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Behavioral Asymmetries among Mother-Infant Dyads of Syntopic Macaques (*Macaca assamensis* and *M. mulatta*) in Shivapuri-Nagarjun National Park, Nepal

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Abstract

The diurnal activity pattern of primates is affected by ecological and social factors including diet selection, distribution, abundance of food sources, social ranks, etc. Daily activity budgets of mothers and infants of the syntopic Assam macaque (*Macaca assamensis*) and rhesus macaque (*Macaca mulatta*) troops were observed in Shivapuri-Nagarjun National Park from September 2017 to January 2018 using focal animal sampling method. Even though both the species were semi-provisioned, activity budgets of rhesus macaques were found more influenced by human activities than the Assam macaques. Rhesus macaque mothers spent significantly more time in feeding and moving than Assam macaque mothers. Conversely, Assam macaque mothers spent significantly more time resting and grooming than that of rhesus macaque. Similarly, Assam macaque infants spent significantly more time in resting whereas rhesus macaque infants spent significantly more time in playing and being groomed. Rank-related differences in activity budgets were found in Assam macaque females whereas those were not significant in rhesus macaques. Sex of the infants did not have significant effect on their activity budgets, except for moving and playing in Assam and rhesus macaque infants, respectively. Feeding, moving, resting and playing behaviors in Assam macaque infants varied with their age whereas such variations were observed in moving and playing behaviors of rhesus macaque infants. However, ranks of the mothers in the troop were not found to be effective factor in determining activity budgets of both Assam and rhesus macaque infants.

Keywords: Activity budgets; Mother-infant dyads; Assam macaque; Rhesus macaque; Nepal

Introduction

Primates are known to adjust their activity budgets to deal with changeable environmental conditions [1]. Studies have shown that non-human primate social behavior is more or less similar to human behavior such as eating, playing, fighting, keeping the baby and others [2]. Primates change their daily behavior according to the environment to ensure their survival. Many studies have shown that the activity budgets vary by several environmental factors including diet, distribution and food sources [3,4].

Primate infants are born dependent on their mother [5]. Mother not only plays an active role in promoting the infant's independence but also regulates own interactions with other infants and members of the group [6,7]. Females with infants must protect their infants from internal threats of individuals of own social group such as harassment/mishandling [8,9] or kidnapping [10] and infanticide; and external threats, such as predation [11-13]. Visual monitoring of infants by mothers is likely to be affected by various factors, including infant age, infant behavior, maternal experience, and dominance rank, and reduces the time available for other important activities [14] such as feeding or grooming.

Two species of macaques have been reported from Nepal: rhesus macaque (*M. mulatta*) and Assam macaque (*M. assamensis*), the latter is the least known non-humanprimate of Nepal [15]. Assam macaques, like rhesus macaques are flexible in habitat types in Nepal from river basins to subtropical hills of Sal forests, mixed deciduous forest, temperate broadleaved forest with rocky outcrops, and along the steep sloped forests along rivers above altitude. However, they are not recorded from Tarai plain and high snowy mountains and human settlements [16]. Rhesus macaques, in Nepal, are found from sub-tropical forests of Tarai to the valleys across higher elevation of Makalu-Barun National Park, Langtang National Park, and coniferous and alpine forests of Rara National Park. They are larger in number in religious parkland jungles and temples [17]. Both Assam and rhesus macaques are diurnal and omnivorous with multi-male and multi-female social troops having ranking system within the troop.

Two species of macaques from Nepal are rarely sharing similar types of microhabitats [16]. Nagarjun forest of Shivapuri Nagarjun National Park in mid-hills of Nepal holds both the species in close spatial extent and similar microhabitats, thus making it an ideal place for comparative behavioral explorations. This study in the Nagarjun forest provides quantitative framework on overall diurnal activity budgets of Assam and rhesus macaque mothers and their infants in semi-provisioned habitat and interspecific comparisons. It contributes to better understanding of how the macaque mothers allocate their time budgets and their activities are affected by human presence. In addition, it also compares the rank related differences in the activity budgets of mothers and infants between the two-macaque species.

