Niche partitioning between Assamese and Rhesus macaques in the Askot landscape of Uttarakhand, Northern India

Dissertation submitted to the Saurashtra University, Rajkot in partial fulfillment of Master's Degree in Wildlife Science (2017)

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Supervisors

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भारतीय वन्यजीव संस्थान
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SUMMARY

1. Closely related species often have similar requirements and these species need to have certain ecological adaptations to live in sympatry. Two congeneric species the Assamese (*Macaca assamensis*) and the rhesus macaque (*Macaca mulatta*) co-occurring in the Askot landscape of Uttarakhand were studied to understand the mechanisms allowing their coexistence.

2. Ecological niche differentiation for the two species was investigated by examining three possible modes of separation: activity pattern, diet and spatial use following observational protocols over a period of five months (December 2016-April 2017). Crop-raiding by macaques often results in human-macaque conflict. With the help of semi-structured interviews, attempts were made to access the level of conflict and people's perception of these two macaque species.

3. Limited niche overlap was found between two primate species across the study duration. The Assamese macaque differed from the rhesus macaque in time spent on various activities. The former spent more time feeding and the latter in resting. Although 44% of all food items were consumed by both the species, only three of the ten major food items were shared. Assamese macaques preferred leaves and had broader niche breadth compared to rhesus macaques who fed more selectively on fruits. There was a significant difference in feeding heights, habitat and roosting site preferences of the two species. Differences in diet choice and roosting sites, in turn, resulted in differences in daily movement and home range of these species. Despite a partial home range overlap, both these species were found to be spatially segregated at a local scale.

4. The extent of niche overlap across winter and spring seasons in the area showed the greatest divergence in the diets of the two species in winter, while diet overlap was more pronounced in spring. As resources were abundant in the spring, an increase in niche overlap may not have lead to competitive interactions.

5. In the study area, both macaques fed on crops grown in the agricultural fields. However, it was found that the losses caused by rhesus macaques were almost twice to that caused by the Assamese macaques as they fed on crops only occasionally. The perception of these macaques was thus a mix of negative and positive emotions but most respondents negatively referred to the macaques as “pests” or their “enemy”.

6. *Synthesis and application*: Knowledge about differential resource use of macaques might help in assigning conservation priorities to the different species and their specific ecological niches along with designing species-specific management strategies. The study was able to distinguish the macaque's tendency to co-exist with humans. The study documented for the first time the behavioural ecology of the unique westernmost population of the Assamese macaque. A more detailed study may be helpful to better understand the adaptive processes along with human-macaque conflict in the area.

Chapter 1

INTRODUCTION

Adaptations of a species to its habitat determine its niche (Grinnell 1917). G. Evelyn Hutchinson popularized the niche concept and provided an explanation for the coexistence of various organisms in a single habitat. He defined a niche as a region in a combination of environment factors and resources used by an organism for its growth, reproduction, and survival (Hutchinson 1957). Competition results in displacement of one species by another, so that it can adapt to distinct modes of life in which it has an advantage over its competitor (Gause 1934). It is generally thought that two species with identical ecological requirements can coexist only when there is a niche separation between the species concerned (Feeroz 2012). The niche concept and understanding the mechanisms that enable similar species to coexist are of pivotal importance in community ecology studies (Rakotondranary and Ganzhorn 2012). Most of the studies done in this context indicate that major factors mediating niche differentiation in sympatric species include activity patterns, diet choice and spatial use of the habitat (Schoener 1974, Schreier et al. 2009).

Primates are a diverse eutherian group of mammals with nearly 400 extant species placed into five distinct groups, largest of which, with 150-odd species of Old World monkeys and apes, inhabits the tropical forests of south Asia along with southeast Asia and Africa (Martin 2012). Macaques are one of the most widespread group of primates in southeast Asia (Abegg and Thierry 2002). It was only during Pleistocene (~2 mya) that most of the macaque species diverged, resulting in similar morphologies observed today. Despite the similarity Fooden (1982) suggested that competition has resulted in ecological or geographical segregation throughout Southeast Asia. Ever since ecological segregation of macaques at a local scale had rarely been studied (Borries et al. 2002).

