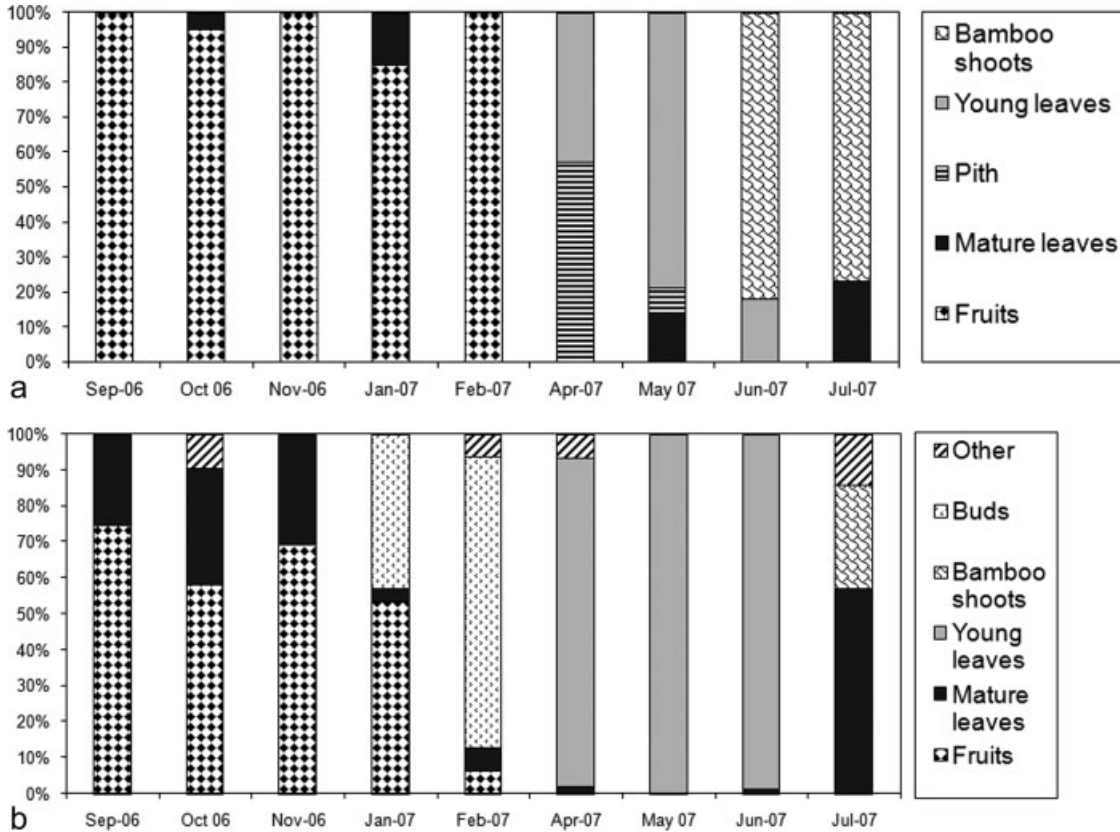


Fig. 7. a) Monthly diet composition for a limited number of months during which feeding sign could be assessed. Lichen use could not be quantified as lichen is rarely found in feeding litter. b) Monthly diet composition based on 15-min scans after excluding lichens. A comparison between the two methods reveals that bamboo shoots and also pith are much more prominent in the data set based on feeding sign.

TABLE 2. Correlation matrix comparing feeding records for lichens with feeding records for plant parts and availability of plant parts

	Availability						Representation in diet			
	Fruit		Young leaves		Fruit and/or young leaf		Fruit		Young leaves	
	DS1	DS2	DS1	DS2	DS1	DS2	DS1	DS2	DS1	DS2
Representation of lichen in diet	0.044	0.252	-0.658**	-0.490*	-0.681**	-0.499*	-0.249	-0.349	-0.668**	-0.616**

Based on inspections of feeding sign, bamboo shoots represent a key food in summer (Fig. 7a), but only a few instances of bamboo shoot consumption appear in the scan samples (Fig. 7b). Although the scan data imply that July is characterized by absence of nutritionally interesting plant foods and high reliance on lichens (96–97% of the feeding records), detritus found in the group’s foraging path demonstrates that lichens are complemented with a substantial amount of bamboo shoots.

Lichens: representation in the diet, distribution, and regeneration

Lichens were consumed in every single month and ranked first in the diet in every month, except in April 2006 (DS15), May 2006 (both DS), April/May 2007 (both DS) when young leaves dominated the diet and August 2006 (DS15) when fruits predominated. Both use of young leaves and availability of young leaves were negatively correlated with percentage of lichen feeding

records (Table 2). There was neither a correlative association between use of lichen and use of fruit nor between use of lichen and availability of fruit. We compared the percentage of time invested in lichen vs. non-lichen feeding between males and females and found for DS15 that males spent significantly more time feeding on lichens than females ($\chi^2 = 4.668$, $df = 1$, $P = 0.018$). However, as for DS30, there was no significant difference between males and females ($\chi^2 = 0.100$, $df = 1$, $P = 0.409$).

The following lichen species were implicated as food by the snub-nosed monkeys at Samage: *Usnea longissima*, *Usnea* sp., *Bryoria confusa*, *Bryoria* cf. *trichodes* cf. ssp. *americana*, *Cetrelia* sp. and 1 unknown species (all Parmeliaceae). Of all the picked lichens that could be identified, 90.1/91.0% were *Usnea* spp. (almost exclusively *U. longissima*; Fig. 8), 8.1/5.1% foliose and 1.8/3.9% *Bryoria* spp.

We conducted some limited “cafeteria-style” trial experiments with a captive subadult male from the local population that was temporarily held at the Samage



Fig. 8. Male *Rhinopithecus bieti* feeding on the lichen *Usnea longissima*. Adult males spent more time feeding on lichens than adult females. Photo by Jed Weingarten. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

Forest Research Station. In a first trial, approximately equal amounts of lichens (*Usnea longissima*) and *Sorbus* sp. fruits/leaves (one of the local monkeys' preferred plant food, Grueter et al., in prep.) were offered concurrently for 41 trials, alternating the sides. In 39 cases, the animal chose lichens, in 2 cases *Sorbus*. In another trial experiment repeated 24 times, *Usnea* and *Bryoria* lichens were offered. In 19 cases the monkey chose *Usnea*, in five cases *Bryoria*. These preliminary results suggest preference for lichens over at least one plant food and preference for *Usnea* over *Bryoria* lichens.

Lichens were available year-round at the site. Seventy-six percent of the sampled trees were covered with lichens (including the mesophytic evergreen broadleaf trees). We tested for a relationship between DBH (diameter at breast height) and lichen load using all the trees except the trees in the mesophytic evergreen broadleaf forest as these have only scant lichen cover. Lichen cover is significantly positively related to DBH ($r_s = 0.312$, $P = 0.001$, $n = 1649$, one-tailed). Canopy volume and lichen load are positively correlated ($r_s = 0.107$, $P = 0.001$, $n = 1649$, one-tailed). So DBH can be seen as a proxy measure for lichen cover. Lichen cover is clearly associated with elevation: the higher the elevation, the larger the lichen load (see Fig. 9).

Different tree types varied with regard to lichen cover (Table 3). Sclerophyllous oaks (*Quercus pannosa*, *Q. rehderiana*) were most densely laden with lichens (lichen-load category 2.1, standard deviation SD 0.8), fol-

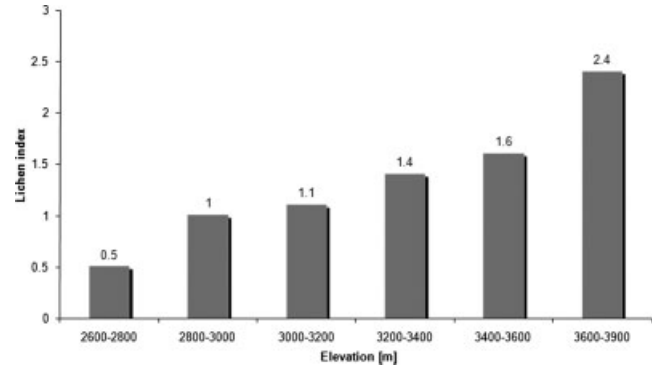


Fig. 9. Lichen index of 1851 trees compared among altitudinal zones at the Samage Forest. For details on how the lichen index was obtained, refer to the text.