Methods

Study Site and Troops

Shivapuri-Nagarjun National Park (SNNP) is located between 27°45' to 27°52'N and 85°15' to 85°30' E. The government of Nepal declared the Shivapuri Watershed and Wildlife Reserve as a national park in 2002 and the Nagarjun forest has been annexed in 2009 AD [18]. It has two isolated forest fragments namely Shivapuri forests and Nagarjun forests covering a sum of 159 square kilometers [19]. The park lies in the transition zone between sub-tropical to temperate regions with more than 1250 species of flowering plants. The park is the true representation of the mid-hills (Figure 1).

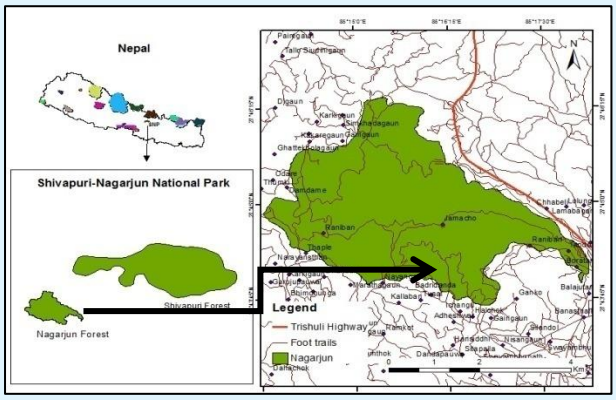

Figure 1: Location of the study site at Nagarjun forest in SNNP [Source: DNPWC, 2010] [19].

This research was conducted within Nagarjun forest which is inhabited by both the macaque species in partially sympatric association. Nagarjun forest is located within 27º43'N to 27º46'N and 8º13'E to 85º18'E, within the elevation range of 1350 to 2732 m covering part of subtropical and lower temperate region and four types of forests namely chir-pine forests, lower mixed hardwood

forests, upper mixed hardwood forests and oak forests [19,20].

Previous studies showed that Nagarjun forest is supporting number of animals of ecological significance. It is estimated that more than 200 rhesus and about 144 Assam macaques inhabit in Raniban periphery of Nagarjun forest [21]. Among these populations, a group of the Assam macaques in army barrack and a group of rhesus macaques inhabiting nearby were studied taking as focal troops. Both the study groups were semi-provisioned, the Assam macaque troop usually fed on the surplus food and discards from the Nepalese army barrack within the forest premises whereas the rhesus macaque troop partly relied on the supplements from the visitors in the Balaju garden area.

The Assam macaque troop consisted of 47 individuals, of which 6 were adult males, 14 adult females, 2 sub-adults male, 10 juveniles male, 2 juveniles female, 7 female infants and 6 male infants. Likewise, the rhesus macaque troop consisted of 37 individuals, of which 4 were adult males, 13 adult females, 4 young females, 1 juvenile male, 4 female infants and 11 male infants. Four mother-infant dyads were selected as focal dyads from each of the Assam and rhesus macaque troops for the study. The dyad selection included two high-ranking mothers and their infants (one male and one female) and two low-ranking mothers and their infants (one male and one female) from each troop. The ages of the mothers and infants were estimated following the methods of Chalise, et al. (2005) [22] and ongoing long-term observations of the troops.

Data Collection and Analysis

Data were collected from September 2017 to January 2018. During the first month, an ethogram was developed and refined (Table 1), and the study subjects were selected. A 15- minute focal sampling was used [23]. The subjects were not observed more than once per hour in order to ensure representative data. The date, hours, members of the dyads and other members of the troops were recorded at the beginning of each focal sample.