The Assamese macaque (*Macaca assamensis*), primarily a forest dwelling species, listed as Near Threatened and the rhesus macaque (*Macaca mulatta*), a wide-ranging species (Wada 2005), listed as Least Concerned by IUCN Red List (2017) co-occur in many parts of East Asia and southeast Asia (Johnsingh and Manjrekar 2012). Askot landscape, where the Assamese macaque was discovered only in 2006, is the westernmost limit of this species locally known as *Kala Bandar*. In select areas here, its distribution is known to overlap with that of the rhesus macaque (Chandola et al. 2006). Sharing the same phylogeny and related closely with similar resource requirements, imply competition between these species for the limited resources in the mountains. The study, therefore, examined the extent of niche overlap and the underlying mechanisms of coexistence of the two macaque species. Major niche dimensions focused on for the study were time, diet and space. Askot is one such mountainous landscape where two seasons: winter and spring were distinguished during the study period. The study, thus, along with looking at co-existence mechanisms tried to draw the patterns of variation in niche overlap across these seasons. Macaques represent a significant crop pest to most of the world's subsistence farmers living in proximity with them (Lee and Priston 2005). Both the species, as was expected, were responsible for serious crop damage in the study area. The study, using semi-structured interviews, thus, tried to find out the extent of conflict and perception of locals towards both the species. It attempted to find out if the two species differed with respect to the crop damage they caused in the landscape.

Literature Review

Niche segregation as an explanation for co-existence has been studied for various taxa including invertebrates (Evans 1983) fishes (Donald and Alger 1993), amphibians (Griffiths 1986), reptiles (Pianka 1973), birds (Martin et al. 2004) and mammals (Fedriani et al. 1999, Bagchi et al. 2003).

Primates have evolved various adaptations which reduce interspecific competition (Sushma and Singh 2006). Collectively a number of studies have been done worldwide to study these adaptations in primates enabling them to co-occur. They are known to consume different plant species, plant parts, plants with varying primary and secondary chemicals and plants in different phenopases (Chapman 1987, Ganzhorn 1989, Sushma and Singh 2006, Yamagiwa and Basabose 2006). Horizontal distribution, vertical stratification, or use of different microhabitats (Ganzhorn 1989, Rakotondranary and

Ganzhorn 2012) are some other ways in which coexisting primate species tend to partition their niche (Lahann 2008).

Niche overlap studies have been conducted on neotropical primates: tamarins and titi monkeys (Nadjafzadeh and Heymann 2008), lemurs (Lahann 2008), Old World monkeys: baboons (Dunbar and Dunbar 1974) mangabeys (Wahungu 1998) and on apes: gorillas and chimpanzees (Tutin and Fernandez 1993). In Asia, a comparative study has been conducted in Bangladesh on northern pig-tailed macaques (*M. leonina*) and rhesus macaques (*M. mulatta*); it concludes that different food preferences and distinction in feeding levels from the ground allow these species to share resources in the same area without major conflict (Feeroz 2012). Another study in the limestone habitats of Nonggang, China reported that dietary overlap between rhesus macaque and Assamese macaque was only slight helping them to co-exist (Zhou et al. 2014)

Few studies have been conducted on resource partitioning between primates in India. One such study in Anaimalai Hills, Karnataka reported that there was a spatial and temporal segregation between sympatric lion-tailed macaques (*Macaca silenus*) and Nilgiri langurs (*Trachypithecus johnii*) (Sushma and Singh 2006). Differential diet was found to be responsible for limited niche overlap between bonnet macaques (*Macaca radiata*), lion-tailed macaques (*M. silenus*), and Hanuman langurs (*Semnopithecus entellus*) in Central Western Ghats, enabling them to co-exist (Singh et al. 2011). Similarly, significant differences in the diet and habitat utilization were held responsible for co-occurrence of three sympatric primate species, namely the stump-tailed macaque (*Macaca arctoides*), northern pig-tailed macaque and the rhesus macaque in the Hollongapar Gibbon Wildlife Sanctuary, Assam (Sharma 2012).

