Effect of Group Size on Time Budgets of Sichuan Snub-Nosed Monkeys (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China

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Abstract Group size influences intragroup scramble competition, which in turn influences time budgets in some primates, and may impact age–sex classes differently. There is a great deal of debate about whether folivorous primates, e.g., colobines, experience significant feeding competition. Unlike most colobines, Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) live in extraordinarily large groups and eat mainly lichens supplemented by seasonal plant food. We examined the effect of group size on time budgets in this species by studying two groups of different sizes in the same habitat in Shennongjia National Nature Reserve, China (study periods: August 2006–July 2008 for the larger group, November 2008–July 2009 for the smaller group). Results showed that the distribution of activities throughout the day did not differ between groups, but that time budgets did differ. Specifically, the monkeys spent more time moving and less time resting in the larger group than in the smaller group. Intergroup comparisons for each age–sex class indicated that adult females (but not adult males or juveniles) in the larger group spent more time moving and less time resting, and tended to spend more time feeding compared to those in the smaller group. The results suggested that increased scramble competition was occurring for adult females in the larger group. We provided preliminary evidence for the existence of intragroup scramble competition in *Rhinopithecus roxellana*.

Keywords Activity pattern · Group size · Intragroup scramble competition · *Rhinopithecus roxellana* · Time budget

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Introduction

The benefits and costs of group living in primates are often debated, and intragroup feeding competition has been widely accepted as one of the main costs (Chapman and Chapman 1996; Clutton-Brock and Harvey 1977; Gillespie and Chapman 2001; Teichroeb and Sicotte 2009; Terborgh and Janson 1986; van Schaik 1983; van Schaik and van Hooff 1983; Wrangham 1980). Intragroup feeding competition can reduce the feeding efficiency of group members via direct contests over food resources (contest competition) or reduction of resources without direct conflict (scramble competition) (Chapman and Chapman 2000; Isbell 1991; Janson 1985, 1988a; Saj and Sicotte 2007; van Schaik and van Noordwijk 1988). Whereas contest competition is relatively easy to measure, e.g., displacements over food, it is much more difficult to detect the existence and degree of scramble competition. Many researchers infer scramble competition from a significant effect of group size on time budgets (Overdorff 1996; Saj and Sicotte 2007; Teichroeb *et al.* 2003; van Schaik *et al.* 1983). Specifically, to compensate for reduced feeding efficiency due to a greater number of feeding members, individuals in larger groups spend more time moving and/or feeding, and/or less time resting than those in smaller groups (Fashing *et al.* 2007; Janson 1988b; Symington 1988; Teichroeb *et al.* 2003).

The effect of group size on time budgets may impact age–sex classes differently owing to differential nutritional requirements. In particular, adult females are usually more sensitive to food availability and feeding competition than other age–sex classes because of their higher nutritional requirements, e.g., for lactating and pregnancy. Female black-and-white colobus (*Colobus vellerosus*), for example, were observed to spend more time feeding than males in larger groups, but this difference was not found in smaller groups (Teichroeb *et al.* 2003). In addition, it is important to control for habitat quality when comparing time budgets between groups of different size (Chapman and Chapman 2000; Saj and Sicotte 2007). A larger group may occupy a higher quality habitat than a smaller group, which could compensate for having more mouths to feed. For example, red colobus (*Colobus badius*) tended to live in larger groups in rain forests and moist woodlands than in drier seasonal habitats (Struhsaker 2000). In such cases, the greater number of feeding individuals in a larger group may not necessarily lead to increased scramble competition, and thus variations in time budgets, compared with a smaller group.

There is a great deal of debate about whether folivores experience significant feeding competition (Harris *et al.* 2010; Isbell 1991; Snaith and Chapman 2007). Unlike frugivores, e.g., *Pan troglodytes* and *Ateles* spp., folivorous species, e.g., colobines, tend to adopt an energy conservation strategy, spending more daytime hours resting and feeding because of the low quality and even distribution of foliage (Stanford 1991; Zhou *et al.* 2007). For folivores, living in larger groups may not influence scramble competition within groups and thus may not influence time budgets (Fashing 2001; Isbell 1991; Koenig *et al.* 1998; Yeager and Kool 2000). An increasing body of evidence, however, suggests that scramble competition may be more important than previously anticipated in some folivorous species and populations (Fashing *et al.* 2007; Gillespie and Chapman 2001; Snaith and Chapman 2008; Teichroeb and Sicotte 2009). Black-and-white colobus monkeys (*Colobus angolensis*) in the Nyungwe Forest, Rwanda, for example, lived in groups

larger than those at any other site, and were found to spend more time feeding and moving, and less time resting than *C. angolensis* at any other site (Fashing *et al.* 2007).

