

DETERMINANTS OF DIFFERENCES IN THE ACTIVITY BUDGETS OF *RHINOPITHECUS BIETI* BY AGE/SEX CLASS AT XIANGGUQING IN THE BAIMAXUESHAN NATURE RESERVE, CHINA

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Abstract: Ecological factors are known to influence the activity budgets of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*). However, little is known about how activity budgets vary between age/sex classes, because the species is difficult to observe in the wild. This study provides the first detailed activity budgets subdivided by age/sex classes based on observations of the largest habituated group at Xiangguqing in Baimaxueshan Nature Reserve. This study was conducted from June 2008 to May 2009. We found that adult females spent more time feeding (44.8%) than adult males (39.5%), juveniles (39.1%), and infants (14.2%). Adult males allocated more time to miscellaneous activities (12.5%) than did adult females (3.8%). Infants were being groomed 6.9% of the time, which was the highest proportion among all age/sex classes. Adults spent more time feeding, while immature individuals allocated more time to moving and other activities. There are several reasons activity budgets may vary by age/sex class: 1) differential reproductive investment between males and females; 2) developmental differences among the age categories; 3) social relationships between members of different age/sex classes, particularly dominance. In addition, group size and adult sex ratio may also impact activity budgets. These variations in activity budgets among the different age/sex classes may become a selective pressure that shapes the development and growth pattern in this species.

Key words: *Rhinopithecus bieti*; activity budgets; age-sex class; reproductive investment

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INTRODUCTION

The temporal distribution of activities has profound implications for the survival and reproduction of animals (Daan and Aschoff, 1982). Diurnal primates must budget their daylight hours in order to complete necessary activities. Factors influencing primate activity budgets are mainly confined to the distribution and abundance of food resources (Clutton-Brock, 1974; Milton, 1980; Oates, 1987; Strier, 1987; Watts, 1988; Zhou et al., 2007), as well as variation in the ambient environment (Hill et al., 2003; Hanya, 2004).

Body size, social rank, energy consumption, locomotion, reproductive investment, and physiological state differ between age/sex classes and significantly influence the time budget of each animal within a group (Altmann, 1980; Key and Ross, 1999; Takahashi, 2002; Vasey, 2005). For example, immature individuals have higher energetic and nutritional needs than adults (Altmann, 1980), resulting in differences in activity patterns among age classes (Watts, 1988). Gestation and lactation make adult females adjust their activity budgets due to higher nutritional requirements than those of mature males (Cox et al., 2004). Additionally, individuals must adjust their activities to maintain coordination with the movements of the rest of the group (Key and Ross, 1999). When food resources are patchily distributed, the subordinate sex needs to feed for a longer time than the dominant one (Foster and Janson, 1985).

The Yunnan snub-nosed monkey (*Rhinopithecus bieti*) is an endangered colobine monkey inhabiting remnant temperate forests in the Hengduan Mountains in northwestern Yunnan and southeastern Tibet (Long et al., 1994). Natural groups of *R. bieti* are large, multilevel societies consisting of many one-male, multi-female units (OMUs) and associated all-male units (AMUs)

(Grueter and van Schaik, 2010). Currently, there are no systematic data on the differences in activity budgets among age/sex classes because of the challenging topography in their high-altitude habitat; low temperatures and the natural shyness of the monkeys towards humans are additional obstacles to full-day follows.

This study aims to provide the first description of between-age/sex class differences in the activity budgets of habituated *R. bieti* in the wild. We use this new information to determine the most important factors influencing the differences in these activity budgets.

MATERIALS AND METHODS

Study site and study group

This study was conducted on a single *R. bieti* group (ca. 480 individuals) at Xiangguqing (99°22'E, 27°37'N), located in the southernmost region of the Baimaxueshan Nature Reserve, PRC. The study site encompasses an area of almost 90 km², which includes multiple habitat types: mixed coniferous and deciduous broadleaf forest (2900-3600 m), subalpine fir forest (*Abies georgei*, 3500-4000 m), montane sclerophyllous oak forest (*Quercus pannosa*, 3200-3500 m), subtropical evergreen broadleaf forest (*Cyclobalanopsis* spp., 2500-3000 m), and pine forest (*Pinus yunnanensis*, 2500-3100 m). The average annual temperature over the course of the study was 9.8 °C, the lowest temperature being -9.3°C in January 2009 and the highest 27.7°C in July 2008 at 3038 m a.s.l. Annual rainfall during the same period was 1371 mm. Temperature and precipitation were strongly seasonal (Li, 2010). We carried out behavioral observations from June 2008 to May 2009.

