ORIGINAL ARTICLE

Overwintering strategy of Yunnan snub-nosed monkeys: adjustments in activity scheduling and foraging patterns

Cyril C. Grueter · Dayong Li · Baoping Ren ·
Ming Li

Abstract Temperate forests are characterized by pronounced climatic and phenological seasonality. Primates inhabiting such environments experience prolonged resource scarcity and low ambient temperatures in winter and are expected to adjust time allocation and foraging behavior so as to maintain their energy balance. We analyzed the activity scheduling of a group of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) based on data collected over 20 months in the high-altitude (>3000 m) Samage Forest, Baimaxueshan Nature Reserve, PRC. The forest consists of evergreen conifers and oaks and deciduous broadleaf trees. The diet varied seasonally, with young leaves preferentially exploited in spring and fruits in summer. The monkeys subsisted on readily available fallback resources (mainly lichens) in winter [Grueter et al. in (Am J Phys Anthropol 140:700–715, 2009)]. We predicted that this switch to a relatively low-quality diet would prompt an increase in feeding effort and decrease in moving effort. We found that the monkeys spent significantly more time feeding in winter than in the other seasons. The monthly time devoted to feeding was also negatively correlated with temperature and positively with percentage of lichens in the diet. Time spent on moving did not vary among seasons or with temperature, but day-journey length was found to be longer on hotter days. Time spent resting was lower in winter and under colder conditions and was also negatively correlated with time spent feeding, indicating that resting time is converted into feeding time during times of ecological stress. These results indicate a strong effect of seasonality on time allocation patterns, constraints on inactivity phases, and the prevalence of an energy-conserving foraging strategy in winter, when costs of thermoregulation were high and the availability of preferred food was low.

Keywords *Rhinopithecus* · China · Foraging strategy · Time budget · Temperate forest

C. C. Grueter (✉)
School of Anatomy, Physiology and Human Biology,
The University of Western Australia, Crawley,
WA 6009, Australia
e-mail: cyril.grueter@uwa.edu.au

D. Li
College of Life Sciences, China West Normal University,
Nanchong 637002, Sichuan, China

B. Ren · M. Li
Key Laboratory of Animal Ecology and Conservation Biology,
Institute of Zoology, Chinese Academy of Sciences,
Beijing 100101, China

Introduction

Primates—indeed all animals—are expected to display an array of adaptive behavioral strategies geared at maintaining their energy balance under variable environmental condition. Numerous studies have shown that primates fine-tune time allocation and ranging effort to the prevailing environmental conditions, most notably food availability and climate (Clutton-Brock 1974; Robinson 1986; Strier 1987; Menon and Poirier 1996; Bocian 1997; Doran 1997; Overdorff et al. 1997; Di Fiore and Rodman 2001; Vasey 2005; Zhou et al. 2007; Masi et al. 2009; N'guessan et al. 2009; González-Zamora et al. 2011). Primates basically have two options when attempting to maintain their daily energy balance (or at least minimize energetic deficits) when faced with a decrease in primary food availability. (1) They invest in traveling that is performed to locate preferred foods (high-return strategy) which, however, entails higher energetic costs and caloric expenditure (MacKinnon 1974;

Milton 1980; Boinski 1987; Barton et al. 1992; Henzi et al. 1992; Palacios and Rodriguez 2001; Sayers and Norconk 2008; Harris et al. 2010). (2) They decrease the distance traveled and/or time spent on traveling and often concomitantly modify their dietary spectrum to incorporate lesser-quality food items (energy expenditure minimization strategy) (Raemaekers 1980; Nakagawa 1989a; Doran 1997; Fleury and Gautier-Hion 1999; Di Fiore and Rodman 2001; Ganas and Robbins 2005; Vasey 2005; Fan and Jiang 2008; Fan et al. 2012). An extreme version of this strategy would be torpor or hibernation, as in cheirogaleid primates (Dausmann et al. 2004). Differential strategies to cope with food scarcity in different seasons have also been recorded (e.g., Ménard and Vallet 1997). The strategy chosen by a particular primate depends on dietary repertoire, digestive needs and capacities, body size, food availability, distribution, and quality. Other factors such as group size (Isbell and Young 1993; Teichroeb et al. 2003) and reproductive state can also influence activity allocation (Dunbar and Dunbar 1988; Matsumoto-Oda and Oda 2001; Dias et al. 2011).

Foraging strategies are bound to differ between tropical- and temperate-living primates, for they occupy fundamentally different habitats. Forested biota in the temperate zone are more marginal in terms of overall primary biomass (Dixon et al. 1994), fruit production (Hanya and Aiba 2010), and the duration of the fruiting season (Ting et al. 2008). Temperate environments are also characterized by striking variations in ambient temperature (e.g., Li et al. 2008), daylight hours (e.g., Ren et al. 2009a) and availability of phenophases (e.g., Grueter et al. 2009), and we would expect primates to show clear behavioral adjustments to such fluctuations in climatic, photoperiodic, and dietetic seasonality. A high-return foraging strategy is usually not an option for temperate-living primates, as profitable resources are virtually absent in their winter habitat (but see Curtin 1975; Sayers and Norconk 2008). Instead, we would anticipate an energy-saving foraging strategy in winter, i.e., a reduction in moving time or a decrease in moving distance (Guo et al. 2007; Mendiratta et al. 2009). Travel generally makes up the largest fraction of an animal's expenditure of nonbasal metabolic energy, and costs associated with relocation are exacerbated when moving up and down steep slopes (Lachica et al. 1997; Hanna 2006). Most temperate-living primates such as some snub-nosed monkey and macaque species are semi-terrestrial or terrestrial and typically live in hilly terrain (Neville 1968; Kirkpatrick and Long 1994; Izumiyama et al. 2003; Grueter et al. 2012b), where a reduction in moving effort would likely entail substantial energetic savings.

Time is a critically limited commodity (Dunbar 1992; Dunbar et al. 2009), and may impact the activity budgets of primates in temperate environments. Short day periods in winter limit the essential activities that can be performed, and scarce food resources and low temperatures create a situation where primates face energetic stress which they may counter by increased feeding effort. Since time is limited, any additional feeding time would have to be taken at the expense of resting time. While some resting is physiologically compulsory for thermoregulation and digestion, some is essentially spare time to be used for inactivity, and it is this latter time that theoretically can be converted into extra feeding time (Dunbar 1992; Dunbar et al. 2009).