Category	Description
Feeding	foraging and feeding food, either natural or human
Moving	locomotion from one place to another for different purposes
Resting	staying in a place, either sleeping or monitoring
Grooming	individuals groom each other, including groomer and groomee
Playing	infants playing alone or with the mother or with other peers
Others	aggression, auto-groom, rear inspection, solicitation, copulation, non-sexual mounting, drink water, vocalizing and other rare behaviors

Table 1: Ethogram with elaboration of used word.

The observations were carried out between 800 to 1600 hours. Proportions of each behavior were calculated per day of observation. One-way ANOVA was used to determine whether time allocated to each of the activities differed significantly among Assam macaques and rhesus macaques. Mann-Whitney U tests (U) was performed for pairwise comparisons of rank-related differences in activity budgets of mothers. Repeated measures by ANOVA were performed to age, sex and rank related differences in activity budgets of infants. Statistical analyses were performed using IBM SPSS Statistics 23 and the significance was tested at $P<0.05$.

Results

Overall Behavioral Differences Between Groups

A total of 1536 focal observation (768 of Assam macaques and 768 of rhesus macaques) were collected, with more than 384 hours of observations. Observations revealed that Assam macaque mothers spent only 28% of their time on feeding whereas rhesus macaque mothers spent 44% of time on it. Similarly, Assam macaque mothers spent 25.29% resting, 16.52% grooming, 11.95% moving and 18.24% in other activities, whereas rhesus macaque mothers spent 26% of time moving, 11% grooming, 10% resting and 9% in other activities (Figure 2).

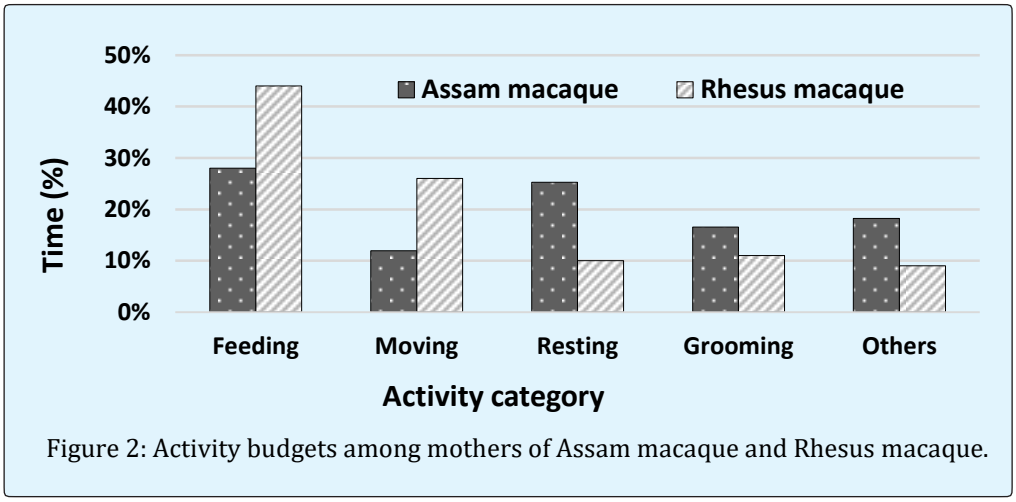

Figure 2: Activity budgets among mothers of Assam macaque and Rhesus macaque.

Significant differences were found in activity budgets among the mothers of Assam and rhesus macaques. Assam macaque mothers allocated significantly more time in resting (1-way ANOVA, $F = 60.45$, $p < 0.001$) and grooming (1-way ANOVA, $F = 5.96$, $p < 0.05$) than the rhesus macaque mothers. On contrary, rhesus macaque mothers spent significantly more time in feeding (1-way ANOVA, $F = 6.27$, $p < 0.046$) and moving (1-way ANOVA, $F = 44.64$, $p < 0.001$) than the Assam macaque mothers (Table 2).