The study group inhabits mixed deciduous broadleaf and conifer forest, as well as cool temperate fir forest, between elevations of 2600-4100 m. This group has been well habituated since 2006 and could be approached to 20-30 m almost every day. The group consists of 47-55 OMUs, the largest of which has 16 members, and one AMU including 40-50 adult males and juvenile males; the adult sex-ratio (M/F) is 1:2.9 (Li, 2010).

Data Collection and Analysis

We spent ten full days each month following the monkey group throughout the study. We collected data on monkey behavior from the time the group woke up in the morning until the monkeys entered their nightly sleeping site. Since the group has been habituated, we were usually able to observe it with the naked eye from distance between 10 and 30 m. However, we sometimes observed subjects via binoculars (10×42) at distances between 50 m and 300 m when the monkey group was far away.

We used instantaneous scan sampling at 15-min intervals (Altmann, 1974) to collect behavioral data. We classified individuals into four age/sex classes based on body size and pelage color: 1) adult males were the largest individuals in the group, with long white hair on their flanks obscuring ischial callosities, a strong con-

trast of black and white hair, hair on the top of the head falling forward, and a long and bushy tail; 2) adult females were smaller, with a body length $\leq \frac{1}{2}$ that of adult males, possessing long black nipples and often being found with infants; 3) juveniles' backs and limbs were light grey, and their tail hair was short; 4) infants were the smallest-sized, had gray-white dominated pelage, and were often observed suckling. We categorized monkey behaviors as feeding, moving, resting, grooming, or other (Table 1). Because of the large size of the study group, we could not observe each individual in the forest. Therefore, we only scanned part of the group during each scan interval.

During the study period, we recorded 1 609 hours of observation over 120 days, obtaining 260 410 total activity records. First, we allocated time to each activity in each scan, expressed as the percentage of scanned individuals engaging in each activity category among the total number of individuals recorded in a scan (Harrison, 1985; Agetsuma and Nakagawa, 1998). We treated each scan budget as an independent data point and used it in subsequent analyses to reduce potential biases (Clutton-Brock, 1977). Then, we calculated hourly activity budgets by averaging scan budgets in an hour. Next, we averaged the hourly budgets in a month to construct monthly activity budgets. Finally, we calculated the annual activity budget of the group by averaging monthly budgets.

Table 1. Group behavior and individual maintenance activities recorded during instantaneous scan sampling.

Category	Description
Feeding	Feed from tree, bush and ground, if moving food must be ingested with 5s
Moving	Locomotion on the ground, bush and tree for more than 5s
Resting	Sitting, lying or sleeping in tree, bush and ground more than 5s
Grooming	Individuals groom each other, including in groomer and groomee
Other	Aggression, playing, autogroom, rear inspection, solicitation, copulation, non-sexual mounting, inspect infant, drink water, vocalizing, and some rare behavior, such as eat snow, sexual interference

We used the Kruskal-Wallis test to compare differences in time spent feeding, moving, resting, grooming and other for each age/sex class. One-way ANOVA test was used to determine whether time allocated to each of the five activities differed significantly among the different age/sex classes. We used Spearman's rank correlation to assess the relationship between feeding time and developmental processes among the different months. All statistical analyses were done using SPSS 15.0 for Windows. Each analysis was two-tailed with $P \leq 0.05$.

RESULTS

Activity budgets among different age/sex classes

During the period of study, adult males were scanned 37 109 times. They spent 39.5% of their time feeding, 24.1% moving, 18.1% resting, 5.9%

grooming, and 12.5% in other activities (Table 2). The maximum proportional time spent feeding in a given month was 44.0% in April. In June 2008, the maximum monthly proportion of time spent moving (32.0%) was observed. Males rested the longest (27.5%) in February 2009. The percentages of time allocated to different activities varied significantly (Kruskal-Wallis test, feeding: $\chi^2=37.30$, $p<0.01$; moving: $\chi^2=71.65$, $p<0.01$; resting: $\chi^2=63.54$, $p<0.01$; other activities: $\chi^2=79.05$, $p<0.01$).