TABLE 3. Lichen load categories for various tree species in the Samage Forest, in descending order

Species	Lichen index
<i>Abies georgei</i> (Pinaceae)	2.47
<i>Quercus pannosa</i> (Fagaceae)	2.46
<i>Picea likiangensis</i> (Pinaceae)	1.81
<i>Pinus yunnanensis</i> (Pinaceae)	1.39
<i>Rhododendron rubiginosum</i> (Ericaceae)	1.38
<i>Tsuga dumosa</i> (Pinaceae)	1.35
<i>Quercus rehderiana</i> (Fagaceae)	1.33
<i>Abies ernestii</i> (Pinaceae)	1.31
<i>Rhododendron anthosphaerum</i> (Ericaceae)	1.30
<i>Salix rehderiana</i> (Salicaceae)	1.28

lowed by conifers (1.8, SD 1.0) and angiosperm trees (excluding sclerophyllous oaks) (0.9, SD 0.7). The differences in lichen load among all three categories are highly significant (ANOVA, $F_{2, 1894} = 341.4$, $P = 0.001$). Dead trees ($n = 40$) supported moderate lichen growth (1.3). The vast majority of lichen feeding was recorded in conifer trees, i.e., 80.1/75.7% conifers, 10.2/13.9% angiosperms, 6.7/7.1% oaks, and 3.0/3.3% dead trees. The regeneration study revealed that lichens need an average of 21.4 years to regrow to the initial length ($n = 14$, after removing one outlier).

DISCUSSION

Dietary strategy of *Rhinopithecus bieti* at Samage and a comparison with other populations

Fallback foods have been operationally defined as foods whose use is negatively correlated with the availability of preferred foods (e.g., Altmann 1998). In line with (Xiang et al., 2007), our data confirm for the *Rhinopithecus bieti* group at Samage that there is a negative correlation between the proportion of lichen in the diet and the availability of young foliage. This inverse relationship indicates that lichens act as a fallback or backup food, and together with the high proportional representation of young leaves in the monkeys' diet during the spring flush, these results provide clear evidence that young foliage is a highly preferred dietary constituent. The results obtained from another study at Xiaochangdu (about 200 km to the north of Samage) show an

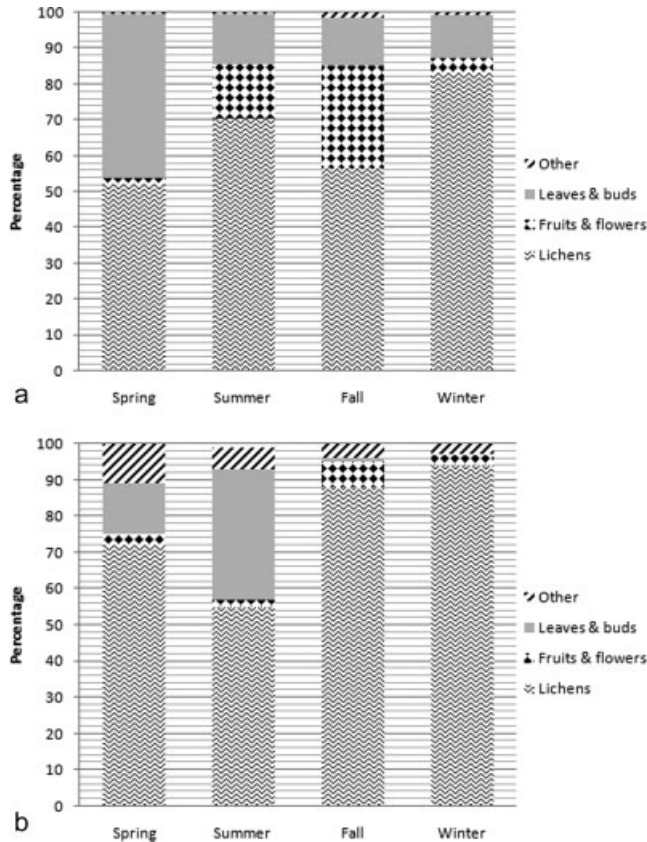


Fig. 10. Seasonal diet composition in percent of the *Rhinopithecus bieti* group at Samage compared with the group at Xiaochangdu. Data for Samage are based on the present study, data for Xiaochangdu are based on (Xiang et al., 2007). The value of 75% lichen feeding at Xiaochangdu represents a weighted mean of two different sampling methods, i.e., group follows and telescope observations; using only data obtained from telescope observations, lichens made up 82% of the total diet.

overall similar dietary pattern, but the lower productivity there (higher altitude and latitude, lower temperature and rainfall and tree species diversity) constrains foraging options and causes differences in a few respects (see Fig. 10). First, at Xiaochangdu, lichens are slightly more important in terms of annual representation in the diet (75 vs. 67%) and basically constitute the only available winter food item. The effect of productivity on lichen use is corroborated by a positive association between altitudinal distribution and proportion of lichen in the diet of different populations (see Fig. 11). Second, fruit plays a more important role in the diet of the monkeys at Samage. Third, young leaves become available later at higher altitudes at Xiaochangdu and are thus part of the early summer diet and not late spring diet as at Samage.

The percentage of feeding records is a proxy for the total time invested in feeding on a particular item and thus indicates the importance of a particular food (Marshall and Wrangham, 2007). Because lichen feeding accounted for about 67% of the diet, lichens are evidently an essential food item. Marshall and Wrangham (2007) have distinguished between two classes of fallback foods, staple and filler fallback foods. According to their definition, staple fallback foods are available perennially, are usually consumed throughout the year, sea-

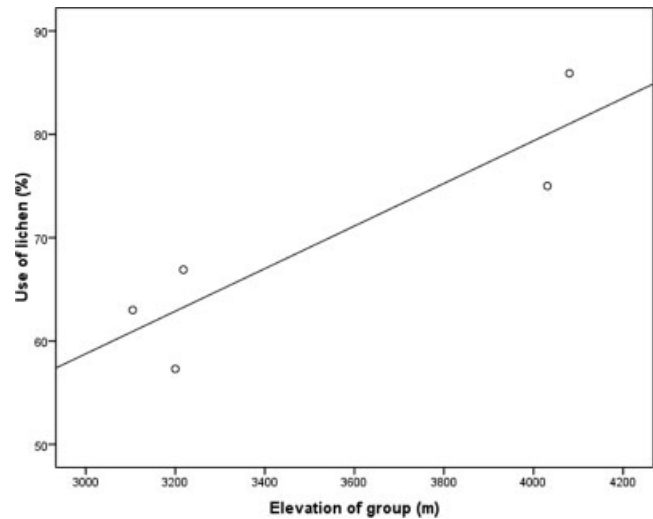


Fig. 11. Correlation between the importance of lichen in diet (percent feeding records) and mean elevation of different study groups of *Rhinopithecus bieti*. Data are based on (this study, Ding and Zhao, 2004; Kirkpatrick, 1996; Liu et al., 2004; Xiang et al., 2007).

sonally can constitute up to 100% of diet, and are uniformly distributed. Filler fallback foods, on the other hand, never make up 100% of the diet, are completely avoided for some time (weeks, months), and are rather patchily distributed. Lichens are eaten in every month and season by *Rhinopithecus bieti* at Samage, albeit with varying percentages, and hence constitute a staple fallback food.

The significance of fruits in the diet reached a peak in late summer/early fall and decreased subsequently. Fruits such as *Sorbus* and *Acanthopanax* persist long into winter and survive frost periods. By feeding intensively on fruit in the fall, the animals can deposit fat which can be drawn upon during the severe winter [compare (Zhao, 1994; Hamada et al., 2003)]. Fruits are, however, a somewhat unreliable resource. In the fall 2006, many rowan (*Sorbus* spp.) fruits suffered from fungus attacks which probably resulted in a diminished fruit supply to the monkeys in winter. A similar case of resource unpredictability has been described for the *Rhinopithecus roxellana* population at the Zhouzhi Reserve: heavy snowfalls in spring 2001 destroyed vast amounts of flowers of plants, so that fruits became scarce in the following fall, and the monkeys were forced to shift to other plant parts (Li et al., 2002).