	Feeding		Moving		Resting		Grooming		Playing		Others	
	F	P	F	P	F	p	F	p	F	p	F	p
AM vs RM	6.27	0.046	44.65	0.001	60.45	0.001	5.96	0.05	-	-	2.430	0.170
AI vs RI	4.034	0.091	2.644	0.155	10.320	0.018	5.681	0.05	23.77	0.003	1.08	0.339

Table 2: Results of one-way ANOVA on activity budgets of mothers and infants of Assam and rhesus macaques.
AM = Assam macaque mothers; RM = rhesus macaque mothers
AI = Assam macaque infants; RI = rhesus macaque infants

Similarly, Assam macaque infants spent highest proportion of time in resting (42%), followed by grooming (19%), equal amount of time in moving and playing (15% each), other activities (6%) and feeding (3%), whereas rhesus macaque infants spent most of their time being groomed (31%), equal amount of time in resting and playing (29% each), moving (6%), other activities (5%) and feeding (2%) (Figure 3).

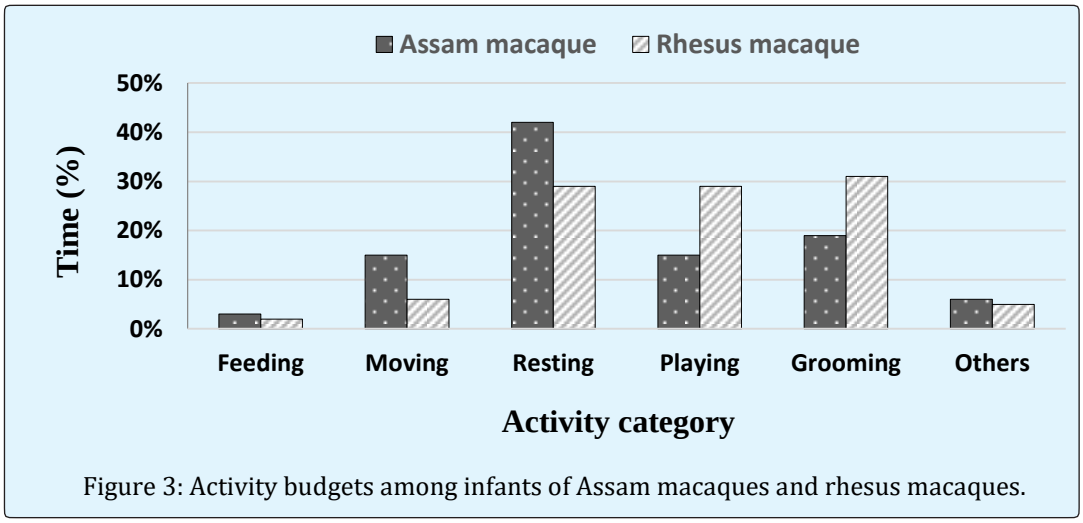

Figure 3: Activity budgets among infants of Assam macaques and rhesus macaques.

No significant differences were found in feeding and moving categories among infants of Assam macaques and rhesus macaques. Significant differences were found only in resting, playing and grooming categories. Assam macaque infants spent significantly more time in resting (1-way ANOVA, $F = 10.32$, $p < 0.018$) than that of the rhesus macaque, whereas rhesus macaque infants spent significantly more time in playing (1-way ANOVA, $F = 23.77$, $p < 0.003$). Similarly, rhesus macaque infants were groomed significantly more often (1-way ANOVA, $F = 5.68$, $p < 0.05$) than the Assam macaque infants.

Rank Related Differences in Activity Budgets among Mothers

Low ranking mothers of Assam macaques spent less time feeding ($U = 28.00$, $p = 0.011$) in comparison to high ranking mothers whereas high ranking mothers spent less moving ($U = 129.50$, $p = 0.001$) and in other activities ($U = 140.00$, $p = 0.001$) than the low-ranking mothers. There were no significant differences in the amount of time high ranking and low-ranking mothers spent in resting ($U = 39.50$, $p = 0.60$) and grooming ($U = 49.00$, $p = 0.184$), though high-ranking mothers spent more time in resting and grooming than the low-ranking mothers (Figure 4).