The Yunnan snub-nosed monkey (*Rhinopithecus bieti*) is an endangered (IUCN 2011) species that is endemic to China and the Tibetan Autonomous Region, living at the eastern edge of the Tibetan plateau (Kirkpatrick 1995). These monkeys occupy the highest altitude of any nonhuman primate (Long et al. 1994; Grueter et al. 2012c), dwelling mostly in alpine mixed broadleaf-conifer and pure conifer forests, where they experience marked oscillations in resource availability due to seasonal changes in temperature and precipitation. Winter is "lean time," when overall resource scarcity is most severe, and fall is "feast time," when fruits are exploited heavily (Grueter et al. 2009). Through several studies it has been established that *R. bieti* turn to fallback resources in winter, or—more specifically—that they increase the amount of time spent feeding on staple fallback foods in times when preferred food resources are absent (Xiang et al. 2007; Grueter et al. 2009). These fallback foods are lichens, which are low quality in the sense that they contain few proteins and are slowly acquired, although they are rich in nonstructural carbohydrates (Kirkpatrick et al. 2001). *Rhinopithecus bieti* and the related Sichuan snub-nosed monkey (*R. roxellana*) have also been shown to modify their activity budgets during periods of climatic and nutritional stress. Among the responses identified are an increase in resting in winter (Ding and Zhao 2004), a decrease in resting on cold days (Xiang et al. 2010a), more feeding and less moving in winter (Guo et al. 2007), and less moving in the cold season (Li 2009). Several studies documented shorter group day-journey lengths in winter when temperatures plunged (Tan et al. 2007; Ren et al. 2009a; Xiang 2005).

Here, we attempt to elucidate a set of adaptive strategies found in this species to deal with an unfavorable seasonal climate and meagre availability of preferred foods. We test two non-mutually-exclusive hypotheses. The *energy-conserving hypothesis* posits that a switch to a relatively low-quality diet prompts an increase in time spent feeding and a decrease in time spent moving. Based on a limited data set, we also test the assumption that day-journey length decreases in winter relative to other seasons. The *time budget constraint hypothesis* posits that a reduction in resting time in winter ensues as a consequence of enhanced foraging needs.

Methods

Study site

This study was conducted between September 2005 and July 2007 in the Samage Forest of Baimaxueshan Nature Reserve, near the village of Gehuaqing in Yunnan Province, PRC (27°34′N, 99°17′E). The terrain at the field site is rugged, with steep slopes and deep valleys. The research area encompasses around 40 km² of forest interspersed with cattle grazing land and ranges in altitude from 2500 to 4000 m (Fig. 1). The total annual rainfall (average of 2005/06 and 2006/07) was 1004 mm and the mean annual temperature was 14.3 °C at the research station at 2450 m (estimated to be around 10 °C within the core area of the range of the study group at 3200 m). Climate varied strikingly with season: winters (December–February) were dry and cold, with a mean ambient temperature of 8.1 °C and total rainfall of only 80 mm, while in summer (June–August) the temperature rose to 20.6 °C and rainfall totaled 470 mm (for details on the climate, see Grueter et al. (2009). Several habitat types have been identified at the study site. Subtropical evergreen forest, confined to wet valleys and pine forest, dominates lower dry slopes (for details on the habitat,

see Li et al. 2008). Pure fir forest tends to take over from mixed forest (with spruce, hemlock, and firs as the dominant gymnosperms, and bamboo and rhododendron featuring in the shrub layer) above ca. 3500 m. Parts of the Samage Forest have been selectively logged, and various human activities such as grazing of cattle and goats and harvesting of nontimber forest products take place inside the reserve. Day length, i.e., the period from time of sunrise to time of sunset (Garmin® eTrex Summit), varied from 10.5 h in December to 13.8 h in June (Fig. 2).

The study group (Gehuaqing group) numbered approximately 410 animals and was partitioned into smaller "harem" subunits containing one male and several females and adolescents (Grueter et al. 2012a). The group is semi-habituated and occupied a home range of 32 km² over the course of 15 months (Grueter et al. 2008). The monkeys' annual diet was composed of 67 % lichens, 16 % young foliage and buds, and 11 % fruits. The diet varied tremendously among seasons: lichens represented the only significant dietary constituent in winter and were eaten in varying quantities throughout the year. The relative dependence on lichens was inversely related to the availability of fruits (which showed a phenological peak in August and September) and young leaves (which were most common in April and May) (Grueter et al. 2009; see also Kirkpatrick and Grueter 2010).

Data collection

Behavioral observations were conducted on 116 days spread relatively evenly across the study period and across seasons, but success in locating the group tended to be higher in spring and summer, when climatic extremes (monsoon rains, snow cover) were less common. A total of 456 observation hours were reached by the end of the study. Total observation hours achieved per season were 148 in spring, 61 in summer, 164 in fall, and 83 in winter.
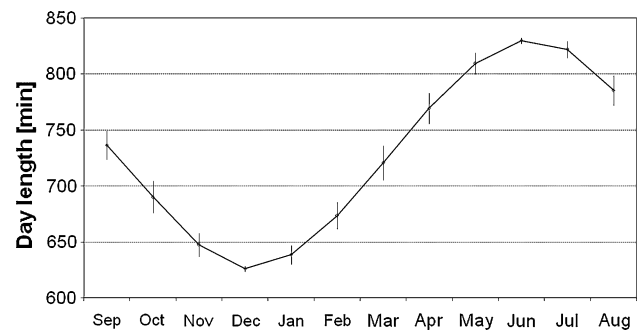

Fig. 1 Topographic map of the study area (delineated by the *dotted line*) in the southern section of Baimaxueshan National Nature Reserve in Yunnan. The *points* represent locations where the study group was recorded during the study period

Fig. 2 Seasonal variation in day length in Gehuaqing, Yunnan (*vertical lines* are standard deviations). Day length was obtained from a Garmin® eTrex Summit GPS receiver. Seasons were defined as spring (March–May), summer (June–August), fall (September–November), winter (December–February)

Observations usually commenced around 9 or 10 am and came to an end when the group moved out of reach or retreated to its sleeping trees. Data were collected with the aid of spotting scopes and binoculars, as the distance from the observer to the group was on average more than 200 m.

Scan sampling (Altmann 1974; Lehner 1996) was the method of choice to quantify the allocation of individuals to different activities. Large spread of the group, dense vegetation, and the semi-terrestrial habitus of the monkeys (Grueter et al. 2012b) resulted in only a fraction of the animals being visible in any given scan. Scans were usually taken every 15 min, but whenever a relatively large number of animals (usually >20) was in view, a 30 min interval was chosen so as to allow a sufficient lag time before commencing a new scan. The behavior and age–sex class of each visible animal was recorded during a scan. The main activity categories used for the purpose of this paper were resting, feeding, and moving. *Resting* included instances of when a monkey was apparently stationary or sleeping, usually while sitting or lying down. Huddling was considered a subcategory of resting and was defined as resting while encompassing another individual with both arms or being encompassed in this manner by another individual. *Moving* included any locomotor behavior, including walking or running that resulted in a monkey changing its spatial position. *Feeding* was defined as searching for, inspecting, and picking food off plants with hand or mouth, manipulating food, putting food into the mouth, and chewing. Feeding did not include inactivity during feeding sessions. Additional behaviors (vigilance, play, grooming, aggression, display) were subsumed under "miscellaneous." Data on the percentage of time the monkeys spent eating different food categories are presented in Grueter et al. (2009).