On an annual basis, mature leaves contributed only negligibly to the diet, but ingestion of deciduous mature leaves as well as deciduous and evergreen mature bamboo leaves was relatively high in the fall, accounting for a maximum of 19% in October when they were eaten along with fruit. To ensure a balanced nutrition, the high percentage of carbohydrate-rich fruit in the fall diet probably needed to be complemented with protein-rich leaves because a ripe-fruit-dominated diet would be incompatible with the pH level requirements to maintain microorganisms and cause fermentative acidosis (Kay and Davies, 1994). In general, mixing dietary items whenever possible is a means by which folivores reduce the impacts of toxins and digestion-inhibiting compounds (e.g., Westoby, 1978).

Outside the fall, the snub-nosed monkeys did not feed much on mature leaves. In spring, they spent up to 93% of their feeding time consuming young foliage. Their strong preference for young leaves is likely due to the fact that young leaves are usually more digestible and generally contain more protein than mature ones (Choo et al., 1981, but see e.g., Schülke et al., 2006). Other vegetative matter such as flowers, bark and tubers were taken in low quantities.

Most of the ingested lichens have a pendulous appearance and belong to the filamentous fruticose ("alec-torioid") lichens, the most notable ones being the light-colored *Usnea longissima* or long-beard lichen and the dark-colored *Bryoria* spp.. Roughly 90% of the lichens selected at our study site were of the genus *Usnea*. The trial experiments revealed a preference for *Usnea*. An *ad lib* observation of a male picking *Usnea* of a bundle composed of both species in an *Abies georgei* tree lends further support to the notion that *Usnea* is favored over *Bryoria*. In striking contrast to our results, Kirkpatrick (1996) found that 92% of the picked lichens were of the genus *Bryoria*. He noted (p 84) that "... *Usnea longissima* did not appear of interest to the langurs; when langurs were in trees holding both *Bryoria* and *Usnea longissima*, the langurs fed almost solely on *Bryoria*." This apparent contrast might perhaps be linked to the fact that *Usnea* is more abundant at moderate altitudes than *Bryoria* (Grueter, unpublished data) and the overall altitudinal range of our focal group at Samage is about 800 m lower than Wuyapiya. Alternatively, this geographical variation in food selection could also reflect cultural variation (Nishida et al., 1983; Zweifel and Bastian, 2007). It is also possible that there is a difference in the chemical properties of *Usnea* and *Bryoria* at the two sites.

As for sex difference in lichen eating, our results are incongruous. Although DS15 indicates that males spent significantly more time feeding on lichens compared with females, no sex differences are apparent in DS30. Males are much larger in body size than females, and larger-bodied primates may be better able to subsist on a generalized (low-quality) staple fallback diet (Gaulin, 1979; Kay, 1984; Haag, 2007). Moreover, females have relatively greater energetic requirements as a result of gestation, lactation and infant carrying which may explain their tendency to feed on more (high-quality) non-lichen foods. However, empirical evidence supporting these assertions is ambiguous (e.g., Strier, 1991; Doran et al., 2002).

Advantages of lichen as a fallback food in relation to vascular plants

Lichens are a symbiotic consortium of fungal and photosynthetic partners and thus do not represent a plant food in the classic sense. The winter dry season poses a nutritional challenge to the hardy snub-nosed monkeys; they are confronted with a lack of preferred plant resources and must choose between abundant lichen and abundant evergreen mature foliage. Evergreen leaves in temperate forests are tough, leathery and chemically defended (Kirkpatrick, 1996). This low palatability thus makes them poor choices of food, so switching to mature leaves in winter is barely an option for the snub-nosed monkeys (but see Curtin, 1975 for *Semnopithecus schistaceus*).

Lichens are a non-seasonal resource and available in abundance. They are also relatively easy to harvest, requiring no extractive or technically difficult foraging

capabilities (although the monkeys sometimes appeared to selectively pick the younger thinner strands out of a bundle of *Usnea*). A fallback strategy involving staple fallback foods is possibly cognitively less demanding than a filler fallback strategy whereby a primate is forced to switch to an otherwise neglected or rarely used resource base during the lean period (compare Russon and Begun, 2004).

The main predictors of colobine food choice are fiber content, protein and tannins. Although tannins and fibers tend to have a negative effect on food choice in colobines, proteins have the reverse effect (Oates et al., 1980; Waterman and Kool, 1994; Fashing et al., 2007a; Hanya et al., 2007). *Rhinopithecus bieti* never or only extremely rarely or accidentally eat conifer needles (this study, Kirkpatrick, 1998; Yang and Zhao, 2001). Gymnosperms have significantly higher loads of fiber and tannin than fruticose lichens (Kirkpatrick, 1996). Moreover, lichens contain virtually no fibrous components such as cellulose or lignin, making them highly digestible (Kirkpatrick, 1996; Kirkpatrick et al., 2001). They are also high in nonstructural carbohydrates which supply digestible energy for thermoregulation in winter (*ibid.*). In addition, lichens are typically rich in vitamin D (e.g., Ellis et al., 1933), and the monkeys possibly satisfy their need for vitamin D through ingestion of lichen. These chemical characteristics may be a key reason why lichens have been chosen as a fallback instead of conifer foliage.

The crude protein content of fruticose lichens is generally low (Kirkpatrick, 1996; Rominger et al., 1996), and for ungulates, it has been suggested that access to non-lichen forage in winter would be beneficial to counteract the protein deficit and potential rumen inhibition incurred from lichen eating (Rominger and Oldemeyer, 1990). *Rhinopithecus bieti* at Samage complement their winter diet with fruits and terrestrial herbs, and this dietary mix may confer more nutritional advantages than a purely lichen-based diet. Usually only leaves are regarded as being high in protein content, but recent studies have demonstrated that fruit may be equally important as sources of protein, even in temperate forests (Li, 2006; Schülke et al., 2006). However, specific phytochemical analyses are needed to determine the nutrient content of the particular fruits being of importance to the snub-nosed monkeys.

Fruticose lichens of the genera *Bryoria* and *Usnea* contain usnic acid, which has antibacterial properties and may hinder digestive processes in the (ungulate) rumen (Brodo and Hawksworth, 1977, compare also Lawrey, 1986). Non-lichen diet supplements may be vital to dilute lichen toxins, or higher-protein food may be required to stimulate microbial activity and enhance passage rates (Rominger and Oldemeyer, 1990). Some lichen taxa, e.g., *Sulcaria virens* are deemed toxic (Wang LS, personal communication). Whenever *Sulcaria* grew along with *Usnea* on a tree, the snub-nosed monkeys in this study obviously singled out *Usnea* and did not handle *Sulcaria* at all. *Sulcaria* was also totally avoided in opportunistic trial experiments, indicating an inherent or learned knowledge of which foodstuffs might be hazardous. With the exception of one study (Kirkpatrick et al., 2001), the physiological basis of lichen consumption in colobines has not been studied and warrants increased attention.

Lichens may also be essential as a source of free water during cold, dry and sunny climate conditions such as

the ones characteristic for the Himalaya foothills. Especially, the dark-colored lichens in the genus *Bryoria* (common at high elevations within the habitat of *Rhinopithecus bieti*) are thought to be good absorbers of solar radiation, thus causing snow to melt and potentially making liquid available for the monkeys (Sharnoff and Rosentreter, 1998).