Female allocated 44.8% of their time to feeding, significantly more time than was devoted to any other activity. Feeding time was significantly variable between months (Kruskal-Wallis test, $\chi^2=26.46$, $p<0.01$).

FM recorded 85 633 activity scans for juveniles. This class spent 39.1% of the time feeding. Moving, resting, grooming and other comprised 30.9%, 19.4%, 4.3% and 6.3% of the time budget, respectively (Table 2). Their feeding time showed

Table 2. Annual mean percentage of time allocated to different activities among the different age-sex categories (Mean \pm SD).

Age/sex category	Feeding	Moving	Resting	Grooming	Other
Male	39.5 \pm 4.1	24.0 \pm 6.3	18.1 \pm 7.0	5.9 \pm 2.1	12.5 \pm 3.4
Female	44.8 \pm 5.0	25.2 \pm 6.0	20.4 \pm 7.9	5.8 \pm 1.6	3.8 \pm 2.9
Juvenile	39.1 \pm 5.0	30.9 \pm 6.3	19.4 \pm 7.8	4.3 \pm 1.4	6.3 \pm 2.9
Infant	44.2 \pm 8.0	30.2 \pm 7.1	30.8 \pm 12.4	6.9 \pm 2.7	17.9 \pm 7.8

Table 3. Results of one-way ANOVA assessment of age-sex category of *R. bieti* at Xiangguqing from June 2008 to May 2009.

Age/sex category	Feeding		Moving		Resting		Grooming		Other	
	F	P	F	P	F	P	F	P	F	P
M vs FM	70.99	0.000	1.866	0.173	5.762	0.017	0.010	0.921	463.73	0.000
M vs. J	0.346	0.557	71.13	0.000	1.788	0.182	5.021	0.035	353.65	0.000
M vs. I	865.21	0.000	50.44	0.000	94.67	0.000	1.063	0.314	69.12	0.000
FM vs. J	78.65	0.000	52.34	0.000	1.038	0.309	6.357	0.019	7.263	0.008
FM vs. I	1256.38	0.000	35.38	0.000	59.51	0.000	1.452	0.241	402.8	0.000
J vs. I	824.29	0.000	0.645	0.423	72.37	0.000	8.959	0.007	348.34	0.000

marked seasonal variation. They allocated 44.9% of their time to feeding in December 2008, but only 32.8% in November 2008.

Infants only allocated 14.2% of their time to feeding, not including time spent suckling. They spent more time eating plants as they grew (Spearman's rank correlation test, $r=0.949$, $n=12$, $p<0.01$). They also engaged in grooming more often (6.9%) than other age-sex classes.

Variation in activity budgets between age/sex classes

Significant differences were detected in activity budgets among the age/sex categories (Fig. 1). Adult females allocated more time to feeding than other individuals (one-way ANOVA test, $F_{1,119}=70.99$, $p<0.01$ for males; $F_{1,119}=78.65$, $p<0.01$ for juveniles; $F_{1,119}=1256.38$, $p<0.01$ for infants). Meanwhile, adult females spent more time resting than adult males ($F_{1,119}=5.762$, $p<0.05$). Juveniles spent the most time moving (one-way ANOVA test, $F_{1,119}=71.13$, $p<0.01$ for males; $F_{1,119}=52.34$, $p<0.01$ for females). Juveniles allocated less time to grooming than did adults (one-way ANOVA test, $F_{1,119}=5.621$, $p<0.05$ for males; $F_{1,119}=6.357$, $p<0.05$ for females). Owing to their developmental requirements, infant rested more often than other age-sex classes (30.8% of the time, one-way ANOVA test, $F_{1,119}=94.67$, $p<0.01$ for males; $F_{1,119}=59.51$, $p<0.01$ for females; $F_{1,119}=72.37$, $p<0.01$ for juveniles) (Table 3). The results also indicated the time allocated to other activities that are significantly different among the four age/sex categories.