Data on daily path length were collected by following the study group from daybreak to nightfall for ten consecutive days in winter (January 14–23, 2007), spring (April 13–22, 2007) and summer (July 12–21, 2007) and 30 consecutive days in the fall (September 1–30, 2006). During these group follows, we took a location record of the group's estimated center every 30 min using a GPS receiver (Garmin® eTrex Summit). *R. bieti* is known to alternate between long-distance movements and concentrated use of relatively small areas (Grueter et al. 2008). Since such uneven ranging may cause biases in monthly estimates of daily travel distance if based on only a few days per month, the following data should be considered preliminary.

Data analyses

In ArcView/ArcGIS® (ESRI), we calculated the daily path length by summing up the distances between each set of sequential coordinates taken at location records. We also calculated the daily range shift, which was defined as the day-to-day straight-line shift of the center of daily home range polygons. The proportional contribution of each behavioral category was calculated for each scan (30 and 15 min scans were lumped together). Proportions were then averaged by month, season (three-month periods), and entire study period.

One-way ANOVA analysis in JMP® 8.0 (SAS Institute Inc.) was used to compare the daily path length in winter with those in the other months. To demonstrate seasonal variation in time allocation to activities, we used day as the unit of analyses for ANOVAs. Using scan as the unit of analyses would have resulted in zero inflation, and month would have resulted in small sample sizes. We visually inspected the distribution of the response variable and its residuals for normality. The assumption of homogeneity of variance was also verified with Levene's test (Sall et al. 2005). We angular transformed the percentage of time spent in different activity categories for ANOVAS. The Tukey–Kramer honestly significant difference was used as an a posteriori procedure for comparing pairs of means after ANOVA (Day and Quinn 1989).

Least squares regression models were run in JMP® to examine the effects of mean monthly temperature and day length on monthly time spent feeding. The importance of lichen in the diet of each month (angular transformed percentages) was included as a covariate in the model. To check if predictors suffered from collinearity, we calculated variance inflation factors (VIF) (Fox and Monette 1992) with the package "car" (Fox 2009) in R (R Development Core Team 2010). Mean monthly temperature and total monthly rainfall were strongly correlated, so we refrained from using both variables in the same model. Standard regression diagnostics were performed as well. Spearman correlation analysis ("cor.test" in R) was used to calculate correlation coefficients for daily path length and climatic variables (monthly rainfall and average monthly temperature), time spent in certain activities (feeding, resting, moving) and monthly temperature, and time spent feeding and resting. Significance levels were set at 0.05.

Results

Time budget

The overall time budget for the entire study period ($n = 1597$ scans) was 38.5 % feeding, 28.5 % resting, 19.1 % moving, and 13.9 % other activities. Time spent resting was significantly different among seasons ($F = 6.87$, $p = 0.0003$, $df = 3, 111$). A Tukey HSD post hoc comparison revealed significant differences in resting time between summer and winter ($p = 0.0001$), fall and
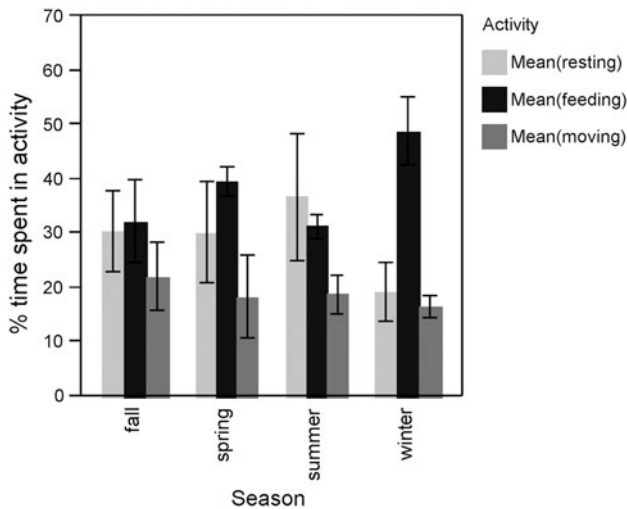
Fig. 3 Seasonal variation in time engaged in various activity states for Yunnan snub-nosed monkeys at Samage. Means and standard deviations are illustrated
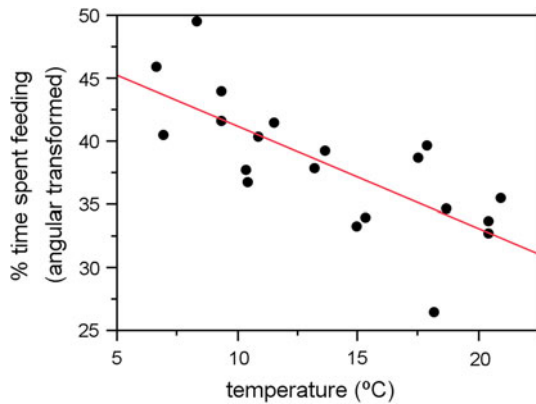

Fig. 4 Correlation between monthly temperature and time spent feeding
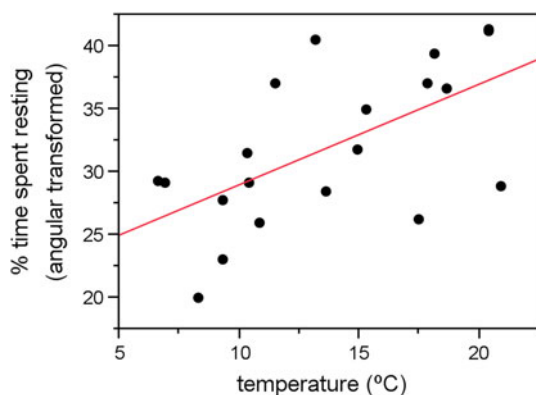

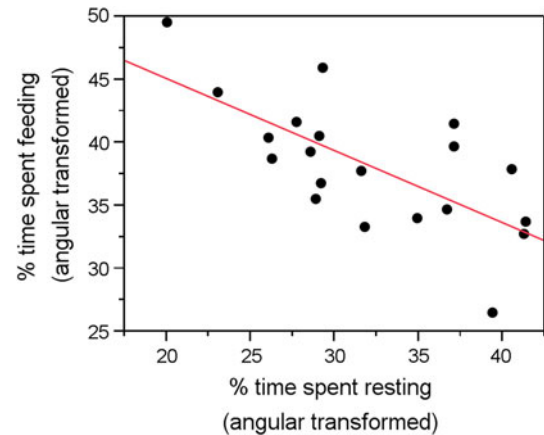**Fig. 5** Correlation between monthly temperature and time spent resting

Fig. 6 Correlation between monthly time spent resting and time spent feeding

winter ($p = 0.0052$) and spring and winter ($p = 0.0146$). Feeding time also differed significantly among the four seasons ($F = 4.62$, $p = 0.0044$, $df = 3, 111$), with significant post hoc results for winter–summer ($p = 0.0098$) and winter–fall ($p = 0.0090$). Moving activity did not show any significant seasonal differences ($F = 1.8075$, $p = 0.1499$, $df = 3,111$) (Fig. 3).