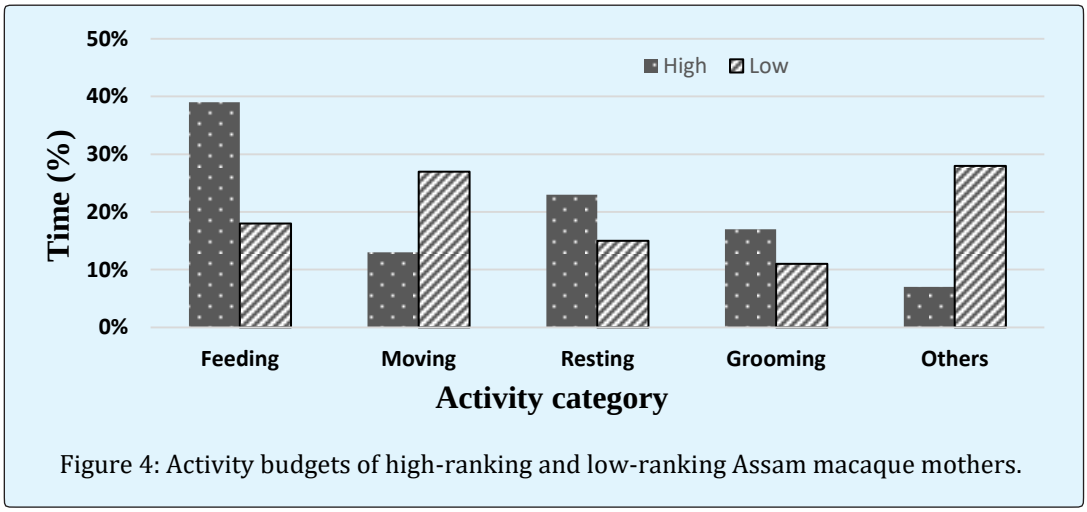

Figure 4: Activity budgets of high-ranking and low-ranking Assam macaque mothers.

Unlike Assam macaques of this study, low-ranking mothers of rhesus macaques spent more time on feeding ($U = 115.50$, $p = 0.012$) than the high-ranking mothers. High-ranking mothers spent more time on moving ($U = 41.50$, $p = 0.078$), resting ($U = 61.50$, $p = 0.544$), grooming ($U = 84.00$, $p = 0.488$) and other activities ($U = 57.00$, $p = 0.386$) than the low-ranking mothers (Figure 5).

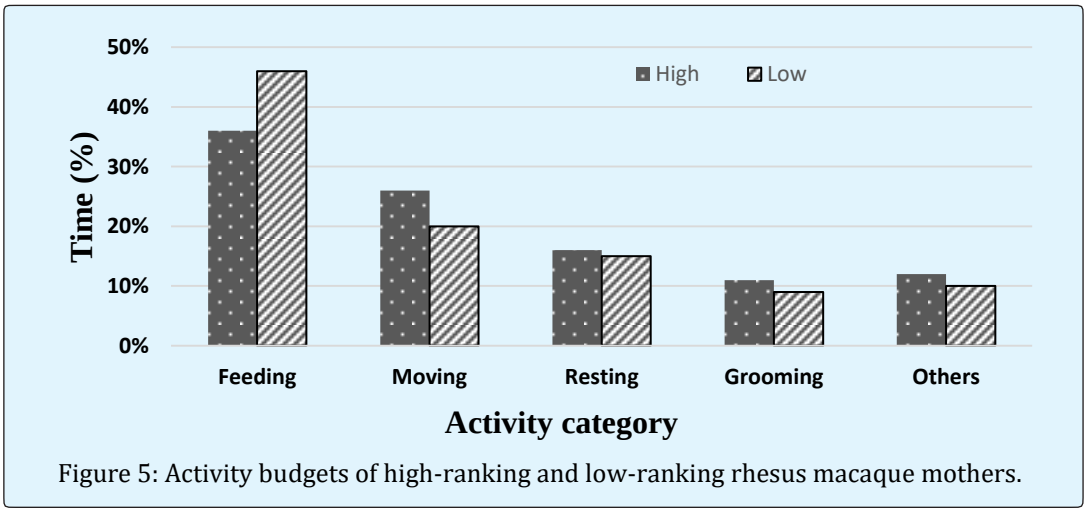

Figure 5: Activity budgets of high-ranking and low-ranking rhesus macaque mothers.