The Sichuan snub-nosed monkey (*Rhinopithecus roxellana*), a China-endemic colobine species, diverges from most colobines in various ecological aspects. Unlike most colobines living in tropical or subtropical forests, it lives in temperate forests in the mountainous areas at high altitudes of 1000–4100 m, which have strong seasonality with cold and snowy winters (Kirkpatrick and Grueter 2010; Li *et al.* 2002a; Ren *et al.* 1998a). This species eats mainly lichens (up to 43% of the overall diet), an uncommon food source for primates and other mammals, supplemented by seasonally available plant food (Guo *et al.* 2007; Li 2006). It lives in two-level groups up to several hundred individuals in size with one-male, multifemale units as the basic social and reproductive level (Ren *et al.* 1998b; Tan *et al.* 2007; Yao *et al.* 2011), whereas most colobines live in small groups containing 3–20 individuals (Bennett and Davies 1994; Oates 1994).

Although *Rhinopithecus roxellana* exhibits an unusual diet and lives in extraordinarily large groups, we do not know whether the monkeys experience scramble competition and how group size affects time budgets because all previous studies have been on a single focal group (Guo *et al.* 2007; Li 2009; Lu and Li 2006). Here we compare the time budgets of two groups of different size in the same habitat, to minimize the confounding effects of food quality and distribution on time budgets and infer whether intragroup scramble competition occurs in this species. We also split time budgets by age–sex class, to see whether group size impacts age–sex classes differently.

Methods

Study Site

The Qianjiaping area (*ca*. 60 km^2) of Shennongjia National Nature Reserve, Hubei, China, has a rugged topography with an elevational range of 1500–2663 m. The vegetation is characterized by deciduous broadleaf and evergreen conifer mixed forest. The climate is highly seasonal. The mean temperature at the elevation of 1700 m ranged from –5.5°C in January to 16.3°C in July. The annual rainfall was *ca*. 1800 mm, with the rainy season between July and September (Li 2006).

Focal Groups

We followed two differently sized groups of *Rhinopithecus roxellana* and collected data on their daily activities. Group counts and determination of group composition were conducted when the monkeys crossed open areas or rivers, or during winters when leaves of deciduous plants fell (age–sex class definition: Li 2007). The larger group had been semihabituated and studied periodically since 1999 (Li 2001, 2006, 2007; Li *et al.* 2002b). We studied this group from August 2006 to July 2008 with the exception of December 2006–February 2007 and February 2008. We could approach the group within 20–30 m and obtained eight group counts. The group contained 236 ± SD 38

individuals, including 106 ± SD 12 adult males, 77 ± SD 18 adult females, 35 ± SD 10 juveniles, and 18 ± SD 5 infants. Unfortunately, we lost this group at the end of July 2008 when it ranged out of the study site and we did not contact it again before the end of the study. We looked for other potential focal groups in the same area and found a much smaller group in November 2008. We followed this group through July 2009, with the exception of February 2009. Before this time, we had not observed this group foraging in the study area. The group had never been habituated and studied, and we could approach it only to within about 100 m. We counted the group six times; it contained 62 ± SD 6 individuals, including 23 ± SD 5 adult males, 22 ± SD 3 adult females, 13 ± SD 3 juveniles, and 4 ± SD 3 infants.

Data Collection

We collected behavioral data via instantaneous scans at 30-min intervals by direct visual observation or with binoculars. For each visible individual (excluding infants) in each scan, we determined its behavior first and then used 5 s to determine its age–sex class. We defined feeding as plucking or manipulating food items (including insects under barks or rocks) using the hand(s) or mouth, or chewing food items. We scored moving if the individual was involved in any locational change, e.g., walking, jumping, and climbing. We recorded moving while feeding as feeding. We recorded resting if the individual was not involved in any locational change and not feeding, e.g., sitting, standing, lying, and autogrooming. We recorded socializing if the individual was involved in any interaction between two or more individuals, e.g., allogrooming, fighting, playing, and mating.

This study complied with protocols approved by the Animal Care Committee of the Hubei Provincial Department of Forestry, and adhered to the legal requirements of Shennongjia National Nature Reserve, Hubei, China.