Time spent moving was not significantly correlated with monthly temperature ($\rho = 0.159$, $p = 0.5038$). Time spent feeding showed a highly significant negative correlation with temperature ($\rho = -0.785$, $p = 4.175 \times 10^{-5}$) (Fig. 4). The multiple regression model with time spent feeding as the dependent variable and several predictor variables was significant ($F = 7.0045$, $p = 0.0032$, $df = 3, 16$). Among the set of predictors, neither day length (estimate = 0.019, SE = 0.025, $p = 0.4534$) nor the importance of lichen in the monkeys' diet (estimate = −0.028, SE = 0.058, $p = 0.6362$) influenced time spent feeding, but temperature did (estimate = −1.076, SE = 0.329, $p = 0.0048$): the cooler the temperature, the more the monkeys fed. Time spent resting was positively correlated with temperature ($\rho = 0.557$, $p = 0.01077$) (Fig. 5). There was a statistically significant negative correlation between time spent resting and time feeding ($\rho = -0.644$, $p = 0.002778$) (Fig. 6).

Daily path length

The mean daily path length was 1514 m (range 212–4216 m). Daily path length was shorter in winter than in the other seasons (spring: 1721 m, summer: 1516 m, fall: 1877 m). Daily path length in winter (985 m) was significantly different from that for the rest of the year ($F = 6.426$, $p = 0.016$, $df = 1, 37$). Daily range shift was also shorter in winter (423 m) than in the other seasons (spring: 723 m, summer: 554 m, fall: 576 m). The amount of daily rainfall

did not correlate with daily path length ($\rho = -0.081$, $p = 0.544$), but temperature did ($\rho = 0.267$, $p = 0.041$).

Discussion

Time allocation of primates in a highly seasonal temperate habitat with a clear season of food dearth is expected to be optimized, as this is crucial to satisfying subsistence requirements and avoiding an energy crisis. In particular, we predicted that a higher reliance on a relatively low-quality diet in winter would bring about an increase in feeding effort and a reduction in moving effort (energy-conserving hypothesis). Additionally, we tested the prediction that the increased feeding requirements and the ensuing greater investment in feeding during the lean season would force the animals to sacrifice resting time (time budget constraint hypothesis). Snub-nosed monkeys are prime examples of primates facing severe seasonal climatic and energetic stress. The foraging strategy of the wild Yunnan snub-nosed monkey population under study in the relatively cold winter was characterized by a high dependence on lichens as a fallback resource (Grueter et al. 2009). The time budget of the monkeys was found to be subjected to marked seasonal changes, and most of the findings were in line with our predictions: we detected an increase in time spent feeding during winter. A reduction in moving effort was shown by a shorter daily path length but not reduced time spent moving. A reduction in winter resting time signals time budget constraints acting on the animals in times of energetic stress.

Adjustments in daily path length and time spent moving

Cutting time spent moving and or shortening the daily distance traveled is likely a means by which primates can gain substantial energy savings in the temperate winter (Nakagawa 1989a; Ménard and Vallet 1997; Hanya 2004; Mendiratta et al. 2009). The opposite strategy, i.e., increasing day range and/or time spent traveling, is rarely used by temperate-living primate species (but see Sayers and Norconk 2008). As for *Rhinopithecus*, there is already evidence for seasonal adjustments in moving time: Guo et al. (2007) reported a clear decrease in moving activity for *R. roxellana* at Zhouzhi in winter (21 % of time budget) as compared to spring (38 %), summer (50 %), and fall (37 %). The same was true for *R. bieti* at Tacheng (Ding and Zhao 2004), albeit less pronounced: 12 % moving in winter, 16 % in spring, 20 % in summer, and 14 % in fall. A study on the same subpopulation by Li (2010) also showed that the monkeys spent less time moving in winter than during other seasons, and that time spent moving was also significantly positively correlated with air temperature. However, there was no effect of season on time allocated to

moving in *R. bieti* at Xiaochangdu (Xiang 2005), which showed rather constant proportions of moving time across seasons. Li (2009) found no seasonal differences in the time spent moving by *R. roxellana* at Shennongjia, but the monkeys spent less time moving in the cold season (November–March) than in the warm season. Moreover, a negative correlation between availability of lichens and time spent moving was interpreted as indirect evidence for an energy-saving strategy (ibid.). In general, the finding that less time is spent on energy-consuming activities in winter is in consensus with most previous studies on snub-nosed monkeys.

Day journey length in temperate snub-nosed monkeys has also been shown to vary with seasons and/or temperature, with shorter travel distances in colder months/winter (Kirkpatrick et al. 1998; Tan et al. 2007; Xiang 2007). Similar results were obtained by Li (2002) and Liu et al. (2004), but seasons were lumped into summer/fall and winter/spring. Ren et al. (2009a) also documented shorter winter day journeys in GPS-collared *R. bieti* at Jinsichang, but only when using the classic four-season classification, not when using the apparently more appropriate three-season classification for that site. In the Qingmuchuan population of *R. roxellana*, for which data are available for only two seasons, there was a significant difference in day-journey length between winter (mean: 676 m/day) and summer (mean: 1020 m/day) (Li et al. 2010b).

Kirkpatrick et al. (1998) surmised that the shorter day-range length of the Wuyapiya band of *R. bieti* in winter may reflect a trade-off between the energetic costs of travel and thermoregulation. Even though nonstructural carbohydrates of tree lichens provide energy for year-round travel at Wuyapiya (ibid.), range-use patterns are also influenced by seasonally changing ambient temperatures. Compared to summer (where energetic costs of long-distance travel can be offset by the higher ambient temperature, ibid.), traveling further entails higher energetic costs in the harsh winter climate because of the additional energetic demands of thermoregulation. These high energetic costs ultimately lead to a decrease in daily travel in winter (ibid.). In times of plenty such as late summer/early fall, when fruits are ripe, however, the lack of energetic constraints allows for more extensive travel and the clumped food distribution (fruits) demands longer foraging trips. The energy obtained from ingesting high-quality resources can then create a positive feedback by acting as a catalyst to sustain further travel. Indeed, preliminary evidence points to longer day journeys in Chinese snub-nosed monkeys during periods when the abundance of plant food items is highest (Li 2002; Tan et al. 2007; Li et al. 2010b; Xiang 2005).

Our results showed that the focal group's daily path length decreased in winter, but time spent moving was unaffected by season. This discrepancy could be due to the

fact that some of the moving activity may have happened in a foraging context, i.e., it was performed in order to find food, and was thus treated as "feeding behavior" in the present analysis. Care should also be taken not to treat daily path length as equivalent to home range size when investigating energy conservation with regard to season. The average monthly distance covered by a group of snub-nosed monkeys can be correlated with monthly home range size (Kirkpatrick et al. 1998; Li 2002; Li 2004; see also Ren et al. 2009b), but the two variables are not necessarily interrelated (Tan et al. 2007; Grueter et al. 2008; Li et al. 2010b; this study). This is because a large range is not an indication of great energetic expenditure the way a longer daily path length is. Thus, daily path length may be the most reliable indicator of the energy expenditure that is subjected to thermoregulatory constraints.