Lichen eating in other primates and other mammals living in temperate habitats

For some primates, lichens are an occasional food item that is eaten in small quantities (e.g., *Colobus guereza*: Harris and Chapman, 2007; *Cercopithecus lhoesti*: Kaplin and Moermond, 2000; *Semnopithecus schistaceus*: Sayers and Norconk, 2008; *Macaca fuscata*: Nakayama et al., 1999; and *Homo sapiens*: Wang, 2004). Habitual lichenivory, though, represents a specialization that among primates is largely restricted to the snub-nosed langurs (*Rhinopithecus bieti*: this study; Wu, 1991; Kirkpatrick, 1996; *R. roxellana*: Li, 2001). Although fruticose lichens are found in various Afri-montane habitats (e.g., Virunga Volcanoes: Owunji et al., 2005; Simen Mountains: Iwamoto and Dunbar, 1983), their cercopithecoïd and hominoid inhabitants such as *Gorilla beringei* and *Theropithecus gelada* do not seem to use this resource at all (Watts, 1984; Grüter and Zinner, 2004). Two exceptions are the colobine *Colobus angolensis* in the montane Nyungwe National Park which ingests substantial amounts of lichen (Vedder and Fashing, 2002) and *Macaca sylvanus* in Algerian oak forests which rely heavily on lichens during winter (Ménard, 1985). Among the Neotropical species, *Oreonax flavicauda* living in high-altitude habitats in Peru have been observed to incorporate yet unspecified amounts of lichens into their diet (Butchart et al., 1995). Another primate species worthy of mention here is *Callimico goeldii*, for which fungus is an important dietary component and comprises more than 50% of the diet in some months (Porter, 2001).

Lichen-eating is also a fallback strategy in ruminants inhabiting temperate mountains and forests. Caribou (*Rangifer tarandus*) and black-tailed deer (*Odocoileus hemionus*) use arboreal lichen—including *Usnea* and relatives—for a fourth or more than a half of their winter diet (Richardson and Young, 1977; Rominger and Oldemeyer 1990; Terry et al., 2000). Musk deer (*Moschus* spp.) have also been reported to feed to a great extent on *Usnea* lichens (Ustinov, 1969; Green, 1987). Lichens also constitute an important winter food for mountain goats (*Oreamnos americanus*) (Fox and Smith, 1988) and North American moose (*Alces alces*) (Thomas, 1990). Among the non-ungulates, northern flying squirrels (*Glaucomys sabrinus*) depend largely on lichens in winter (Maser et al., 1986). What becomes evident from this taxonomic summary is that the great majority of bulk feeders on lichens have a sacculated stomach.

Implications of lichenivory for social organization and structure

In theory, we would expect declining group sizes in more seasonal and marginal habitats as a result of declining productivity, i.e., smaller and fewer food patches (Plavcan et al., 2005; van Schaik and Brockman, 2005). Alternatively, foods in more seasonal areas are

available in greater abundance (albeit of lower quality) and thus are not worth a fight and allow large groups to form (*ibid.*). Exploiting abundant or superabundant and evenly distributed resources on an annual basis reduces the ecological costs of long-term grouping and dampens feeding competition of the scramble type (*sensu* Wrangham, 1979; van Schaik and van Noordwijk 1988; Yeager and Kool, 2000; Steenbeek and van Schaik, 2001; Marshall and Wrangham, 2007). The cornucopia of lichen and the fact that lichens are rarely if ever depleted in a patch at once (Grueter, personal observation) is evidence for weak competition and is thought to permit the formation and maintenance of “super-groups” in snub-nosed monkeys (Kirkpatrick et al., 1998). The cascading effects on social dynamics (competitive regime etc.) remains to be elucidated in detail, but spatially dispersed foods are hypothesized to generate weak or non-existent dominance hierarchies (Wrangham, 1980; van Schaik, 1989; Isbell, 1991). Snub-nosed monkeys still appear to experience competition to some degree when focusing on contestable and preferred plant foods such as preferred fruit items which create the foundation for competition (Grueter et al., in prep.). This competition is likely enhanced during the lean season when fruits become increasingly scarce (compare Wrangham, 1980; van Schaik and Brockman, 2005).

Moreover, it has also been proposed that lichens’ slow regeneration time selects for the formation of large bands because aggregating in super-groups and collective foraging is a means of avoiding depleted patches of food (Kirkpatrick et al., 1998). This hypothesis, the Cody-Altman hypothesis (Rodman, 1988), has thus far, however, rarely been invoked as a likely explanation of grouping in primates in general and its plausibility is seriously compromised because of its group selection argumentation (Harcourt and Stewart, 2007). Hence, we argue that lichenivory allows the creation of bands, but does not induce it.

In a striking socioecological parallel to the snub-nosed monkeys, two populations of montane-living *Colobus angolensis* show extensive consumption of lichens and live in extremely large groups of several hundred (Fashing et al., 2007b). Lichen eating *Colobus angolensis* living in huge groups with 500+ animals have also been reported for the montane forests of Kahuzi-Biega (J Yamagiwa, pers. comm.). While the internal structure and functional basis of these groupings remains unclear, lichens may at least play a role in facilitating the formation of super-groups in *Colobus angolensis* (Fashing et al., 2007b).

Implications for three-dimensional use of space

If temperature was the primary determinant of altitude use, the snub-nosed monkeys would stay at the lowest altitudes in winter where temperature is higher. At Samage, it was found that they remain at moderately high altitudes in winter despite freezing winter nights. No significant difference in mean altitude of the group between fall and winter was detected (Li et al., 2008). This unexpected result is best explained with dietary needs: lichen density is higher at higher elevations (this study), and lichen intake mitigates the negative effects of increased thermal stress associated with staying at high elevations.

Implications for ranging and foraging strategies

According to standard foraging theory (Norberg, 1977; Stephens and Krebs, 1986), primates of the temperate zone facing food crunches during the winter bottleneck period basically have two options to maintain daily food intake: they may invest in traveling and thereby incurring higher energetic costs and caloric expenditure to acquire a sufficient quantity of the preferred foods (high-returns foods). Alternatively, they can modify their dietary spectrum by incorporating lesser-quality fallback foods, and concomitantly show a decrease in moving. The first strategy, the "high-returns strategy" is adopted by only a few temperate-living primates (e.g., Curtin, 1975; Bleisch, 1995; Sayers and Norconk, 2008). The second strategy, the energy-saving strategy, appears to be the norm (e.g., Mehlman, 1986; Nakagawa, 1989; Ménard and Vallet, 1997; Ding and Zhao, 2004; Xiang, 2005; Guo et al., 2007). The particular tactic a given primate resorts to depends largely on whether prolific food items are available in winter. Because temperate biota are usually characterized by a virtual absence of profitable resources (with the exception of long-persisting winter fruits), a high-returns strategy is usually not an option.

Rhinopithecus bieti at Samage also feed on winter fruits. Tracking these diffusely distributed and energetically profitable fallback fruits might be the impetus for them to move out of their core area and visit peripheral patches of forest ("short-term habitat shifting") after fruit resources had been depleted in more central areas of the home range. These forays may have caused them to keep a large home range in winter (Grueter et al., 2008b). On the other hand, they showed a decreased day journey length in winter as a consequence of cold temperatures (Grueter et al., in prep). With regard to optimal foraging models, the winter strategy pursued by *R. bieti* at Samage is a mixture of both: their subsistence on lichens as a fallback (this study; Kirkpatrick, 1996; Ding and Zhao, 2004) and reduced day journey length basically comply with the energy-minimizing strategy, but visiting peripheral areas in search of thinly dispersed fruit is consistent with the high-returns strategy.

Implications for anatomy of the masticatory apparatus

Fallback foods have been hypothesized to be strong selective forces on morphology (Rosenberger, 1992; Marshall and Wrangham, 2007). The relatively robust mandible of the Chinese Rhinopiths as opposed to *Trachypithecus* and *Macaca* has probably evolved as a phenotypic adaptation to the tough staple fallback food available in their marginal arid temperate habitat (Pan et al., 2008). Fruticose lichens most likely have fracture properties unlike those of young leaves or unripe fruits. To render the lichens' cell contents accessible to digestion, prolonged chewing and strong mastication force are probably necessary (Jablonski et al., 1998). Testing the mechanical properties of lichens using established field protocols (Lucas et al., 2001; Wright et al., in press) is suggested as an avenue for future study.

