Differences in the Activity Budgets of Yunnan Snub-Nosed Monkeys (*Rhinopithecus bieti*) by Age-Sex Class at Xiangguqing in Baimaxueshan Nature Reserve, China

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Key Words

Rhinopithecus bieti · Activity budgets · Age-sex class · Reproductive investment

Abstract

The activity budgets of primates reflect their survival strategy. Despite existing data on the activity budgets of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), little is known about how activity budgets vary between age-sex classes. This study provides the first detailed activity budgets subdivided by age-sex class, based on observations of the largest habituated group of *R. bieti* 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%). Females allocated significantly more time to feeding than to any other activity. Adult males allocated more time to miscellaneous activities (12.5%) than adult females (3.8%). Juveniles allocated less time to grooming than adults. Infants were being groomed 6.9% of the time, 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 why activity budgets can vary by age-sex class: (1) differential reproductive investment between males and females; (2) developmental differences among the age categories, and (3) social relationships between members of different age-sex classes, particularly dominance. These variations in activity budgets among the different age-sex classes may become a selective pressure in this species.

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Introduction

The temporal distribution of an animal's activities has profound implications for its survival and reproduction [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; Watts, 1988; Zhou et al., 2007] as well as variation in the ambient environment [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; 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 [Fox et al., 2004]. Additionally, individuals must adjust their activities to coordinate their movements with those 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].

Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) are endangered colobine monkeys that inhabit remnant temperate forests in the Hengduan Mountains in north-western Yunnan and south-eastern Tibet [Long et al., 1994; Li et al., 2013]. *R. bieti* occurs in large, multilevel social groups consisting of many one-male, multi-female units (OMUs) and associated all-male units [Grueter and van Schaik, 2010]. Activity budgets have been published for some geographical populations of this species [Ding and Zhao, 2004; Xiang et al., 2009]. However, there is no systematic data on differences in activity budgets among age-sex classes; the challenging topography of their high-altitude habitat, low temperatures and the natural shyness of the monkeys towards humans are obstacles to full-day follows. This study aims to provide the first description of variability and differences between age-sex classes in the activity budgets of habituated *R. bieti* in the wild. Finally, we try to identify the most important factors that affect individual activity budgets.

Methods

Study Site and Study Group

This study was conducted on a single *R. bieti* group (approx. 480 individuals) at Xiangguqing (99°22' E, 27°37' N), located in the southernmost region of Baimaxueshan Nature Reserve, Yunnan Province, PR China. The study site encompasses an area of almost 90 km², which includes multiple habitat types: mixed coniferous and deciduous broad-leaf forest (2,900–3,600 m), subalpine fir forest (*Abies georgei*, 3,500–4,000 m), montane sclerophyllous oak forest (*Quercus pannosa*, 3,200–3,500 m), subtropical evergreen broad-leaf forest (*Cyclobalanopsis* spp., 2,500–3,000 m) and pine forest (*Pinus yunnanensis*, 2,500–3,100 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 3,038 m a.s.l. Annual rainfall during the same time was 1,371 mm. Temperature and precipitation were strongly seasonal [Li, 2010]. We carried out behavioural observations from June 2008 to May 2009.

The study group inhabits mixed deciduous broad-leaf and conifer forest, as well as cool temperate fir forest, between elevations of 2,600 and 4,100 m. This group has been well habitu-

Table 1. General group behaviour and individual maintenance activities recorded during instantaneous scan sampling

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

ated since 2006 and could be approached to 20–30 m almost every day. The group consisted of 47–55 OMUs, the largest of which had 16 members, and 1 all-male unit including 40–50 adult males and juvenile males; the adult sex ratio (male:female) was 1:2.9 [Li, 2010].

Data Collection and Analysis

We spent 10 full days each month following the monkey group throughout the study. We collected data on monkey behaviour from the time the group woke up in the morning until the monkeys entered their nightly sleeping site. Since the group had been habituated, we were usually able to observe it with the naked eye at distances between 10 and 30 m. However, we sometimes observed subjects using binoculars (10 × 42) from distances between 50 and 300 m when the monkey group was far away. We used instantaneous scan sampling at 15-min intervals to collect behavioural data [Altmann, 1974]. Each scan was carried out either horizontally, alternating between ‘left to right’ and ‘right to left’, or between ‘ground to tree’ and ‘tree to ground’, depending on how the troop was dispersed. We classified individuals into 4 age-sex classes based on body size and pelage colour: (1) adult males, the largest individuals in the group, with long white hair on their flanks obscuring ischial callosities, a strong contrast of black and white hair, hair on the top of the head falling forward, and a long and bushy tail; (2) adult females, with a body length no more than half that of adult males, possessing long black nipples and often being found with infants; they usually have an interbirth interval of no more than 20 months, and lactation continues until the infant reaches about 1.5 years; (3) juveniles, whose backs and limbs were light grey, with short hairs on the tail, and (4) infants, born from March to May every year – these were the smallest, had predominantly grey and white pelage, and were often observed suckling. Immature individuals included both juveniles and infants. We categorized monkey behaviours 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 h of observation over 120 days, obtaining 260,546 total activity records. These may be divided into 145,732 records for adults (37,109 for adult males and 108,623 for adult females) and 114,814 for immature individuals. In order to avoid bias stemming from uneven data collection, activity pattern numbers were averaged for each hour before mean daily activity budgets were computed for each month and annual budgets [Agetsuma and Nakagawa, 1998; Xiang et al., 2010]. We treated each scan budget as an independent data point and used it in subsequent analyses to reduce potential biases [Clutton-Brock, 1977].