Age and Sex Related Differences in Activity Budgets of the Infants

Male and female infants of the Assam macaque did not differ significantly in the amount of time they spent in feeding, resting, playing, grooming and in other activities, however they varied significantly in amount of time they spent in moving (Table 5). Male infants spent more time moving than the female infants. An interaction was found between the sex of the infants and time spent in different activity categories at different ages, which resulted in male infants of 6 months of age spending more time in feeding while the female infants of 6 months of age spent more time in resting. Male infants at the age of 3 months spent more time in moving, on the other hand female infants during same age spent more time being groomed and in other activities. Similarly, male infants of the age 5-6 months spent more time on playing than the female infants. Not so significant interaction was found between the rank of the mother and age of the infants (Table 5). Only infants of high-ranking mothers spent significantly more time moving than the infants of low-ranking mothers. There were no significant differences in time spent in feeding, resting, playing, grooming and in other activities between the infants born to different ranking mothers (Table 5).

Activity categories	Effect or Interaction	Description	F-value
Feeding	Sex	F > M	F (1, 22) = 0.402
	Sex * Age	M > F (6 months)	F (3, 16) = 3.428**
	Rank * Age	H > L	F (1, 18) = 0.118
Moving	Sex	M > F	F (1, 22) = 4.059**
	Sex * Age	M > F (3 months)	F (3, 16) = 1.827**
	Rank * Age	H > L	F (1, 18) = 1.164**
Resting	Sex	F > M	F (1, 22) = 0.720
	Sex * Age	F > M (6 months)	F (3, 16) = 1.154**
	Rank * Age	L > H	F (1, 18) = 0.315
Playing	Sex	M > F	F (1, 22) = 1.513
	Sex * Age	M > F (5-6 months)	F (3, 16) = 1.758**
	Rank * Age	L > H	F (1, 18) = 1.328
Grooming	Sex	F > M	F (1, 22) = 0.679
	Sex * Age	F > M (3 months)	F (3,16) = 0.914
	Rank * Age	H > L	F (1, 18) = 1.368
Others	Sex	F > M	F (1, 22) = 0.011
	Sex * Age	F > M (3 months)	F (3,16) = 0.441
	Rank * Age	L > H	F (1, 18) = 0.074

Table 5: ANOVA table for effects and interactions of sex and age of infants and ranks of mothers in activity budgets of Assam macaque infants.
M: Males; F: Females; L: Low-ranking; H: High-ranking. ** The value is significant at 0.05.

Male and female infants of any age and born to different ranking mothers of rhesus macaques did not differ significantly in the amount of time they spent in feeding. Though the infants born to high ranking mothers spent more time in feeding than the low-ranking mothers, the difference was not significant (Table 6). Male infants of 3 months age spent more time playing and that of 6 months spent significantly more time moving than the female infants. Likewise, infants born to low ranking mothers spent significantly more time in moving and playing than the infants born to high ranking mothers. However no significant differences were found between male and female infants of different ages born to different ranking mothers in grooming and other activities.