While daily temperature had a significant positive effect on the daily distance traveled by the study group, rainfall did not. Raemaekers (1980) found for tropical lar gibbons and siamangs an inverse correlation between rainfall and daily path length, and the same was the case in mountain gorillas (Ganas and Robbins 2005; Grueter et al., unpublished). While the snub-nosed monkeys tended to remain stationary during heavy downpours as well as snowstorms, they still moved around during drizzling rain and light snowfall (Grueter, personal observation). Corresponding to our findings, there was no effect of rainfall on daily path length in the Jinischang group of *R. bieti* (Ren et al. 2009a). Xiang (2005), however, found a significant positive correlation between monthly rainfall and daily path length, but this could have been a spurious pattern driven by the positive correlation between rainfall and food availability. *R. roxellana* at Shennongjia were found to move shorter distances on rainy/snowy days, but only in winter and spring (Li et al. 2005). Possible confounders affecting daily path length are human activities such as mushroom and medicine collection, to which the monkeys respond with escape, leading to longer travel distances (Li et al. 2005; Xiang 2005).

Adjustments in feeding efforts

Increased feeding effort in winter and/or times of low temperature has likely been selected to compensate for a lower quality diet, shorter day length, and/or to gain energy for thermoregulation. An increase in feeding time as a response to low food availability has been documented for various primates, both tropical-living (Doran 1997; Alberts et al. 2005; Zhou et al. 2007; N'guessan et al. 2009; Harris et al. 2010) and temperate-living (Nakagawa 1989b; Agetsuma 1995; Guo et al. 2007; Sayers and Norconk 2008; Mendiratta et al. 2009; but see Ménard and Vallet 1997; Hanya 2004). In the case of *Rhinopithecus*, there is a general tendency for increased food intake in harsh times.

Both *R. bieti* at Tacheng and Xiaochangdu fed more in winter (Tacheng: 37 %, Xiaochangdu: 57 %) than in spring (Tacheng: 31 %, Xiaochangdu: 45 %) and summer (Tacheng: 30 %, Xiaochangdu: 48 %), but not fall (Tacheng: 42 %, Xiaochangdu: 57 %) (Ding and Zhao 2004; Xiang et al. 2010a). Guo et al. (2007) reported a striking increase in feeding activity in a wild group of *R. roxellana* at Zhouzhi in winter (66 %) as compared to the other seasons (spring: 37 %, summer: 26 %, fall: 15 %). Contrary to our results, no significant correlations were found between feeding time and temperature in *R. bieti* at Xiaochangdu (Xiang et al. 2010a). Our multiple regression analysis revealed that temperature explained more variation in monthly feeding time than other variables, implying that feeding effort is maximized under cold conditions, with resulting thermoregulatory benefits.

Under very precarious conditions such as very low temperatures or persistent snowfalls we would expect temperate primates to enhance insulation by reducing feeding time and allotting some of the feeding time to resting. In our study, on January 17 2007, for example, we recorded continuous snowfall throughout the day at the altitude at which the group stayed. Consequently, the group did not show any movements at all on that day and remained at the same position from morning until evening. Japanese macaques in the Shiga Heights sometimes did not move at all under snowy conditions (Wada 1975; Wada and Tokida 1981), and feeding time was reduced on Yakushima when the temperature was low (Hanya 2004). Primates also have the option to delay their morning foraging session on cold days in order to decrease exposure to the elements. *Rhinopithecus bieti* stayed in their sleeping trees longer in winter than during other seasons (Liu and Zhao 2004; Li et al. 2010a) and when there were heavy snowfalls (Li et al. 2010a; Xiang et al. 2010b). Similar observations have been made in Hanuman langurs (Bishop 1975), black spider monkeys (Wallace 2001), and Barbary macaques (Mehlman 1986).

Adjustments in resting time

Resting behavior showed strong seasonal and temperature-related variation, with significantly less time devoted to resting in winter than in the other seasons, and a positive correlation between resting time and temperature. These results correspond to those of other *Rhinopithecus* field studies: Guo et al. (2007) recorded a significantly lower amount of resting behavior in winter, and Xiang et al. (2010a) recorded less resting on colder days. Along the same lines, temperate Arunachal macaques responded to winter stress with reduced resting (Mendiratta et al. 2009). However, a lack of seasonal variation in resting activity was noted in *R. roxellana* at Shennongjia (Li 2009).

Interestingly, two nonsimultaneous studies on *R. bieti* in Tacheng disclosed the opposite pattern: more resting in winter (Ding and Zhao 2004) and a significant negative correlation between resting time and temperature (Li 2010). These findings are striking in light of the fact that the Tacheng group (alternatively referred to as the Xiangguqing group) shares the same forest block with our focal group and thus experiences similar environmental pressures in winter, although human disturbance (including human interference in the ranging and foraging behavior of the Tacheng group) may be at the root of these discrepant findings.

Resting time was negatively correlated with feeding time in the present study, which implies that the need for enhanced feeding acts as a constraint on resting time (cf. Agetsuma and Nakagawa 1998; Li 2009; see also Kurup and Kumar 1993). This result fits with the hypothesis that resting time is a source of spare time that can be converted into extra feeding time (Dunbar 1992; Dunbar et al. 2009). Nevertheless, folivores always require a certain minimum of resting time to ferment their ingesta (cf. van Soest 1982). Li (2009) argued that snub-nosed monkeys may need less resting time for the digestion of lichens, but this seems rather unlikely since leaves (a more typical fallback food for primates) and lichens are considered physiological equivalents in terms of digesta passage (Kirkpatrick et al. 2001).

Cross-site comparisons

Data are scarce, but it appears that more time is invested in food acquisition and less time in resting by *R. bieti* in the relatively unproductive forests of Xiaochangdu in Tibet, where temperatures are lower and lichens are even more important in the monkeys' diet [82 % at Xiaochangdu vs. 67 % at Samage (Xiang et al. 2007; Grueter et al. 2009)] compared to the lusher forests at the more southerly locations Samage/Tacheng and Fuhe (Table 1). The higher percentage of feeding was not related to group-size-associated foraging constraints (cf. Snaith and Chapman 2007), as group size was not correlated with feeding time

($\rho = 0.7$, $p = 0.2333$, $n = 5$; group size data from Grueter 2012). Within-species variation in activity budgets in relation to habitat productivity has also been reported in other primates (Iwamoto and Dunbar 1983; Agetsuma and Nakagawa 1998; Li and Rogers 2004). It has been postulated that this variation is due to either the greater energy requirements needed to maintain a constant body temperature in colder habitats or the lower energy gain rates from low-quality foods (Iwamoto and Dunbar 1983; Agetsuma and Nakagawa 1998). However, interstudy differences in methodology and visibility may also impact the results.