Implications for conservation

Lichens are only sporadically collected by humans in the area as foods and fire kindling. However, dead standing trees are usually festooned with considerable

amounts of lichen and are regularly climbed by the snub-nosed monkeys for the purpose of acquiring this resource (this study, see also Li, 2006), so the occasional removal of dead trees by villagers as a source of firewood has a negative impact on the lichen biomass.

The present results on lichen regeneration are preliminary in nature and based on a limited sample size, but together with the data provided by (Kirkpatrick, 1996), they tentatively signify that renewal rates are extremely slow and lichens need decades to recover from harvesting. Moreover, cursory inspection revealed that in areas through which the monkeys had recently passed, branches were not devoid of lichen. However, the snub-nosed monkeys live in a highly fragmented habitat and at some sites suffer from artificial range restricting as a means of attracting tourists, which increases their susceptibility to depletion effects. Thus, depletion over the long-term may be a realistic scenario. Even though no quantitative data on the potential problem of lichen depletion are available for this site or any other inhabited by snub-nosed monkeys, it is reasonable to assume that continued lichen consumption or destruction exceeding annual production would result in a decreased standing crop.

Usnea longissima is the single most numerous food constituent in the diet of the snub-nosed monkeys at Samage. The abundance of this resource likely sets the carrying capacity of the community. That primate populations are limited by the availability of their key fallback resource has been empirically demonstrated (e.g., Marshall and Leighton, 2006). The odds of the snub-nosed monkeys' survival are to a large degree dependent on the preservation of this critical resource. That habitat change or a decline of the major fallback food can cause local extinctions has been exemplified by the Amboseli *Cercopithecus aethiops* (Alberts et al., 2005). As for *Rhinopithecus bieti*, it is alarming that exactly this species of lichen has been found to be vulnerable and susceptible to human-induced environmental changes, e.g., a dramatic decline in European forests has been attributed to air pollution in general and sulphur dioxide in particular (Esseen et al., 1981; Seaward, 1987). Lichens lack a protective cuticle and roots and thus absorb substances from the atmosphere via dry and wet deposition (Purvis et al., 2007).

China is the world's largest emitter of sulphur dioxide (Smith et al., 2001), and lichens are likely most at risk of deterioration in the industrialized and heavily polluted Eastern and Central areas of China. Nevertheless, it is conceivable that the eastern Himalayas could still be affected, in the way that for example the Arctic is a sink for atmospheric pollution generated in the heavily industrialized north temperate regions (Klein and Vlasova, 1992). This would have a devastating and irreversible effect on the last remaining population of this highly endangered and charismatic primate. While hard data on lichen depletion and deterioration are not available for this area at the moment, this is an alarm signal that should be taken seriously and hopefully promotes more in-depth research in this field.

Choice of fallback foods and foraging strategies of other temperate-living monkeys

Broadly speaking, different evolutionary lineages have developed different solutions to the problem of seasonal food scarcity. Phylogenetic constraints and resource

Taxon	Site	Citation	Fallback Food Item							
			Lichen	Buds	Bark	Mature leaves	Conifer foliage	Herbs / Grasses	Fruits / Seeds	USOs
COLOBINAE										
<i>Rhinopithecus bieti</i>	Samage	This study								
<i>Rhinopithecus bieti</i>	Xiaochangdu	Xiang et al. 2007								
<i>Rhinopithecus bieti</i>	Wuyapiya	Kirkpatrick 1996								
<i>Rhinopithecus roxellana</i>	Shennongjia	Li 2006								
<i>Rhinopithecus roxellana</i>	Zhouzhi	Guo et al. 2007								
<i>Rhinopithecus roxellana</i>	Baihe	Kirkpatrick unpubl.								
<i>Rhinopithecus brelichi</i>	Mt Fanjing	Bleisch and Xie 1998								
<i>Semnopithecus schistaceus</i>	Langtang	Sayers and Norconk 2008								
<i>Semnopithecus schistaceus</i>	Simla/Hatto	Sugiyama 1976								
<i>Semnopithecus schistaceus</i>	Junbesi	Curtin 1975								
CERCOPITHECINAE										
<i>Macaca sylvanus</i>	Akfadou	Menard and Vallet 1997								
<i>Macaca sylvanus</i>	Djurdjura	Menard and Vallet 1997								
<i>Macaca sylvanus</i>	Rif	Mehlman 1988								
<i>Macaca thibetana</i>	Mt Emei	Zhao 1996								
<i>Macaca mulatta</i>	Murree Hills	Golstein and Richard 1989								
<i>Macaca mulatta</i>	Taihang Mts	Qu et al. 1993								
<i>Macaca fuscata</i>	Kinkazan	Nakagawa 1989								
<i>Macaca fuscata</i>	Shiga Heights	Wada and Ichiki 1980								
<i>Macaca fuscata</i>	Shimokita	Izawa 1971; Wada 1964								
<i>Macaca fuscata</i>	Yakushima	Hanya 2004								
<i>Papio ursinus</i>	Giant's Castle	Whiten et al. 1987								

Fig. 12. A tabular overview of fallback foods in temperate-old World Monkeys. Two north temperate primate species are not included as no data on their respective dietary regime are available: *Macaca munzala* (Sinha et al., 2006) and *Trachypithecus geei* (Srivastava, 2006; Wangchuk et al., 2003). Among the south temperate primates, only the montane-living *Papio hamadryas ursinus* is included. “Fruits/seeds” include acorns and pine nuts, “herbs/grasses” include grass shoot bases. “Yakushima” refers to the high-altitude sites only. The data were extracted from the following sources: (Curtin, 1975; Goldstein and Richard, 1989; Guo et al., 2007; Hanya, 2004; Izawa, 1971; Kirkpatrick, 1996; Kirkpatrick and Gu, 1999 (Ecology and conservation of golden monkeys *Rhinopithecus roxellana* at Baihe Nature Reserve (Min Mountains, Sichuan), Unpublished report; Li, 2006; Mehlman, 1988; Ménard and Vallet, 1997; Nakagawa, 1989; Qu et al., 1993; Sayers and Norconk, 2008; Sugiyama, 1976; Wada, 1964; Wada and Ichiki, 1980; Whiten et al., 1987; Xiang et al., 2007; Zhao, 1996).

availability during the lean season are probably key determinants of the kinds of fallback foods that are used. Overall, buds and bark are the dominant fallback foods of temperate-living primates, followed by herbs (see Fig. 12). With the single exception of fruit, fallback foods in temperate environments are to a large degree congruent with winter foods. Fruits emerge in the fall and often remain available long into winter. So winter fruits are often preferred and thus not fallback foods *sensu stricto*. Some colobines forage on winter fruits/seeds (e.g., Guo et al., 2007; this study), while this strategy is surprisingly uncommon among cercopithecines. On the other hand, mature leaves (including gymnosperm needles) act as fallback foods in macaques (e.g., (Mehlman, 1988)), but are hardly of importance for temperate-living “leaf monkeys.” Mature leaves are eaten as fallback foods by only a few temperate taxa, and unexpectedly, mature leaves were not an essential fallback food for colobines with the single exception of *Semnopithecus schistaceus* (Curtin, 1975; Sayers and Norconk, 2008). For no single colobine species do mature leaves constitute the principal resource base in winter (see Fig. 12). The stereotype of colobines as “leaf monkeys” thus does not hold in this case. Apart from the foods listed in Figure 12, crop raiding is another means by which monkeys buffer themselves from food shortages and is exhibited by some temperate monkeys (e.g., *Macaca mulatta*: Teas et al., 1980).

There are also examples of convergences in fallback strategies in distantly related taxa inhabiting ecologically similar habitats in different biogeographic regions. A case example are North African *Macaca sylvanus* populations and Central Asian *Rhinopithecus bieti* populations. Both incorporate considerable amounts of lichen in

their diet in winter, despite divergent anatomy and physiology of the gastrointestinal tract (forestomach fermentation in snub-nosed monkeys and caeco-colic fermentation in macaques (Lambert, 1998). With regard to the exploitation of conifer foliage, however, the two differ drastically: Barbary macaques in high altitude fir forests at the Ghomoran Rif show a clear feeding adaptation to the firs by being able to rely on fir foliage during the cold, snowy winters (Mehlman, 1988). However, no evidence of needle leaf feeding has been accrued in *Rhinopithecus bieti* (this study) despite the abundance of this particular resource in its habitat. Early reports of needle eating (e.g., Mu and Yang, 1982) have almost certainly been misinterpreted, because no subsequent study has substantiated the initial records.