Activity categories	Effect or Interaction	Description	F-value
Feeding	Sex	M = F	F (1, 22) = 0.005
	Sex * Age	M = F	F (3, 16) = 2.066
	Rank * Age	H > L	F (3, 16) = 0.364
Moving	Sex	M > F	F (1, 22) = 1.541
	Sex * Age	M > F (6 months)	F (3, 16) = 4.302**
	Rank * Age	L > H	F (3, 16) = 5.390**
Resting	Sex	F > M	F (1, 22) = 3.790
	Sex * Age	F > M (3 months)	F (3, 16) = 2.437
	Rank * Age	H > L	F (3, 16) = 2.559
Playing	Sex	M > F	F (1, 22) = 5.840**
	Sex * Age	M > F (3 months)	F (3, 16) = 0.648**
	Rank * Age	L > H	F (3, 16) = 2.098**
Grooming	Sex	F > M	F (1, 22) = 2.324
	Sex * Age	F > M (3 months)	F (3, 16) = 0.774
	Rank * Age	L > H	F (3, 16) = 1.109
Others	Sex	F > M	F (1, 22) = 0.852
	Sex * Age	M > F (6 months)	F (3, 16) = 1.260
	Rank * Age	L > H	F (1, 20) = 2.354

Table 6: ANOVA table for effects and interactions of sex and age of infants and ranks of mothers in activity budgets of rhesus macaque infants.
M: Males; F: Females; L: Low-ranking; H: High-ranking. ** The value is significant at 0.05.

Discussion

Overall Behavioral Differences between the Assam and Rhesus Macaque Groups

The activity budgets of both Assam macaques and rhesus macaques seemed to have been influenced by the availability of food. Both Assam macaque and rhesus macaque mothers devoted greater percentage of time in feeding than other activities in order to accumulate energy reserves. The results of this study were consistent with those from other primates [24-26].

Studies on other primates have shown that lactating females devote a greater proportion of their time to feeding than do non-reproductive and pregnant females [27,24]. The activity budgets of rhesus macaque mothers in this study appeared to be affected similarly, as they spent more time in foraging and feeding than the Assam macaque mothers. Frequent availability and access to food might account for this fact, as rhesus macaques were more habituated and in direct contact with the human beings than the Assam macaques. Also, since rhesus macaques were in direct contact with human beings, they had to move more frequently than the Assam macaques, which required special energetic demands. Thus, rhesus macaque females fed more in order to compensate the energy loss, consequently, higher feeding activities caused lower resting behavior. This is supported by Kurup and Kumar (1993) [28] which states that feeding is inversely related to resting. The rhesus macaques of this study spent lesser time in resting than the Assam macaques and the conspecific urban troops in Bangladesh [29].

A number of studies have suggested that females modify their activity budgets during pregnancy or lactation [30-33]. Assam macaque mothers were found to spend more time in resting and grooming than the rhesus macaque mothers. Grooming was associated with the resting. Assam macaque mothers spent more time in grooming as found in the cases of Long-tailed macaques [34,35]. On contrary, rhesus macaque mothers spent lesser time resting and grooming, which differed from the study carried out in Cayo Santiago rhesus group [36]. This

might also be due to frequent invasions of human beings in macaque habitat. Rhesus macaques hardly got longer time to rest and groom in a single place and had to move frequently to escape from human beings, which resulted in them moving more often than resting and grooming.

The study showed that there were no significant differences in the feeding and moving behaviors of Assam macaque infants and rhesus macaque infants. This is not surprising as infants were still being carried by their mothers and their travel and rest was dependent on the mothers' activity patterns. Infants of both species allocated similar time budgets in feeding and moving. While mothers fed, infants had opportunities to learn how and what to eat by observing her from close range in both species [37]. Thus, infants were found to replicate the activity of the mothers, even though they were unable to consume the food materials properly. As reported for other primate species [24,38], infants were found to be responsible for maintaining proximity to their mothers as they frequently approached their mothers when left by the mothers.

Assam macaque infants spent more time on resting than rhesus macaque infants which might be the result of more arboreal nature of Assam macaque than the rhesus macaques spending much of their time on ground. Since rhesus macaque infants spent lesser time on resting, they were engaged more in playing activities – both solitary and social. Although rhesus macaque mothers spent lesser time in grooming, whenever they did, they mostly groomed their infants, as grooming behavior between mother and baby can strengthen the relationship between them [39,34].