Data Analysis

Before data analysis, we discarded data for the 3 mo of August–October for the larger group because there were no data for the smaller group in these months, and combined the data for the months that were sampled twice for the larger group. Because we did not have scans from dawn to dusk for all observation days, we first divided the daytime hours into 2-h intervals (06:00–18:00 h for November–January and 06:00–20:00 h for March–July). We then calculated 2-h time budgets, i.e., the proportion of records of each behavior among the total records of all behaviors, for each group (the whole group and each age–sex class, respectively), and took the means to estimate time budgets over the study period. We compared 2-h time budgets between the two groups via a Kolmogorov–Smirnov test to see if group size affected the distribution of activities throughout the day. We conducted the same tests for each age–sex class between the two groups. Similarly, we estimated monthly time budgets by averaging 2-h time budgets for each group (the whole group and each age–sex class, respectively). We compared monthly time budgets between the two groups using a Mann–Whitney U test. We conducted the same tests for each age–sex class between the two groups. We performed all tests in SPSS 17.0. Tests were two tailed with a significance level of 0.05.

Results

Overall Time Budgets

We recorded 948 scans over 198 d (monthly range: 6–20 days, 27–151 scans) for the larger group and 859 scans over 127 d (monthly range: 6–25 d, 45–187 scans) for the smaller group. Overall, the monkeys in the larger group spent 28.1% of the day feeding, 39.2% moving, 27.2% resting, and 5.4% socializing, and those in the smaller group spent 25.5% of the day feeding, 34.5% moving, 33.8% resting, and 6.2% socializing (overall time budgets for each age–sex class: Table I).

Activity Pattern Throughout the Day

We found no difference in the distribution of activities throughout the day between the two groups (Kolmogorov–Smirnov test, whole groups: $Z = 0.71$, $P = 0.70$ for feeding; $Z = 0.36$, $P > 0.99$ for moving; $Z = 0.61$, $P = 0.86$ for resting; $Z = 1.20$, $P = 0.11$ for socializing; adult females: $Z = 0.89$, $P = 0.40$ for feeding; $Z = 0.88$, $P = 0.42$ for moving; $Z = 0.84$, $P = 0.48$ for resting; $Z = 1.19$, $P = 0.12$ for socializing; adult males: $Z = 1.01$, $P = 0.26$ for feeding, $Z = 0.59$, $P = 0.88$ for moving; $Z = 0.76$, $P = 0.61$ for resting; $Z = 1.18$, $P = 0.13$ for socializing; juveniles: $Z = 0.69$, $P = 0.72$ for feeding; $Z = 0.42$, $P > 0.99$ for moving; $Z = 0.80$, $P = 0.55$ for resting; $Z = 1.19$, $P = 0.12$ for socializing). Both groups showed a similar activity pattern throughout the day: feeding increased from the early morning (06:00–08:00 h), occurred at a peak level in the morning (08:00–12:00 h), reduced to the lowest level around midday (12:00–14:00 h), increased again and reached another peak in the late afternoon (16:00–18:00 h), and decreased toward the end of the day; moving had the same pattern as feeding, while resting showed the opposite exactly; most socializing occurred around the midday (12:00–14:00 h) and in the early afternoon (14:00–16:00 h) (Fig. 1).

Table I Overall time budgets of two differently sized groups of *Rhinopithecus roxellana* in Shennongjia National Nature Reserve, China (study periods: August 2006–July 2008 for the larger group, November 2008–July 2009 for the smaller group)