CONCLUSIONS

Snub-nosed monkeys (*Rhinopithecus bieti*) feed on lichens throughout the year, but the proportional representation of this item increased dramatically in winter when preferred edible plant foods became rare. These primates are unique for having the capacity to rely to such a large extent on a single resource base during the long precarious winter. This high reliance on lichen is simply a consequence of the fact that in their ecologically challenging environment there is a shortage of dietetically valuable vegetative matter, i.e., digestible mature deciduous foliage (due to leaf shedding in the fall). It is probably reasonable to assume that in most of the habitats occupied by *R. bieti* there is no other fallback resource besides lichens that can provide the basis for their continued survival. An array of threats such as habitat disturbance, fragmentation, anthropogenic range

restriction, slow regeneration time of lichen, depletion and environmental pollution seriously compromise viability of the remaining populations.

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LITERATURE CITED

- Alberts SC, Hollister-Smith JA, Mututua RS, Sayialel SN, Muruthi PM, Warutere JK, Altmann J. 2005. Seasonality and long-term change in a savanna environment. In: Brockman D van Schaik C, editors. Seasonality in primates: studies of living and extinct human and non-human primates. New York: Cambridge University Press. p 157–195.
- Altmann J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227–267.
- Altmann SA. 1998. Foraging for survival. Chicago: Chicago University Press.
- Bleisch W. 1995. Conservation of the Guizhou golden monkey. In: Xia W, Zhang Y, editors. Primate research and conservation. Beijing: China Forestry Publishing House. p 150–156.
- Brockman DK, van Schaik CP, editors. 2005. Seasonality in primates: studies of living and extinct human and non-human primates. New York: Cambridge University Press.
- Brodo IM, Hawksworth DL. 1977. Aleatoria and allied genera in North America. *Opera Bot* 42:1–164.
- Butchart SHM, Barnes R, Davies CWN, Fernandez M, Seddon N. 1995. Observations of two threatened primates in the Peruvian Andes. *Prim Cons* 16:15–19.
- Choo GM, Waterman PG, McKey DB, Gartlan JS. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. *Oecologia* 49:170–178.
- Cramer W, Kicklighter DW, Bondeau A, Moore III B, Churkina G, Nemry B, Ruimy A, Schloss AL, and the Participants of the Potsdam NPP Model Intercomparison. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biol* 5, Suppl 1:1–15.
- Curtin RA. 1975. The socio-ecology of the common langur, *Presbytis entellus* in the Nepal Himalaya. Ph.D. thesis. Berkeley: University of California.
- Ding W, Zhao QK. 2004. *Rhinopithecus bieti* at Tacheng, Yunnan: diet and daytime activities. *Int J Primatol* 25:583–598.
- Doran DM, McNeilage A, Greer D, Bocian C, Mehlman P, Shah N. 2002. Western lowland gorilla diet and resource availability: new evidence, cross-site comparisons, and reflections on indirect sampling methods. *Am J Primatol* 58:91–116.
- Ellis NR, Palmer LJ, Barnum GL. 1933. The vitamin content of lichens. *J Nutr* 6:443–454.
- Esseen P-A, Ericson L, Lindström H, Zackrisson O. 1981. Occurrence and ecology of *Usnea longissima* in central Sweden. *Lichenologist* 13:177–190.
- Fashing PJ, Dierenfeld ES, Mowry CB. 2007a. Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of *Colobus guereza* in Kakamega Forest, Kenya. *Int J Primatol* 28:673–703.
- Fashing PJ, Mulindahabi F, Gakima J-B, Masozera M, Mununura I, Plumptre A, Nguyen N. 2007b. Activity and ranging patterns of Angolan black-and-white colobus (*Colobus angolensis ruwenzorii*) in Nyungwe Forest, Rwanda: possible costs of large group size. *Int J Primatol* 28:529–550.
- Fox JL, Smith CA. 1988. Winter mountain goat diets in Southeast Alaska. *J Wildl Manage* 52:362–365.
- Gaulin SJC. 1979. A Jarman/Bell model of primate feeding niches. *Hum Ecol* 7:1–19.
- Geist V. 1978. Life strategies, human evolution, environmental design: toward a biological theory of health. New York: Springer.
- Goldstein SJ, Richard AF. 1989. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int J Primatol* 10:531–567.
- Green MJB. 1987. Diet composition and quality in Himalayan Musk deer based on faecal analysis. *J Wildl Manage* 51:880–892.
- Grueter CC, van Schaik CP, Ren B, Wei F. 2008a. Towards an understanding of the social system of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) [abstract]. *Primate Eye* 96:317.
- Grueter CC, Li D, van Schaik CP, Ren B, Long Y, Wei F. 2008b. Ranging of *Rhinopithecus bieti* in the Samage Forest, China. I. Characteristics of range use. *Int J Primatol* 29:1121–1145.
- Grüter CC, Zinner D. 2004. Nested societies. Convergent adaptations in snub-nosed monkeys and baboons? *Prim Rep* 70:1–98.
- Guo S, Li B, Watanabe K. 2007. Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. *Primates* 48:268–276.
- Haag L. 2007. Responses to food scarcity: a comparative study of white-bearded gibbons (*Hylobates albibarbis*) and Bornean orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan, Indonesia [Master's thesis]. Zurich: University of Zurich.
- Hamada Y, Hayakawa S, Suzuki J, Watanabe K, Ohkura S. 2003. Seasonal variation in the body fat of Japanese macaques *Macaca fuscata*. *Mammal Study* 28:79–88.
- Hanya G. 2004. Diet of a Japanese macaque troop in the coniferous forest of Yakushima. *Int J Primatol* 25:55–71.
- Hanya G, Kiyono M, Takafumi H, Tsujino R, Agetsuma N. 2007. Mature leaf selection of Japanese macaques: effects of availability and chemical content. *J Zool* 273:140–147.
- Hanya G, Noma N, Agetsuma N. 2003. Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. *Primates* 44:51–59.
- Harcourt AH, Stewart KJ. 2007. Gorilla society: conflict, compromise, and cooperation between the sexes. Chicago: University of Chicago Press.
- Harris TR, Chapman CA. 2007. Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates* 48:208–221.
- Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behaviour among primates. *Behav Ecol* 2:143–155.
- Iwamoto T, Dunbar RIM. 1983. Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. *J Anim Ecol* 52:357–366.
- Izawa K. 1971. Japanese monkeys living in the Okoppe Basin of the Shimokita Peninsula: the first report of the winter follow-up survey after the aerial spraying of herbicide. *Primates* 12:191–200.
- Jablonski NG, Pan RL, Chaplin G. 1998. Mandibular morphology of the doucs and snub-nosed monkeys in relation to diet. In: Jablonski NG, editor. The natural history of the doucs and snub-nosed monkeys. Singapore: World Scientific. p 105–128.
- Kaplin BA, Moermond TC. 2000. Foraging ecology of the mountain monkey (*Cercopithecus lhoesti*): implications for its evolutionary history and use of disturbed forest. *Am J Primatol* 50:227–246.
- Kay RF. 1984. On the use of anatomical features to infer foraging behavior in extinct primates In: Rodman P, Cant J, editors. Adaptations for foraging in nonhuman primates: contributions to an organismal biology of prosimians, monkeys, and apes. New York: Columbia University Press.