Avenues for future research

How individual energy budgets change across seasons has not yet been assessed in any population of *Rhinopithecus*. Ideally, we would need data on actual food intake/energy intake (instead of time spent feeding as a proxy, cf. Schülke et al. 2006) across seasons to corroborate the findings presented here. Nakagawa (1997) found that daily intake of gross energy in Japanese macaques on Kinkazan was significantly lower in winter than in spring and fall (see also Tsuji et al. 2008, who accentuate that energy balance can vary over shorter time frames and that sporadic data collection every month may not accurately reflect energy balance). Sayers et al. (2010) found that the profitability (energy/handling time or protein/handling time) of Himalayan langur foods taken during late fall, winter, and early spring were considerably lower overall than those taken during the rest of the year. The increase in feeding effort we observed in *R. bieti* during winter may be partly related to the longer handling time and slower acquisition rate of lichens (Kirkpatrick 1996; Kirkpatrick and Grueter 2010).

It is possible that massive fruit ingestion is deposited as fat and thus represents an adaptive overwintering strategy (cf. Zhao 1994; Hanya et al. 2006; Garcia et al. 2011), but this is yet to be demonstrated for snub-nosed monkeys. The kind of behavioral adaptations that primates have evolved to reduce heat loss in cold winter conditions, such as huddling (Takahashi 1997; Li et al. 2010a), basking in the

Table 1 Comparison of the proportions of time allocated to different activities among groups of *R. bieti*

Site (latitude)	Activities (%)				References
	Feed	Move	Rest	Other	
Xiaochangdu (29°15′)	49	20	18	13	Xiang et al. (2010a)
Wuyapiya (28°30′)[a]	32	36	22	10	Kirkpatrick (1996)
Samage (27°34′)	38	19	29	14	This study
Xiangguqing (Tacheng) (27°36′)	35	15	33	17	Ding and Zhao (2004)
Xiangguqing (Tacheng)	39	27	21	13	Li (2010)
Fuhe (26°25′)	30	15	41	14	Liu et al. (2004)

[a] The annual activity budget for Wuyapiya may have been influenced by an underrepresentation of the data collected in winter

sun (Long et al. 1998: Danzy et al. 2011), and selecting weather-protected sleeping sites (Tsuji 2011), also deserve further investigation. So far, physiological approaches to measuring energetic and climatic stress in snub-nosed monkeys in winter have also been untapped. Physiological stress could be assessed by documenting changes in biomarkers such as urinary C-peptides (Harris et al. 2010) and glucocorticoid levels (Beehner and McCann 2008), as well as changes in metabolic rates (cf. Signer et al. 2011).

Conclusion

In this contribution to the theme issue on temperate primates, we explored overwintering strategies of Yunnan snub-nosed monkeys in a strongly seasonal temperate-montane forest habitat in China. The monkeys subsisted primarily on lichens in winter (Grueter et al. 2009), a dietary adaptation to seasonal food scarcity that was accompanied by an increase in feeding effort. There was also some evidence for a decrease in moving effort in winter, as shown by shorter daily path lengths. These results confirm that the most common strategy for primates facing climatic and resource stress in temperate habitats is to alter their dietary spectrum by including lesser-quality fallback foods and to adopt an energy-saving time budget strategy (e.g., Ding and Zhao 2004; Guo et al. 2007; Lai et al. 2012; Mehlman 1986; Ménard and Vallet 1997; Nakagawa 1989a; Kowalewski et al. 2012). We also documented a decrease in resting time in winter, which we interpret as a direct consequence of greater investment in feeding, thus supporting the time budget constraint hypothesis (Dunbar 1992).

References

Agetsuma N (1995) Foraging strategies of Yakushima macaques (*Macaca fuscata yakui*). Int J Primatol 16:595–609

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. Primates 39:275–289

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 DK, van Schaik CP (eds) Seasonality in primates. Cambridge University Press, Cambridge, pp 157–195

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Barton RA, Whiten A, Strum SC, Byrne RW, Simpson AJ (1992) Habitat use and resource availability in baboons. Anim Behav 43:831–844

Beehner JC, McCann C (2008) Seasonal and altitudinal effects on glucocorticoid metabolites in a wild primate (*Theropithecus gelada*). Physiol Behav 95:508–514

Bishop N (1975) Social behavior of langur monkeys (*Presbytis entellus*) in a high altitude environment (Ph.D. dissertation). University of California, Berkeley

Bocian C (1997) Niche separation of black-and-white colobus monkeys (*Colobus angolensis* and *C. guereza*) in the Ituri Forest (Ph.D. dissertation). City University of New York, New York

Boinski S (1987) Habitat use by squirrel monkeys (*Saimiri oerstedi*) in Costa Rica. Folia Primatol 49:151–167

Clutton-Brock TH (1974) Activity patterns of red colobus (*Colobus badius tephrosceles*). Folia Primatol 21:161–187

Curtin RA (1975) The socio-ecology of the common langur, *Presbytis entellus*, in the Nepal Himalaya (Ph.D. dissertation). University of California, Berkeley

Danzy J, Grobler JP, Freimer N, Turner T (2011) Sunning: a behavioral response to seasonal climatic change in South African vervet monkeys. Am J Phys Anthropol 144(Suppl. 52):120

Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2004) Hibernation in a tropical primate. Nature 429:825–826

Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. Ecol Monogr 59:433–463

Di Fiore A, Rodman PS (2001) Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. Int J Primatol 22:449–480

Dias PAD, Rangel-Negrín A, Canales-Espinosa D (2011) Effects of lactation on the time-budgets and foraging patterns of female black howlers (*Alouatta pigra*). Am J Phys Anthropol 145:137–146

Ding W, Zhao Q-K (2004) *Rhinopithecus bieti* at Tacheng, Yunnan: diet and daytime activities. Int J Primatol 25:583–598

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185–190

Doran D (1997) Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. Int J Primatol 18:183–206

Dunbar RIM (1992) Time: a hidden constraint on the behavioral ecology of baboons. Behav Ecol Sociobiol 31:35–49

Dunbar RIM, Dunbar P (1988) Maternal time budgets of gelada baboons. Anim Behav 36:970–980

Dunbar RIM, Korstjens AH, Lehmann J (2009) Time as an ecological constraint. Biol Rev 84:413–429

Fan P-F, Jiang X-L (2008) Effects of food and topography on ranging behavior of black crested gibbon (*Nomascus concolor jingdongensis*) in Wuliang Mountain, Yunnan, China. Am J Primatol 70:871–878

Fan P-F, Ai H-S, Fei H-L, Zhang D, Yuan S-D (2012) Seasonal variation of diet and time budget of eastern hoolock gibbon (*Hoolock leuconedys*) living in a northern montane forest. Primates (this issue)

Fleury M, Gautier-Hion A (1999) Seminomadic ranging in a population of black colobus (*Colobus satanas*) in Gabon and its ecological correlates. Int J Primatol 20:491–509

Fox J (2009) car: companion to applied regression (R package version 1.2–14). http://cran.r-project.org/web/packages/car/