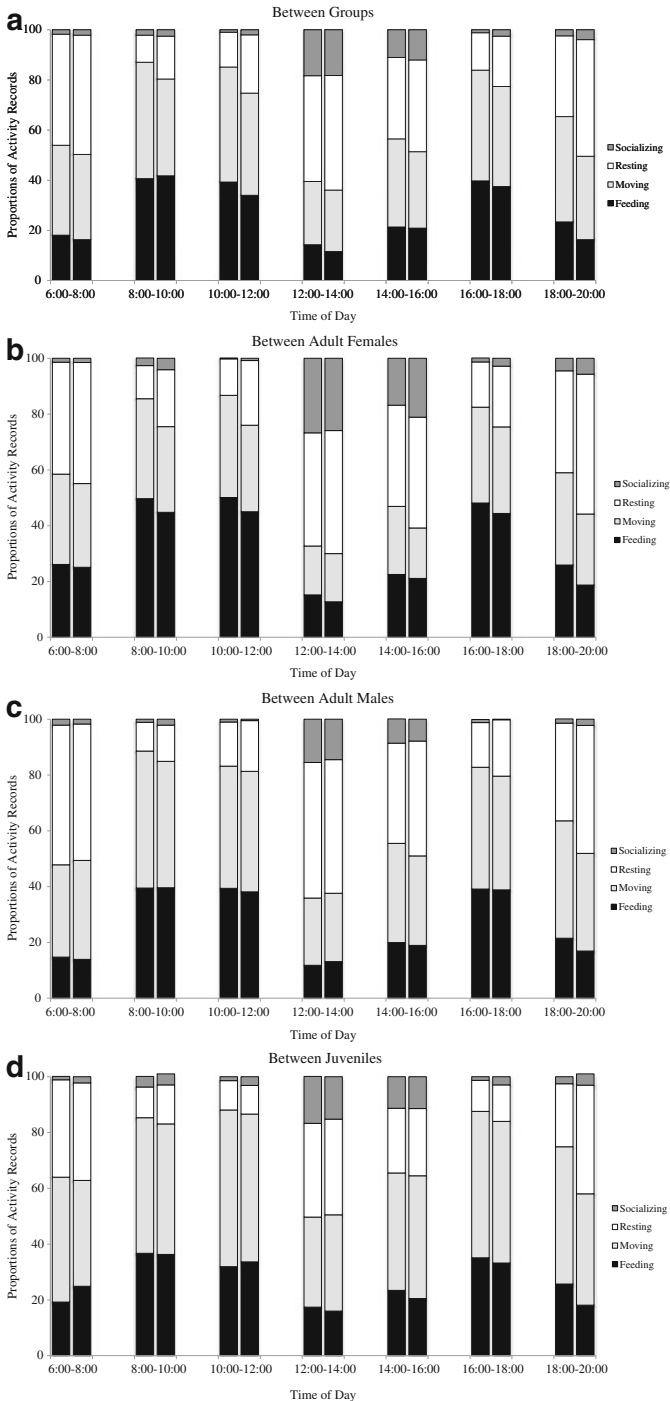|	Age–sex class	Feeding (%)	Moving (%)	Resting (%)	Socializing (%)
Larger group	Whole group	28.1	39.2	27.2	5.4
	Adult females	33.9	30.5	27.8	7.7
	Adult males	26.5	38.8	30.2	4.4
	Juveniles	27.1	46.5	21.0	5.5
Smaller group	Whole group	25.5	34.5	33.8	6.2
	Adult females	30.3	26.2	34.7	8.8
	Adult males	25.6	36.6	33.6	4.1
	Juveniles	26.1	43.8	24.3	6.1

Fig. 1 Comparison of activity pattern throughout the day between two differently sized groups of *Rhinopithecus roxellana* in Shennongjia National Nature Reserve, China (study periods: August 2006–July 2008 for the larger group, November 2008–July 2009 for the smaller group; within each time interval the first bar represents the larger group, the second the smaller group).

Monthly Time Budgets

The monkeys spent more time moving (Mann–Whitney U test, $U = 16.0$, $P < 0.05$, $N = 8$ for both groups) and less time resting ($U = 14.0$, $P < 0.05$) on average in the larger group than in the smaller group. There was no difference in the time spent feeding ($U = 25.0$, $P = 0.31$) or socializing ($U = 38.0$, $P = 0.62$) between the two groups (Fig. 2a).

Adult females spent more time moving ($U = 13.0$, $P < 0.05$, $N = 8$ for both groups) and less time resting ($U = 8.5$, $P < 0.01$), and tended to spend more time feeding ($U = 19.5$, $P = 0.08$) on average in the larger group than in the smaller group. Again, there was no difference in the time spent socializing between the two groups ($U = 36.0$, $P = 0.51$) (Fig. 2b).

There was no difference in the time allocated to any behavior by adult males or juveniles between the two groups (adult males: $U = 37.0$, $P = 0.56$ for feeding; $U = 27.5$, $P = 0.34$ for moving; $U = 33.0$, $P = 0.36$ for resting; $U = 39.5$, $P = 0.75$ for socializing; juveniles: $U = 41.0$, $P = 0.80$ for feeding; $U = 22.0$, $P = 0.19$ for moving; $U = 34.0$, $P = 0.41$ for resting; $U = 43.0$, $P = 0.93$ for socializing; $N = 8$ for both groups) (Fig. 2c, d).