- Kay RNB, Davies AG. 1994. Digestive physiology. In: Davies AG, and Oates JF, editors. *Colobine monkeys: their ecology, behaviour and evolution*. Cambridge: Cambridge University Press. p 229–249.
- Kirkpatrick RC. 1996. Ecology and behavior of the Yunnan snub-nosed langur (*Rhinopithecus bieti*, Colobinae). Ph.D. dissertation. Davis: University of California.
- Kirkpatrick RC. 1998. Ecology and behavior in snub-nosed and douc langurs. In: Jablonski NG, editor. *The natural history of the doucs and snub-nosed monkeys*. Singapore: World Scientific Press. p 155–190.
- Kirkpatrick RC, Long YC, Zhong T, Xiao L. 1998. Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *Int J Primatol* 19:13–51.
- Kirkpatrick RC, Zou RJ, Dierenfeld ES, Zhou HW. 2001. Digestion of selected foods by Yunnan snub-nosed monkey *Rhinopithecus bieti* (Colobinae). *Am J Phys Anthropol* 114:156–162.
- Klein DR, Vlasova TJ. 1992. Lichens, a unique forage resource threatened by air pollution. *Rangifer* 12:21–27.
- Knott CD. 2005. Energetic responses to food availability in the great apes: implications for hominin evolution. In: Brockman DK, van Schaik CP, editors. *Seasonality in primates: studies of living and extinct human and non-human primates*. New York: Cambridge University Press. p 351–378.
- Lambert JE. 1998. Primate digestion: interactions among anatomy, physiology and feeding ecology. *Evol Anthropol* 7:8–20.
- Latham RE, Ricklefs RE. 1993. Continental comparisons of temperate-zone tree species diversity. In: Ricklefs RE, Schluter D, editors. *Species diversity in ecological communities*. Chicago: University of Chicago Press. p 294–314.
- Lawrey JD. 1986. Biological role of lichen substances. *Bryologist* 89:111–122.
- Li BG, Zhang P, Watanabe K, Tan CL, Fukuda F, Wada K. 2002. A dietary shift in Sichuan snub-nosed monkeys. *Acta Theriol Sin* 23:358–360.
- Li D, Grueter CC, Ren B, Long Y, Li M, Peng Z, Wei F. 2008. Ranging of *Rhinopithecus bieti* in the Samage Forest, China. II. Use of land cover types and altitudes. *Int J Primatol* 29:1147–1173.
- Li Y. 2001. The seasonal diet of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia Nature Reserve, China. *Folia Primatol* 72:40–43.
- Li Y. 2006. Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. *Am J Primatol* 68:217–233.
- Li ZX, Ma SL, Hua CH, Wang YX. 1982. The distribution and habit of the Yunnan golden monkey, *Rhinopithecus bieti*. *J Hum Evol* 11:633–638.
- Liu Z, Ding W, Grüter CC. 2004. Seasonal variation in ranging patterns of Yunnan snub-nosed monkeys *Rhinopithecus bieti* a Mt. Fuhe, China. *Acta Zool Sin* 50:691–696.
- Long Y, Kirkpatrick C, Zhong T, Xiao L. 1996. Status and conservation strategy of the Yunnan snub-nosed monkey. *Chin Biodiv* 4:145–152 (in Chinese with English abstract).
- Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee PKD, Osorio D, Yamashita N, Yuen TDB. 2001. Field kit to characterize physical, chemical, and spatial aspects of potential primate foods. *Folia Primatol* 72:11–25.
- Marshall AJ, Leighton M. 2006. How does food availability limit the population density of white-bearded gibbons? In: Hohmann G, Robbins MM, Boesch C, editors. *Feeding ecology in apes and other primates*. Cambridge: Cambridge University Press. p 313–335.
- Marshall AJ, Wrangham RW. 2007. Evolutionary consequences of fallback foods. *Int J Primatol* 28:1219–1235.
- Maser C, Maser Z, Witt JW, Hunt G. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. *Can J Zool* 64:2086–2089.
- Mehlman PT. 1986. Population ecology of the Barbary macaque (*Macaca sylvanus*) in the fir forests of Ghomara, Moroccan Rif Mountains. Ph.D. thesis. Toronto: University of Toronto.
- Mehlman PT. 1988. Food resources of the wild Barbary macaque (*Macaca sylvanus*) in high-altitude fir forest. Ghomaran Rif, Morocco. *J Zool* 214:469–490.
- Ménard N. 1985. Le régime alimentaire de *Macaca sylvanus* dan différent habitats d'Algérie: I-régime en chênaie décidue. *Rev d'Ecol (Terre Vie)* 40:451–466.
- Ménard N, Vallet D. 1997. Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. *A J Primatol* 43:285–304.
- Morrison ML, Marcot BG, Mannan RW. 1998. *Wildlife-habitat relationships: concepts and applications*. Madison: University of Wisconsin Press.
- Mu W, Yang D. 1982. A primary observation on the group figures, moving lines and food of *Rhinopithecus bieti* at the east side of Baima Snow Mountain. *Acta Theriol Sin* 2:125–131 (in Chinese with English abstract).
- Mueller-Dombois D, Ellenberg H. 1974. *Aims and methods of vegetation ecology*. New York: Wiley.
- Nakagawa N. 1989. Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan Island during winter. *Primates* 30:441–460.
- Nakayama Y, Matsuoka S, Watanuki Y. 1999. Feeding rates and energy deficits of juvenile and adult Japanese monkeys in a cool temperate area with snow coverage. *Ecol Res* 14:291–301.
- Nishida T, Wrangham RW, Goodall J, Uehara S. 1983. Local differences in plant-feeding habits of chimpanzees between the Mahale Mountains and Gombe National Park, Tanzania. *J Hum Evol* 12:467–480.
- Norberg PA. 1977. An ecological theory on foraging time and energetics and costs of optimal food searching method. *J Anim Ecol* 46:511–529.
- Oates JF, Waterman PG, Choo GM. 1980. Food selection in the South Indian leaf-monkey. *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45:45–56.
- Owiunji I, Nkuutu D, Kujirakwinja D, Liengola I, Plumtre AJ, Nsanzurwimo A, Fawcett K, Gray M, McNeilage A. 2005. *The biodiversity of the Virunga Volcanoes*. Report. New York: Wildlife Conservation Society.
- Pan R, Xuelong J, Milne N. 2008. Mandibular morphometric variation among Chinese cercopithecoids and the unique structure of the snub-nosed monkey (*Rhinopithecus*) mandible. *Primates* 49:195–203.
- Plavcan JM, van Schaik CP, McGraw WS. 2005. Seasonality, social organization, and sexual dimorphism in primates In: Brockman DK, van Schaik CP, editors. *Seasonality in primates: studies of living and extinct human and non-human primates*. New York: Cambridge University Press. p 401–441.
- Porter LM. 2001. Dietary differences among sympatric Callitrichinae in Northern Bolivia: *Callimico goeldii*, *Saguinus fuscicollis* and *S. labiatus*. *Int J Primatol* 22:961–992.
- Purvis OW, Seaward MRD, Loppi S. 2007. Lichens in a changing pollution environment: an introduction. *Env Poll* 146:291–292.
- Qu WY, Zhang YZ, Manry D, Southwick CH. 1993. Rhesus monkeys (*Macaca mulatta*) in the Taihang mountains. Jiayuan County, Henan, China. *Int J Primatol* 14:607–621.
- Raven PH, Wu ZY. 1994–2005. *Flora of China*. Beijing: Science Press.
- Richardson DHS, Young CM. 1977. Lichens and vertebrates In: Seaward MRD, editor. *Lichen ecology*. London: Academic Press.
- Rodman PS. 1988. Resources and group sizes of primates. In: Slobodchikoff CN, editor. *The ecology of social behavior*. San Diego: Academic Press. p 83–108.
- Rominger EM, Oldemeyer JL. 1990. Early-winter diet of woodland caribou in relation to snow accumulation. Selkirk Mountains, British Columbia, Canada. *Can J Zool* 68:2691–2694.
- Rominger EM, Robbins CT, Evans MA. 1996. Winter foraging ecology of woodland caribou in northeastern Washington. *J Wildl Manage* 60:719–728.
- Rosenberger AL. 1992. Evolution of feeding niches in the New World Monkeys. *Am J Phys Anthropol* 88:525–562.
- Russon AE, Begun DR. 2004. Evolutionary origins of great ape intelligence: an integrated view. In: Russon AE, Begun DR, editors. *The evolution of thought: evolutionary origins of great ape intelligence*. Cambridge: Cambridge University Press. p 353–368.