Of 260 546 activity records, there are 145 732 records for adults and 114 814 for immature individuals. Activity budgets were quite different between adults and immature individuals (Fig. 2). Adults allocated much more time to feeding

(one-way ANOVA test, $F_{1,239}=27.27$, $p<0.01$). However, immature individuals spent more time moving ($F_{1,239}=16.62$, $p<0.01$), resting ($F_{1,239}=6.179$, $p<0.05$) and doing other activities ($F_{1,239}=5.466$, $p<0.05$) than adults.

DISCUSSION

As observed in several other primate species (Clutton-Brock, 1977; Masi et al., 2009), activity budgets varied among age/sex classes of *R. bieti* at Xiangqing. In this study, adult females spent more time feeding and resting than males or juveniles. In contrast, adult males allocated more time to other activities than adult females and juveniles. There are several reasons why such differences may arise. Reproductive investments differ considerably between males and females, particularly in mammals. Female reproductive strategies may require them to spend more time feeding, owing to the added energetic costs associated with pregnancy, lactation and infant transport (Demment, 1983; Vasey, 2005). It has been suggested that the energetic requirements of reproduction may affect female activity budgets, especially for animals in which females are smaller than males and therefore have a higher metabolic requirement capacity ratio (Demment, 1983). Female energy requirements increase 25% during pregnancy and 50% during lactation (Portman, 1970). Coelho (1974) and Coelho et al. (1979) reported that a pregnant and lactating female primate's metabolic values and energy costs are estimated to increase 1.25 times and 1.5 times, respectively. A number of studies have suggested females modify their activity budgets during pregnancy or lactation (Dunbar, 1983; Harrison, 1983; Dunbar and Dunbar, 1988; Rose 1994; Stevenson et al., 1994). Female yellow baboons (*Papio cynocephalus*) compensated in various ways to maintain

their energetic requirements (Altmann, 1980). Ruffed lemurs (*Varecia variegata*) that are lactating spend more time feeding than those that are not (Morland, 1990). Sauther (1998) reported that pregnant ring-tailed lemurs (*Lemur catta*) eat more energy rich foods than conspecific males. In this study, *R. bieti* showed significant sex differences in activity budgets of adults that obviously are related to different degrees of reproductive investment. Kirkpatrick et al. (1998) reported that the ratio of infants to adult females in *R. bieti* was 1.0:2.3 at the end of the birth season, which suggests that the interbirth interval is approximately two years. Thus, most adult females observed in a given year are either pregnant or lactating. Females spend more time feeding and resting than males, indicative of both their higher energy requirements and the increased need to conserve energy during pregnancy or lactation.

Differential ability to perform certain activities, special energetic demands at particular stages of development, and unequal energetic costs and benefits lead to changes in activity budgets of individuals age. Juveniles in this study fed similarly to adults. Although juveniles are smaller and weigh less than do adults, the energy required per unit body weight does not decrease (McNab, 1978). Thus, juveniles need to spend enough time feeding to meet the costs of growth (Clutton-Brock, 1977; Key and Ross, 1999). The variation in ability related to age-specific cognitive, memory, and fine motor performance between juveniles and adults influences activity budgets. For instance, studies of Japanese macaques (*Macaca fuscata*) showed juveniles spend a significantly larger proportion of their time searching for food than adult females (Agetsuma, 2001; Hanya et al., 2003). Juvenile *R. bieti* in this study allocated more time to moving than adults, which may indicate they need more time to look for food. Perhaps juveniles are less efficient foragers than adults are. Due to the limita-

tions of development, infants only infrequently fed upon plants in this study. Why did infants spend the most time grooming among all of the age/sex classes in this study? Xi et al. (2008) reported that infant golden snub-nosed monkeys (*R. roxellana*) were cared for by all of the members in their OMU at Zhouzhi, in Shaanxi province. We also found that adult males, adult females, and juveniles in one OMU all groomed the infants in the wild. Thus, they likely have more chances to groom than the other categories.