Discussion

The results of this study should be interpreted cautiously. Although we tried to control for the influence of habitat quality by studying two groups of different sizes in the same area, we did not study the two groups at the same time. Food availability and distribution may have differed in the two study periods (August 2006–July 2008 for the larger group and November 2008–July 2009 for the smaller group). Further, we did not control for the amount of data collected in each month and for each group, which may have introduced biases into our results. Nevertheless, we found no effect of group size on the distribution of activities throughout of the day in this study of *Rhinopithecus roxellana* in Shennongjia. The activity pattern throughout the day was similar to previous findings in the Qinling population of this species, with two peaks of feeding and moving in the morning and the afternoon, and one peak of resting and socializing around the midday (Lu and Li 2006). We found a significant effect of group size on time budgets. Specifically, the monkeys spent more time moving and less time resting in the larger group than in the smaller group, suggesting that the individuals in the larger group experienced more scramble competition and lower feeding efficiency. Further, intergroup comparison for each age–sex class showed that adult females spent more moving and less time resting, and tended to spend more time feeding in the larger group than in the smaller group, whereas these differences in time budgets were not found in adult males or juveniles. This result suggested that adult females in the larger group experienced more scramble competition but adult males and juvenile did not. Indeed, the absence of data in August–October and February may have led to an underestimation of feeding competition because in addition to lichens, the monkeys eat mainly fruits and seeds (the most patchily distributed and least available food items) in these months (Li 2006).

The results of this study suggest that adult females in the larger group needed to increase foraging efforts to meet their energetic requirements but adult males and
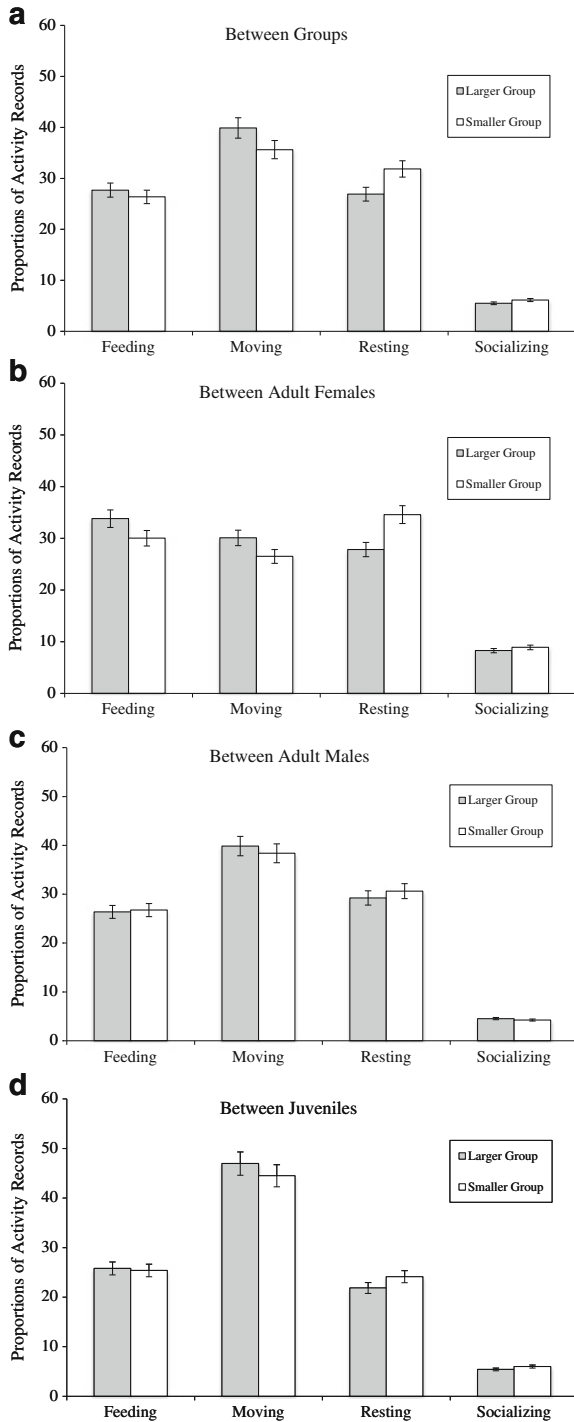
Fig. 2 Comparison of monthly time budgets between two differently sized groups of *Rhinopithecus roxellana* in Shennongjia National Nature Reserve, China (study periods: August 2006–July 2008 for the larger group, November 2008–July 2009 for the smaller group).