Rank Related Differences in Activity Budgets of Mothers

Among social mammals, dominance hierarchies determine the activity budgets of various age/ sex classes to a certain extent [40].It seems clear that dominance status has social significance, at least in certain species, even though no single unifying concept has been found to explain all primate sociality [41]. The influence of rank was found more in Assam macaques than in rhesus macaques. Dominance rank among the adult females of Assam macaques clearly influenced their feeding behavior. Low-ranking mothers were clearly at disadvantages in feeding competition at the provisioning site, as found in the studies of other provisioned populations [42-45]. Because of being at disadvantage in feeding site, low-ranking mothers of Assam macaques moved more frequently than the high-ranking mothers, as opposed to various studies carried out in Japanese macaques [46-49]. As suggested by Agetsuma and Nakagawa (1998), there might be a trade-off among feeding, moving and grooming time. As a result of spending more time resting, high-ranking mothers of Assam macaques were found to be more involved in grooming as well.

On contrary, no significant influence of ranks was found in activity budgets of rhesus macaque mothers. This result contradicted with the study carried out in Japanese macaques [49]. Only significant differences were found in moving and resting between medium ranking and low-ranking mothers. Again, this might be the result of more human interference and availability of food resources in wider space. As rhesus macaques mostly spent their time in garden area, surrounded by human beings, they were more habituated with human beings, as oppose to Assam macaques, which were shyer in nature. Also, there were more waste food materials available in wider range, resulting in less competition for food. Thus, rhesus macaque mothers of this study spent almost equal amount of time in all activities. The time allocated for different activities by different ranking mothers of the rhesus macaque contradicted with that of Japanese macaques [49] which might be the result of smaller group size. As suggested by van Schaik, et al. (1983) [50], among long-tailed macaques, an increase in group size leads to less favorable time budgets, the rhesus macaques of this study were smaller in group size, which led to more favorable time budgets.

Age and Sex Related Differences in Activity Budgets of Infants

Studies conducted in captivity and in the wild have shown that macaque mothers adjust their behavior according to effects of socio- demographic factors such as their age and experience, dominance rank, aggression received by themselves and their infants, sex of the infant, and size and composition of their family [51-55]. Sex differences were apparent in moving behavior of Assam macaque infants and playing behavior of rhesus macaque infants but not in other activities. Male infants moved more often than the female infants of Assam macaques. Also, mothers of male infants left their infants more frequently than the mothers of female infants. In rhesus macaques, male infants played for longer periods of time than the female infants as in the cases of Blue monkeys [56] and Olive Baboons [57]. In case of Assam macaques, male infants started feeding or playing with food items more often than the female infants by the time they were

6 months of age whereas in rhesus male and female infants of any age did not differ in feeding behavior. Sex and age also had effect on resting behavior of infants of Assam macaques but not the rhesus macaques. Female infants of Assam macaques spent more time resting at the age of 6 months than the male infants same age. Female's social status may also impact the nutrition and growth of infants because of feeding in the proximity to the mother [58]. On contrary, ranks didn't seem to influence the feeding time of infants. Infants of high ranking females of Assam macaque tend to be more secure and have greater freedom of movement within the group. They have less dependence on their mothers and even have more varied and greater experience than infants born to low-ranking mothers. On the other hand, infants of low ranking females of rhesus macaques moved more often than the infants of high ranking mothers. Unlike the study carried out in stump-tailed macaques by Zothansiama and Solanki (2015) [59], rhesus macaques of this study showed lesser influence of maternal-status. No interactions of age, sex and rank was found in time the infants of both Assam macaques and rhesus macaques were groomed.

Conclusion

The study conclude that the daily activity budgets of Rhesus macaques were more influenced by human presence than that of Assam macaques, even though habitat of both species were semi-provisioned. Assam macaques were found to be more inactive than the Rhesus macaques. Rhesus macaques frequently came in direct contact of human beings, whereas direct interactions rarely occurred between Assam macaques and humans. In Nepal case, the protected species Assamese monkey can co-exists with common rhesus monkeys and significance population around the capital city.

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