One-way ANOVA was used to determine whether time allocated to each of the 5 activities differed significantly among the different age-sex classes. All statistical analyses were done using SPSS 15.0 for Windows. Each analysis was 2-tailed with $p \leq 0.05$.

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

Age-sex category	Feeding	Moving	Resting	Grooming	Other
Male	39.5 $\pm$ 4.9	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	14.2 $\pm$ 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 1-way ANOVA on 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. F	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
F vs. J	78.65	0.000	52.34	0.000	1.038	0.309	6.357	0.019	7.263	0.008
F vs. I	1,256.38	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

M = Male; F = female; J = juvenile; I = infant.

Results

Activity Budgets among Different Age-Sex Classes

Adult males spent 39.5% of their time feeding, 24.1% moving, 18.1% resting, 5.9% grooming and 12.5% in other activities (table 2). Females allocated 44.8% of their time to feeding, which was more than the time allocated to other activities (1-way ANOVA, $F_{4, 476} = 246.21$, $p < 0.01$). Juveniles spent 39.1% of the time feeding. Moving, resting, grooming and other comprised 30.9, 19.4, 4.3 and 6.3% of their time budget, respectively (table 2). Infants allocated only 14.2% of their time to feeding, not including the time spent suckling. They were also groomed 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 age-sex categories (table 2). Adult females allocated the most time to feeding (1-way ANOVA, $F_{1, 238} = 70.99$, $p < 0.01$ for males; $F_{1, 238} = 78.65$, $p < 0.01$ for juveniles; $F_{1, 238} = 1,256.38$, $p < 0.01$ for infants) and spent more time resting than adult males ($F_{1, 238} = 5.762$, $p < 0.05$). Juveniles spent more time moving as compared to other age-sex classes (1-way ANOVA, $F_{1, 238} = 71.13$, $p < 0.01$ for males; $F_{1, 238} = 52.34$, $p < 0.01$ for females)

Fig. 1. Comparison of activity budgets between adults and immature individuals of *R. bieti* at Xiangguqing from June 2008 to May 2009.

and allocated less time to grooming than did adults (1-way ANOVA, $F_{1,238} = 5.021$, $p < 0.05$ for males; $F_{1,238} = 6.357$, $p < 0.05$ for females). Infants rested more often than other age-sex classes (30.8% of the time, 1-way ANOVA, $F_{1,238} = 94.67$, $p < 0.01$ for males; $F_{1,238} = 59.51$, $p < 0.01$ for females; $F_{1,238} = 72.37$, $p < 0.01$ for juveniles; table 3).

Variation in Activity Budgets between Adults and Immature Individuals

Activity budgets differed significantly between adults and immature individuals (fig. 1). Adults allocated more time to feeding (1-way ANOVA, $F_{1,478} = 27.27$, $p < 0.01$). However, immature individuals spent more time moving ($F_{1,478} = 16.62$, $p < 0.01$), resting ($F_{1,478} = 6.179$, $p < 0.05$) and doing other activities ($F_{1,478} = 5.466$, $p < 0.05$) than did adults.

Discussion

As observed in several other primate species [Clutton-Brock, 1977; Masi et al., 2009], the activity budgets of *R. bieti* varied among age-sex classes at Xiangguqing. In this study, adult females spent more time feeding and resting than either 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. Females' 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 impact females' activity budgets, especially for animals in which females are smaller than males and therefore have a higher metabolic requirement capacity ratio [Demment, 1983]. Females' energy requirements increase by 25% during pregnancy and by 50% during lactation [Portman, 1970]. Coelho et al. [1979] reported that pregnant primates' and lactating primates' metabolic values and energy costs are estimated to increase 1.25 and 1.5 times, respectively. A number of studies have suggested that females modify their activity budgets

during pregnancy or lactation [Harrison, 1983; Dunbar and Dunbar, 1988; Rose, 1994; Stevenson et al., 1994]; for instance, 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. 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 2 years. Almost every infant nurses in their first year of life [Li D.Y., unpubl. data]. Thus, most adult females observed in a given year are likely to be either pregnant or lactating. Females spend more time feeding and resting than males, indicative of both their higher energy requirements and 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 as individuals age. Juveniles in this study fed similarly to adults. Although juveniles are smaller and weigh less than 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 impacts 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 [Agatsuma, 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. Juveniles may be less efficient foragers than adults. Due to the limitations 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 that unit's infants in the wild [Li D.Y., unpubl. data]. Thus, infants likely have more chances to groom than older individuals.

Finally, 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 McNeillage [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 [Masi et al., 2009]. As a result, females may need more time to forage and may also resort to eating 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 1 all-male unit (40–50

adult males and juvenile males), and the adult sex ratio (male vs. female) was 1.0:2.9 [Li D.Y., unpubl. data]. The adult sex ratio of *R. bieti* was smaller at Xiangguqing than that of 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 8 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 behaviours at Xiangguqing [Li D.Y., unpubl. data]. 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 which shapes the development and growth patterns of this species. The characteristic social functions of individuals in primate groups can change their behavioural patterns, consequently affecting their activity budgets.

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