juveniles did not need to do so. To compensate for greater energy expenditure, adult females in the larger group could have acquired more energy from the increase in the time spent feeding; alternatively, adult females in the larger group may have increased food intake rates or have taken in food of greater quality (Schülke *et al.* 2006; Zinner 1999). Adult females in the larger group increased foraging efforts probably owing to faster depletion of food patches, i.e., lower encounter rate with food, due to a greater number of feeding members (Chapman and Chapman 2000). In support of this, during the present study, we also conducted a preliminary survey of food distribution for *Rhinopithecus roxellana* at our study site (*unpubl. data*). We found that woody plants accounting for ≥5.0% of the seasonal diet only occupied small proportions of the total tree basal area (varying from 4.2% in summer to 11.5% in winter) and of the total shrub ground cover (varying from 1.3% in autumn to 13.9% in spring), and that only 11.5% of the trees and 18.9% of the shrubs were covered by food lichens. These results were consistent with previous finding of high selectivity for uncommon seasonal plant food items by *Rhinopithecus roxellana* at our study site (Li 2006), and suggested the possibility of easy depletion of food patches.

Another species of the same genus, the Yunnan snub-nosed monkey (*Rhinopithecus bieti*), is also endemic to temperate forests in the mountainous areas of China and lives in large groups composed of several one-male, multifemale units (Kirkpatrick 1996). *Rhinopithecus bieti* has also been observed to eat lichens, and the dietary proportion of lichens ranges from about 60 % to 80% in different populations (Ding and Zhao 2004; Grueter *et al.* 2009a; Kirkpatrick 1996). *Rhinopithecus bieti* in the Samage Forest was observed to be highly selective of diverse seasonal plant food items and completely deplete some food (leaf) patches, suggesting the possible costs of living in large groups (Grueter *et al.* 2009a). Compared to the Samage Forest and Shennongjia, lichens were much more abundant at Wuyapiya and were the primary food for *Rhinopithecus bieti* (Kirkpatrick 1996). Kirkpatrick (1996) hypothesized that *Rhinopithecus bieti* at Wuyapiya experienced very low intragroup scramble competition due to the ubiquitous availability and large patch size of lichens. However, the very slow renewal rate (>15 yr) of lichens implied that lichen patches at Wuyapiya might also be easily depleted (Grueter *et al.* 2009b; Kirkpatrick 1996).

We found no difference in the time spent socializing between the two groups, unlike previous findings in some other species wherein the time spent socializing increased with group size, i.e., potential social partners (Dunbar 1992; Teichroeb *et al.* 2003). The individuals of the same social unit usually stay much closer to each other than to those of other units in *Rhinopithecus roxellana*, and most social interactions occur among the individuals within units (Zhang *et al.* 2006). The frequency of social interactions, therefore, may not be related to the size of a group, but to the number of individuals in a social unit. Unfortunately, we were unable to determine the sizes of social units because individual recognition was difficult in this study.

Conclusion and Future Studies

Our study provided preliminary evidence for the existence of intragroup scramble competition in *Rhinopithecus roxellana*. This may have significant effects on fitness. Individuals may have increased mortality, lower developmental rate, and lower

reproductive rate in larger groups than in smaller groups (Borries *et al.* 2008; Chapman and Chapman 2000; Dittus 1979; Isbell 1991). The following aspects should be considered to obtain a better understanding of this issue in this lichenivorous–folivorous–frugivorous primate. First, food depletion indicators need to be determined, such as patchiness of food distribution, food patch size, and distance between food patches, which directly link with feeding competition (Chapman and Chapman 2000; Isbell 1991). Second, primates may have other ways to cope with energetic demands and intragroup scramble competition in addition to adjusting their time budgets. For example, rest huddling is a way to cope with thermoregulatory costs (Hanya 2004), and was noted both in *Rhinopithecus roxellana* in this study and in *R. bieti* at Wuyapiya (Kirkpatrick 1996). Groups of different sizes and age–sex classes may differ in the frequency of this behavior. Third, with the presence of intragroup scramble competition, individuals in larger groups may also acquire more energy by increasing food intake rates or eating food of greater quality to compensate for greater energetic demands (Schülke *et al.* 2006; Zinner 1999). Fourth, and finally, owing to more rapid depletion of food patches, individuals in larger groups may increase day-range length or home-range size to find adequate food supplies (Chapman and Chapman 2000; Gillespie and Chapman 2001; Isbell 1991; Saj and Sicotte 2007; Teichroeb and Sicotte 2009).

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