Fox J, Monette G (1992) Generalized collinearity diagnostics. J Am Stat Assoc 87:178–183

Ganas J, Robbins MM (2005) Ranging behavior of the mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda: a test of the ecological constraints model. Behav Ecol Sociobiol 58:277–288

Garcia C, Huffman MA, Shimizu K, Speakman JR (2011) Energetic consequences of seasonal breeding in female Japanese macaques (*Macaca fuscata*). Am J Phys Anthropol 146:161–170

González-Zamora A, Arroyo-Rodríguez V, Chaves OM, Sánchez-López S, Aureli F, Stoner KE (2011) Influence of climatic variables, forest type, and condition on activity patterns of Geoffroyi's spider monkeys throughout Mesoamerica. Am J Primatol 73:1189–1198

Grueter CC (2012) The biology of snub-nosed monkeys, douc langurs, proboscis monkeys and simakobus. Nova, Hauppauge (in press)

Grueter CC, Li D, van Schaik CP, Ren B, Long Y, Wei F (2008) Ranging of *Rhinopithecus bieti* in the Samage Forest, China. I. Characteristics of range use. Int J Primatol 29:1121–1145

Grueter CC, Li D, Ren B, Wei F, Xiang Z, van Schaik CP (2009) Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. Am J Phys Anthropol 140:700–715

Grueter CC, Li D, Ren B, Wei F (2012a) Insights into the social system of Yunnan snub-nosed monkeys. In: Tan CL, Grueter CC, Wright BW (eds) Odd-nosed monkeys: recent advances in the study of the forgotten colobines. Springer, New York

Grueter CC, Li D, Ren B, Xiang Z, Li M (2012b) Substrate use and postural behavior of free-ranging snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan. Integr Zool (accepted)

Grueter CC, Li D, Ren B, Xiang Z, Li M (2012c) Food abundance is the main determinant of high-altitude range use in snub-nosed monkeys. Int J Zool 2012, Article ID 739419

Guo S, Li B, Watanabe K (2007) Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. Primates 48:268–276

Hanna J (2006) Climbing energetic in primates: implications for primate locomotor evolution (Ph.D. dissertation). Duke University, Durham

Hanya G (2004) Seasonal variations in the activity budget of Japanese macaques in the coniferous forest of Yakushima: effects of food and temperature. Am J Primatol 63:165–177

Hanya G, Aiba S-I (2010) Fruit fall in tropical and temperate forests: implications for frugivore diversity. Ecol Res 25:1081–1090

Hanya G, Kiyono M, Yamada A, Suzuki K, Furukawa M, Yoshida Y, Chijiiwa A (2006) Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. Primates 47:275–278

Harris TR, Chapman CA, Monfort SL (2010) Small folivorous primate groups exhibit behavioral and physiological effects of food scarcity. Behav Ecol 21:46–56

Henzi SP, Byrne RW, Whiten A (1992) Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. Int J Primatol 13:601–629

Isbell LA, Young TP (1993) Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. Behav Ecol Sociobiol 32:377–385

IUCN (2011) IUCN Red List of Threatened Species, version 2011.1. http://www.iucnredlist.org. Accessed 5 June 2012

Iwamoto T, Dunbar RIM (1983) Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. J Anim Ecol 52:357–366

Izumiyama S, Mochizuki T, Shiraishi T (2003) Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. Ecol Res 18:465–474

Kirkpatrick RC (1995) The natural history and conservation of the snub-nosed monkeys (genus *Rhinopithecus*). Biol Cons 72:363–369

Kirkpatrick RC (1996) Ecology and behavior of the Yunnan snub-nosed langur (*Rhinopithecus bieti*, Colobinae) (Ph.D. dissertation). University of California, Davis

Kirkpatrick RC, Grueter CC (2010) Snub-nosed monkeys: multilevel societies across varied environments. Evol Anthropol 19:98–113

Kirkpatrick RC, Long YC (1994) Altitudinal ranging and terrestriality in the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). Folia Primatol 63:102–106

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

Kowalewski M, Raño M, Fernández V, Zunino G (2012) Behavioral and ecological adaptations of black and gold howler monkeys living in seasonal forests in Southern South America: the influence of abiotic factors. Primates (this issue)

Kurup GU, Kumar A (1993) Time budget and activity patterns of the lion-tailed macaque (*Macaca silenus*). Int J Primatol 14:27–39

Lachica M, Barroso FG, Prieto C (1997) Seasonal variation of locomotion and energy expenditure in goats under range grazing conditions. J Range Manage 50:234–238

Lai C-M, Lin M-F, Chang C-I, Su H-H (2012) Activity budget and food chemical analysis of Taiwanese macaques (*Macaca cyclopis*) in northern Taiwan. Primates (this issue)

Lehner PN (1996) Handbook of ethological methods, 2nd edn. Cambridge University Press, Cambridge

Li Y (2002) The seasonal daily travel in a group of Sichuan snub-nosed monkey (*Pygathrix roxellana*) in Shennongjia Nature Reserve, China. Primates 43:271–276

Li Y (2004) The effect of forest clear-cutting on habitat use in Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia Nature Reserve, China. Primates 45:69–72

Li Y (2009) Activity budgets in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. Curr Zool 55:173–179

Li D (2010) Time budgets, sleeping behavior and diet of the Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) at Xiangguqing in Baimaxueshan Nature Reserve (Ph.D. dissertation). Northwest University, Xi'an

Li Z, Rogers ME (2004) Habitat quality and activity budgets of white-headed langurs in Fusui, China. Int J Primatol 25:41–54

Li Y, Liao M, Yu J, Yang J (2005) Effects of annual change in group size, human disturbances and weather on daily travel distance of a group in Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia Nature Reserve, China. Biodiv Sci 13:432–438

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 D, Ren B, Grueter CC, Li B, Li M (2010a) Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. Am J Primatol 72:1092–1099

Li Y, Jiang Z, Li C, Grueter CC (2010b) Effects of seasonal folivory and frugivory on ranging patterns in *Rhinopithecus roxellana*. Int J Primatol 31:609–626

Liu Z, Zhao Q (2004) Sleeping sites of *Rhinopithecus bieti* at Mt. Fuhe, Yunnan. Primates 45:241–248

Liu Z, Ding W, Grueter CC (2004) Seasonal variation in ranging patterns of Yunnan snub-nosed monkeys *Rhinopithecus bieti* at Mt. Fuhe, China. Acta Zool Sin 50:691–696

Long Y, Kirkpatrick RC, Zhong T, Xiao L (1994) Report on the distribution, population, and ecology of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). Primates 35:241–250

Long YC, Kirkpatrick RC, Xiao L, Zhong T (1998) Time budgets of the Yunnan snub-nosed monkey (*Rhinopithecus* [*Rhinopithecus*] *bieti*). In: Jablonski NG (ed) The natural history of the doucs and snub-nosed monkeys. World Scientific, Singapore, pp 279–289

MacKinnon J (1974) The behaviour and ecology of wild orangutans (*Pongo pygmaeus*). Anim Behav 22:3–74