Finally, the functional and status differences among age/sex classes lead to variation in activity budgets. For example, adult male OMU leaders allocated more time to other activities than adult females at Xiangguqing. They may need to invest more time monitoring the environment for predators, maintaining unit cohesion, preventing infanticide, and mate guarding the females in their OMU. Doran and McNeilage (2001) suggested that male gorillas showed a similar pattern of variation in their activity budgets. Dominance hierarchies determine the activity budgets of various age/sex classes to a certain extent (Foster and Janson, 1985). In gorillas, large dominant males spend less time feeding than do adult females and juveniles, because dominant males are able to exclude the females and juveniles from preferred food patches (Dittus, 1979; Masi et al., 2009). As a result, females may need more time to forage and may also resort to eating some lower-quality foods.

In addition, group size and adult sex ratio also have an important influence on the activity budgets of different individuals. Xiangguqing has the largest troop of *R. bieti* in the wild. The troop is comprised of 47-55 OMUs and an AMU (40-50 adult males and juvenile males), and the adult sex ratio (male vs. female) was 1.0:2.9. The adult sex ratio of *R. bieti* was smaller at Xiangguqing than both conspecifics at Wuyapiya (1.0:3.1) and *R. roxellana*

at Zhouzhi (1.0:3.7) (Kirkpatrick et al., 1998; Tan et al., 2007). During the study period, we observed eight instances of male replacement, in which an existing OMU leader was deposed by a challenger, and we found that males allocated 6.1% of their time to aggressive behaviors at Xiangguqing. Thus, we observed high levels of male-male competition in this group. That adult males spent more time engaged in other activities than adult females may be indicative of this competition.

In summary, variations in activity budgets among the different age/sex classes may become

a selective pressure that shapes the development and growth patterns of this species. The characteristic social functions of individuals in primate groups can determine their behavioral patterns, consequently affecting their activity budgets.

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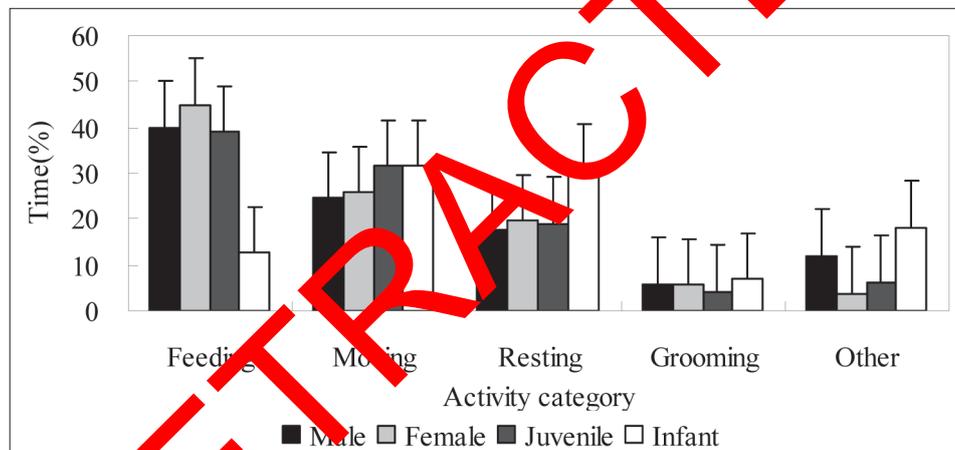


Fig. 1. Proportion of time spent on different activities by age and sex category of *R. bieti* at Xiangguqing from June 2008 to May 2009.