- Sayers K, Norconk M. 2008. Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. *Int J Primatol* 29:509–530.
- Schülke O, Chalise MK, Koenig A. 2006. The importance of ingestion rates for estimating food quality and energy intake. *Am J Primatol* 68:951–965.
- Seaward MRD. 1987. Effects of quantitative and qualitative changes in air pollution on the ecological and geographical performance of lichens. In: Hutchinson T, Meema K, editors. The effects of atmospheric pollutants on forests, wetlands and agricultural ecosystems. Berlin: Springer. p 439–450.
- Sharnoff S, Rosentreter R. 1998. Lichen use by wildlife in North America. Available at: <http://www.lichen.org/fauna.html>.
- Sinha A, Kumar RS, Datta A, Madhusudan MD, Mishra C. 2006. In search of the Munzala: behavioural ecology and conservation of a newly-discovered primate, the Arunachal Macaque *Macaca munzala*, in western Arunachal Pradesh, north-eastern India. *Int J Primatol* 27, Suppl 1: Abstr. #429.
- Smith SJ, Pitcher H, Wigley TML. 2001. Global and regional anthropogenic sulfur dioxide emissions. *Glob Planetary Change* 29:99–119.
- Srivastava A. 2006. Ecology and conservation of the golden langur. *Trachypithecus geei*, in Assam, India. *Prim Cons* 21:163–170.
- Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited. *Behav Ecol Sociobiol* 49:100–110.
- Stephens DW, Krebs JR. 1986. Foraging theory. Princeton: Princeton University Press.
- Strier KB. 1991. Diet in one group of woolly spider monkeys, or muriquis (*Brachyteles arachnoides*). *Am J Primatol* 23:113–126.
- Struhsaker TT, Leland L. 1977. Palmtree smashing by *Cebus a. apella* in Colombia. *Biotropica* 9:124–126.
- Su Y, Ren R, Yan K, Li J, Zhou Y, Zhu Z, Hu Z, Hu Y. 1998. Preliminary survey of the home range and ranging behavior of golden monkeys (*Rhinopithecus roxellana*) in Shennongjia National Natural Reserve, Hubei, China. In: Jablonski NG, editor. The natural history of the doucs and snub-nosed monkeys. Singapore: World Scientific Press. p 255–268.
- Sugiyama Y. 1976. Characteristics of the ecology of the Himalayan langurs. *J Hum Evol* 5:249–277.
- Suzuki A. 1965. An ecological study of wild Japanese monkeys in snowy areas-focused on their food habits. *Primates* 10:103–148.
- Tan CL. 2000. Behavior and ecology of three sympatric bamboo lemur species (genus *Haplemur*) in Ranomafana National Park, Madagascar. Ph.D. thesis. State University of New York at Stony Brook.
- Teas J, Richie T, Taylor H, Southwick C. 1980. Population patterns and behavioral ecology of rhesus monkeys (*Macaca mulatta*) in Nepal. In: Lindburg DG, editor. The macaques: studies in ecology, behavior and evolution. New York: Van Nostrand Reinhold. p 247–262.
- Terborgh J, Goldizen AW. 1985. On the mating system of the cooperatively breeding saddle-backed tamarin (*Saguinus fuscicollis*). *Behav Ecol Sociobiol* 16:293–299.
- Terry EL, McLellan BN, Watts GS. 2000. Winter habitat ecology of mountain caribou in relation to forest management. *J Appl Ecol* 37:589–602.
- Thomas DC. 1990. Moose diet and use of successional forests in the Canadian Taiga. *Alces* 26:24–29.
- Unknown. 1972. Iconographia Cormophytorum Sinicorum. Beijing: Science Press.
- Ustinov SK. 1969. On the feeding of *Moschus moschiferus* L. and its adaptations to conditions for food searches. *Zool Zh* 48:1558–1563.
- van Schaik CP. 1989. The ecology of social relationships amongst female primates. In: Standen V, Foley RA, editors. Comparative socioecology: the behavioural ecology of humans and other mammals. Oxford: Blackwell. p 195–218.
- van Schaik CP, Brockman DK. 2005. Seasonality in primate ecology, reproduction, and life history: an overview. In: Brockman DK, van Schaik CP, editors. Seasonality in primates: studies of living and extinct human and non-human primates. New York: Cambridge University Press. p 3–20.
- van Schaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Ann Rev Ecol Syst* 24:353–377.
- van Schaik CP, van Noordwijk MA. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour* 105:77–98.
- Vedder A, Fashing PJ. 2002. Diet of a 300-member Angolan colobus monkey (*Colobus angolensis*) supergroup in the Nyungwe Forest, Rwanda [abstract]. *Am J Phys Anthropol Suppl* 34:159.
- Wada K. 1964. Some observations on the life of monkeys in a snowy district of Japan. *Physiol Ecol* 12:151–174 (in Japanese).
- Wada K, Ichiki Y. 1980. Seasonal home range use by Japanese monkeys in the Shiga Heights. *Primates* 21:468–483.
- Wang L-S. 2004. *Bryoria confusa* (lichenized Ascomycota, Parmeliaceae) as a food for man and monkey in Sichuan and Yunnan, China. *Lichenology* 3:25–26.
- Wangchuk T, Inouye DW, Hare MP. 2003. A new subspecies of golden langur (*Trachypithecus geei*) from Bhutan. *Folia Primatol* 74:104–108.
- Waterman PG, Kool KM. 1994. Colobine food selection and plant chemistry. In: Davies AG, Oates JF, editors. Colobine monkeys: their ecology, behaviour, and evolution. Cambridge: Cambridge University Press. p 251–284.
- Watts DP. 1984. Composition and variability of mountain gorilla diets in the Central Virungas. *Am J Primatol* 7:323–356.
- Westoby M. 1978. What are the biological bases of variable diets? *Am Nat* 112:627–631.
- Whiten A, Byrne RW, Henzi SP. 1987. The behavioral ecology of mountain baboons. *Int J Primatol* 8:367–388.
- Wrangham RW. 1979. On the evolution of ape social systems. *Soc Sci Inf* 18:334–368.
- Wrangham RW. 1980. An ecological model of female bonded primate groups. *Behaviour* 75:262–300.
- Wright BW, Ulibarri L, O'Brien J, Sadler B, Prodhon R, Covert HH, Nadler T. 2008. It's tough out there: variation in the toughness of ingested leaves and feeding behavior among four Colobinae in Vietnam. *Int J Primatol* 29:1455–1466.
- Wu B. 1991. Survey and analysis of feeding habits of *Rhinopithecus bieti*. *Acta Anthropol Sin* 10:357–371 (in Chinese with English abstract).
- Xiang Z-F. 2005. The ecology and behavior of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*, Colobinae) at Xiaochangdu in Honglaxueshan National Nature Reserve, Tibet, China. Ph.D. thesis. Kunming Institute of Zoology, Kunming.
- Xiang Z-F, Huo S, Xiao W, Quan R-C, Grueter CC. 2007. Diet and feeding behavior of *Rhinopithecus bieti* at Xiaochangdu, Tibet: adaptations to a marginal environment. *Am J Primatol* 69:1141–1158.
- Yang S, Zhao Q-K. 2001. Bamboo leaf-based diet of *Rhinopithecus bieti* at Lijiang, China. *Folia Primatol* 72:92–95.
- Yeager CP, Kool K. 2000. The behavioral ecology of Asian colobines. In: Whitehead PF, and Jolly CJ, editors. Old world monkeys. Cambridge: Cambridge University Press. p 497–521.
- Zhao Q-K. 1994. Seasonal changes in body weight of *Macaca thibetana* at Mt. Emei, China. *Am J Primatol* 32:223–226.
- Zhao Q-K. 1996. Etho-ecology of Tibetan macaques at Mount Emei, China. In: Fa JE, Lindburg DG, editors. Evolution and ecology of macaque societies. New York: Cambridge University Press. p 263–289.
- Zweifel N, Bastian M. 2007. Geographic variation in orangutan diet: how important is culture? In: Vančátová M, Vančáta V, editors. Book of abstracts of the 2nd Congress of the European Federation for Primatology. Prague. p 66.