Masi S, Cipolletta C, Robbins MM (2009) Western lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. Am J Primatol 71:91–100

Matsumoto-Oda A, Oda R (2001) Activity budgets of wild female chimpanzees in different reproductive states. J Ethol 19:17–21

Mehlman P (1986) Population ecology of the Barbary macaque (*Macaca sylvanus*) in the fir forests of Ghomara, Moroccan Rif Mountains (Ph.D. dissertation). University of Toronto, Toronto

Ménard N, Vallet D (1997) Behavioral responses of Barbary macaques (*Macaca sylvanus*) to variations in environmental conditions in Algeria. Am J Primatol 43:285–304

Mendiratta U, Kumar A, Mishra C, Sinha A (2009) Winter ecology of the Arunachal macaque *Macaca munzala* in Pangchen Valley, Western Arunachal Pradesh, Northeastern India. Am J Primatol 71:939–947

Menon S, Poirier FE (1996) Lion-tailed macaques (*Macaca silenus*) in a disturbed forest fragment: activity patterns and time budget. Int J Primatol 17:969–985

Milton K (1980) The foraging strategy of howler monkeys: a study in primate economics (Ph.D. dissertation). Columbia University Press, New York

N'guessan AK, Ortmann S, Boesch C (2009) Daily energy balance and protein gain among *Pan troglodytes verus* in the Taï National Park, Côte d'Ivoire. Int J Primatol 30:481–496

Nakagawa N (1989a) Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan Island during winter. Primates 30:441–460

Nakagawa N (1989b) Feeding strategies of Japanese monkeys against deterioration of habitat quality. Primates 30:1–16

Nakagawa N (1997) Determinants of the dramatic seasonal changes in the intake of energy and protein by Japanese monkeys in a cool temperate forest. Am J Primatol 41:267–288

Neville MK (1968) Ecology and activity of Himalayan foothill rhesus monkeys (*Macaca mulatta*). Ecology 49:110–123

Overdorff DJ, Strait SG, Telo A (1997) Seasonal variation in activity and diet in a small-bodied folivorous primate, *Hapalemur griseus*, in southeastern Madagascar. Am J Primatol 43:211–223

Palacios E, Rodriguez A (2001) Ranging pattern and use of space in a group of red howler monkeys (*Alouatta seniculus*) in a southeastern Colombian rainforest. Am J Primatol 55:233–251

R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Raemaekers J (1980) Causes of variation between months in the distance traveled daily by gibbons. Folia Primatol 34:46–60

Ren B, Li M, Long Y, Wei F (2009a) Influence of day length, ambient temperature, and seasonality on daily travel distance in the Yunnan snub-nosed monkey at Jinsichang, Yunnan, China. Am J Primatol 71:233–241

Ren B, Li M, Long Y, Wu R, Wei F (2009b) Home range and seasonality of Yunnan snub-nosed monkeys. Integr Zool 4:162–171

Robinson JG (1986) Seasonal variation in use of time and space by the wedge-capped capuchin monkey, *Cebus olivaceus*: implications for foraging theory. Smithson Contr Zool 431:1–60

Sall J, Creighton L, Lehman A (2005) JMP start statistics: a guide to statistics and data analysis using JMP® and JMP IN® software, 3rd edn. SAS Institute Inc., Cary

Sayers K, Norconk MA (2008) Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: diet, activity patterns, and resources. Int J Primatol 29:509–530

Sayers K, Norconk MA, Conklin-Brittain NL (2010) Optimal foraging on the roof of the world: Himalayan langurs and the classical prey model. Am J Phys Anthropol 141:337–357

Schülke O, Chalise M, Koenig A (2006) The importance of ingestion rates for estimating food quality and energy intake. Am J Primatol 68:951–965

Signer C, Ruf T, Arnold W (2011) Hypometabolism and basking: the strategies of Alpine ibex to endure harsh over-wintering conditions. Funct Ecol 25:537–547

Snaith TV, Chapman CA (2007) Primate group size and interpreting socioecological models: do folivores really play by different rules? Evol Anthropol 16:94–106

Strier KB (1987) Ranging behavior of woolly spider monkeys, or muriquis, *Brachyteles arachnoides*. Int J Primatol 8:575–591

Takahashi H (1997) Huddling relationship in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. Primates 38:57–68

Tan CL, Guo S, Li B (2007) Population structure and ranging patterns of *Rhinopithecus roxellana* in Zhouzhi National Reserve, Shaanxi, China. Int J Primatol 28:577–591

Teichroeb JA, Saj TL, Paterson JD, Sicotte P (2003) Effect of group size on activity budgets of *Colobus vellerosus* in Ghana. Int J Primatol 24:743–758

Ting S, Hartley S, Burns KC (2008) Global patterns in fruiting seasons. Glob Ecol Biogeogr 17:648–657

Tsuji Y (2011) Sleeping-site preferences of wild Japanese macaques (*Macaca fuscata*): the importance of nonpredatory factors. J Mammal 92:1261–1269

Tsuji Y, Kazahari N, Kitahara M, Takatsuki S (2008) A more detailed seasonal division of the energy balance and the protein balance of Japanese macaques (*Macaca fuscata*) on Kinkazan Island, northern Japan. Primates 49:157–160

van Soest PJ (1982) The nutritional ecology of the ruminant. Cornell University Press, Ithaca

Vasey N (2005) Activity budgets and activity rhythms in red ruffed lemurs (*Varecia rubra*) on the Masoala Peninsula, Madagascar: seasonality and reproductive energetics. Am J Primatol 66:23–44

Wada K (1975) Ecology of wintering among Japanese monkeys in Shiga Heights and its adaptive significance. Physiol Ecol 16:9–14

Wada K, Tokida E (1981) Habitat utilization by wintering Japanese monkeys (*Macaca fuscata fuscata*) in the Shiga Heights. Primates 22:330–348

Wallace RB (2001) Diurnal activity budgets of black spider monkeys, *Ateles chamek*, in a southern Amazonian tropical forest. Neotrop Prim 9:101–107

Xiang Z (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. dissertation). Kunming Institute of Zoology, Kunming

Xiang Z, Huo S, Xiao W, Quan R, Grueter CC (2007) Diet and feeding behavior of *Rhinopithecus bieti* at Xiaochangdu, Tibet: adaptations to a marginal environment. Am J Primatol 69:1141–1158

Xiang Z, Huo S, Xiao W (2010a) Activity budget of *Rhinopithecus bieti* at Tibet: effects of day length, temperature and food availability. Curr Zool 56:650–659

Xiang Z, Nie S, Chang Z, Wei F, Li M (2010b) Sleeping sites of *Rhinopithecus brelichi* at Yangaoping, Guizhou. Int J Primatol 31:59–71

Zhao Q-K (1994) Seasonal changes in body weight of *Macaca thibetana* at Mt. Emei, China. Am J Primatol 32:223–226

Zhou QH, Wei FW, Huang CM, Li M, Ren BP, Luo B (2007) Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. Int J Primatol 28:657–671