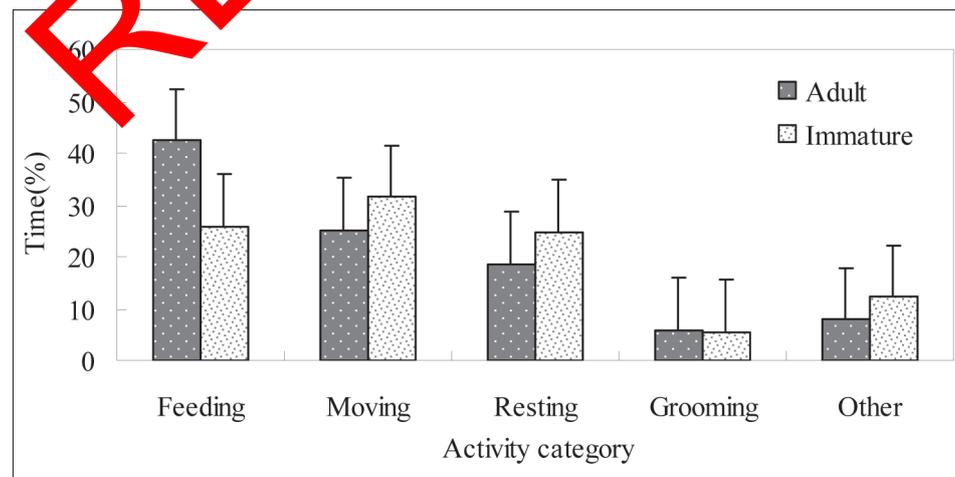


Fig. 2. Comparison of activity budgets between adults and immature individuals of *R. bieti* at Xiangguqing from June 2008 to May 2009.

REFERENCES

- Agetsuma, N. and N. Nakagawa (1998). Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. *Primates* **39**, 275-289.
- Agetsuma, N. (2001). Relation between age-sex classes and dietary selection of wild Japanese monkeys. *Ecol. Res.* **16**, 759-763.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227-267.
- Altmann J. (1980). *Baboon Mothers and Infants*, 242. Harvard University Press, Cambridge
- Clutton-Brock, T.H. (1974). Activity patterns off red colobus (*Colobus badius tephrosceles*). *Folia Primatol.* **21**, 161-187.
- Clutton-Brock, T.H. (1977). Some aspects of intraspecific variation in feeding and ranging behaviour in primates. In: *Primate Ecology*, (Ed. T. H., Clutton-Brock) , 557-579. Academic Press, New York.
- Coelho, A.M. (1974). Socio-bioenergetics and sexual dimorphism in primates. *Primates* **15**, 263-269.
- Coelho, A.M., Bramblett, C.A. and L.B. Quick (1979). Activity patterns in howler and spider monkeys: an application of socio-bioenergetic methods. In: *Primate Ecology and Human Origins: Ecological Influences on Social Organization*, (Eds. I. S. Bernstein and E. O. Smith) , 175-194. Garland, New Daan, S. and J. Aschoff (1982). Circadian contributions to survival. In: *Vertebrate Circadian Systems, Structure and Physiology*, (Eds. J. Aschoff, S. Dassen and G. Groos), 305-321. Springer, New York.
- Demment, M. W. (1983). Feeding ecology and the evolution of body size of baboons. *Afr. J. Ecol.* **21**, 229-233.
- Doran, D.M. and A. McNeilage (2001). Subspecific variation in gorilla behaviour: the influence of ecological and social factors. In: *Mountain Gorillas: Three Decades of Research at Karisoke*, (Eds. M. M. Robbins, P. Sicoff and K. J. Stewart), 123-149. Cambridge University Press, Cambridge.
- Dunbar, R.I.M. (1983). Structure of gelada baboon reproductive units. IV. Integration at group level. *Z. Tierpsychol.* **63**, 265-282.
- Dunbar, R.I.M. and P. Dunbar (1988). Maternal time budget of gelada baboons. *Anim. Behav.* **36**, 970-980.
- Foster, S.A. and C.H. Janson (1985). The relationship between seed size and establishment conditions in tropical woody plant. *Ecology* **66**,773-780.
- Fox, E., van Schaik, C. P., Sitompul, A. and D. Wright (2004). Intra- and interpopulational differences in orangutan (*Pongo pygmaeus*) activity and diet: implications for the invention of tool use. *Am. J. Phys. Anthropol.* **125**,162-174.
- Grueter, C.C. and C.P. van Schaik (2010). Evolutionary determinants of modular societies in colobines. *Behav. Ecol.* **21**, 63-71.
- Hanya, G., Noma, N. and N. Agetsuma (2003). Altitudinal and seasonal variations in the diet of Japanese Macaques in Yakushima. *Primates* **44**, 51-59.
- 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.
- Harrison, M. J. S. (1983). Age and sex differences in the diet and feeding strategies of the green monkey *Cercopithecus sabaecus*. *Anim. Behav.* **31**, 967-977.
- Harrison, M. J. S. (1985). Time budget of the green monkeys, *Cercopithecus sabaecus*: some optimal strategies. *Int. J. Primatol.* **6**, 351-376.
- Hill, R.A., Barrett, L., Gaynor, D., Weingrill, T., Dixon, P., Payne, H. and S. P. Henzi (2003). Day length, latitude and behavioural flexibility in baboons (*Papio cynocephalus ursinus*). *Behav. Ecol. Sociobiol.* **53**, 278-288.
- Key, C. and C. Ross (1999). Sex differences in energy expenditure in non-human primates. *Proc. R. Soc. Lond. B.* **266**, 2479-2485.
- Kirkpatrick, R.C., Long, Y.C., Zhong, T. and L. Xiao (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *Int. J. Primatol.* **19**, 13-51.
- Jiang, D. Y. (2010). Time budgets, sleeping behavior and diet of the Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) at Xianningqing in Baimaxueshan Nature Reserve. Ph.D, dissertation. North West University, Xi'an.
- Long, Y.C., Kirkpatrick, R.C., Zhong, T. and L. Xiao (1994). Report on the distribution, population and ecology of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). *Primates* **35**, 241-250.
- Masi, S., Cipolletta, C. and M. M. Robbins (2009). West lowland gorillas (*Gorilla gorilla gorilla*) change their activity patterns in response to frugivory. *Am. J. Primatol.* **71**, 91-100.
- McNab, B.K. (1978). The energetics of arboreal folivores: the problem of feeding on a ubiquitous food source. In: *The Ecology of Arboreal Folivores*, (Ed. G. Montgomery), 153-162. Smithsonian Institution Press, Washington.
- Milton, K. (1980). The foraging strategy of howler monkeys: a study in primate economics. Columbia University Press, New York.
- Morland, H. S. (1990). Parental behavior and infant development in ruffed lemurs (*Varecia variegata variegata*). *Am. J. Primatol.* **20**, 253-265.
- Oates, J.F. (1987). Food distribution and foraging behavior. In: *Primate societies* ,(Eds. B. B. Smuts, D. L. Cheney, R. N. Seyfarth, R. W. Wrangham and T.T. Struhsaker T.T.), 197-209. University of Chicago Press, Chicago.
- Portman, O.W. (1970). Nutritional requirements of non-human primates. In: *Feeding and Nutrition of Non-human Primates*, (Ed. R.S. Harris), 87-116. Academic Press, New York.
- Rose, L.M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *Int. J. Primatol.* **15**, 95-114.
- Sauter, M. L. (1998). Interplay of phenology and reproduction in ring-tailed lemurs: implications for ring-tailed lemur conservation. *Folia Primatol.* (Suppl) **69**, 309-320.

- Stevenson, P.R., Quinones, M.J. and J.A. Ahumada (1994). Ecological strategies of woolly monkeys (*Lagothrix lagotricha*) at Tinigua National Park, Columbia. *Am. J. Primatol.* **32**, 123-140.
- Strier, K.B. (1987). Activity budget of woolly spider monkeys, or muriquis (*Brachyteles arachnoids*). *Am. J. Primatol.* **13**, 385-395.
- Tan, C.L., Guo, S.T. and B.G. Li (2007). Population structure and ranging patterns of *Rhinopithecus roxellana* in Zhouzhi National Reserve, Shaanxi, China. *Int. J. Primatol.* **28**, 577-591.
- Takahashi, H. (2002). Female reproductive parameters and fruit availability: factors determining onset of estrus in Japanese macaques. *Am. J. Primatol.* **57**, 141-153.
- 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.
- Watts, D.P. (1988). Environmental influences on mountain gorilla time budgets. *Am. J. Primatol.* **15**, 295-312.
- Xi, W.Z., Li, B.G., Zhao, D.P., Ji, W.H. and P. Zhang (2008). Benefits to female helpers in wild *Rhinopithecus roxellana*. *Int. J. Primatol.* **29**, 593-600.
- Zhou, Q.H., Wei, F.W., Huang, C.M., Li, M., Ren, B.P. and B. Luo (2007). Seasonal variation in the activity patterns and time budgets of *Trachypithecus jingxi* in the Nonggang Nature Reserve, China. *Int. J. Primatol.* **28**, 657-671.

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