Availability of resources decides the dietary separation between species (Chapman 1987). Diet differentiation between chimpanzees and gorillas increased when fruit became scarce in winters (Tutin and Fernandez 1993). Similar trends have been found for other sympatric species as well (Schreier et al. 2009, Singh et al. 2011). On the flip side, a study done in Brazil mentions that overlap between food types consumed by the saddleback tamarins (*Saguinus fuscicollis*) and red-cap moustached tamarins (*S. mystax*) was higher during periods of lowest fruit availability when species resorted to a common food supply (Peres 1996).

Sufficient knowledge about the adaptations in primates enabling them to co-exist is lacking in India, more specifically in a mountainous landscape. Community studies like this may provide an insight into the kind of association between the two co-existing primates (Burton and Chan 1996). It may also help in assigning conservation priorities to the different species and their specific ecological niches (Mittermeier and Vanroosmalen 1981). A considerable variation exists within genus *Macaca* in their tendency to exploit anthropogenic environments (Lee and Priston 2005) This study in this context will be able to distinguish the macaque's propensity to co-exist with humans.

1.2 Objectives

a. To understand the extent of niche overlap and mechanisms of resource partitioning between two congeneric primate species: Assamese and rhesus macaque in the Askot landscape of Uttarakhand

b. To assess the extent of human-macaque conflict in the Askot landscape of Uttarakhand based on people’s perception

Chapter 2

STUDY AREA

The study was carried out in the Askot Landscape (29'46'45" to 30'27'45" N and 81'01'53'' to 80'16'25" E) located in the Western Himalaya in the Pithoragarh district of Uttarakhand. The study area forms a part of the Himalaya Biogeographic zone and West Himalaya Province (2B) (Rodgers and Panwar 1988). In the north, the area is demarcated by Tibet, and Kali River separates it from Nepal in the southeast. The western boundary is formed by left banks of Gori River (Samant et al. 1998). The landscape is a mixture of lower, middle and upper Himalayas. Elements of the Western Himalaya, the Central Himalaya and the Tibetan Plateau converge in this landscape making it regionally important site for species richness and biological distinctiveness. The landscape supports a wide variety of plants, mammals and bird species. Gori basin is known to be the orchid hotspot in the Western Himalaya. Bhotia and Ban Rajis are well-known tribes in the area contributing to its ethnic diversity (Dhar et al. 1997).

A segment of Askot range covering an area of 6.78 km^2 (29° 48' 53" to 29° 46' 46" N and 80° 21' 18" to 80° 23' 6" E) was chosen as intensive study area (Figure 1). The area was selected on the basis of information provided by locals regarding the places frequented by the two macaque species and the comparative ease of working in those areas. Elevation of the area ranged from 645 to 1741 m AMSL. The temperature varied from a minimum of 2˚C in winter to a maximum of 42˚C in spring (Figure 2). Average winter (December-February) and spring (March, April) temperatures were 13.7˚C and 20.9˚C respectively. Forest patch in the study site formed a part of the Paiyann Reserved Forest. The river Goriganga flowed on the western side of the study area, a road ran parallel to it. Area was characterized by steep slopes, northwest and southwest was the major aspect classes in the study area.

As per Champion and Seth (1968) classification, four dominant forest types were present in the study area:

a) Montane Valley Sal forest (3C/C2a(i)) having *Shorea robusta, Terminalia tomentosa, Litsea monopetala* and *Mallotus phillippensis* as dominant species.
b) Moist Mixed deciduous forest (3C/c3) with dominant species of *Toona ciliata, Syzygium cumini, Diploknema butyrace, Olea glandulifera*, *Ougeinia oojeinensis*, *Engelhardtia spicata Murraya koenigii*, *Emblica officinalis*, *Terminalia* and *Bauhinia spp.*
c) Himalayan Chir Pine forest (9/C1b) with *Pinus roxburghii, Glochidion velutinum* and *Wood fordia fruticosa* as dominant species.
d) Banj Oak forest (12/C1a) comprising of species namely *Quercus leucotrichophora, Myrica esculenta, Dendrobium spp., Lyonia ovalifolia* and *Sinarundinaria falcate*.

Apart from these four dominant vegetation types some small patches were characterized by Subtropical Riverine Forest (8C/c1) with *Macaranga pustulata*, *Syzygium cumini*, *Castanopsis tribuloides*, *Maesa indica* as dominant species. Species of *Macaranga* in the Gori valley represented the westernmost limit for these plant communities.

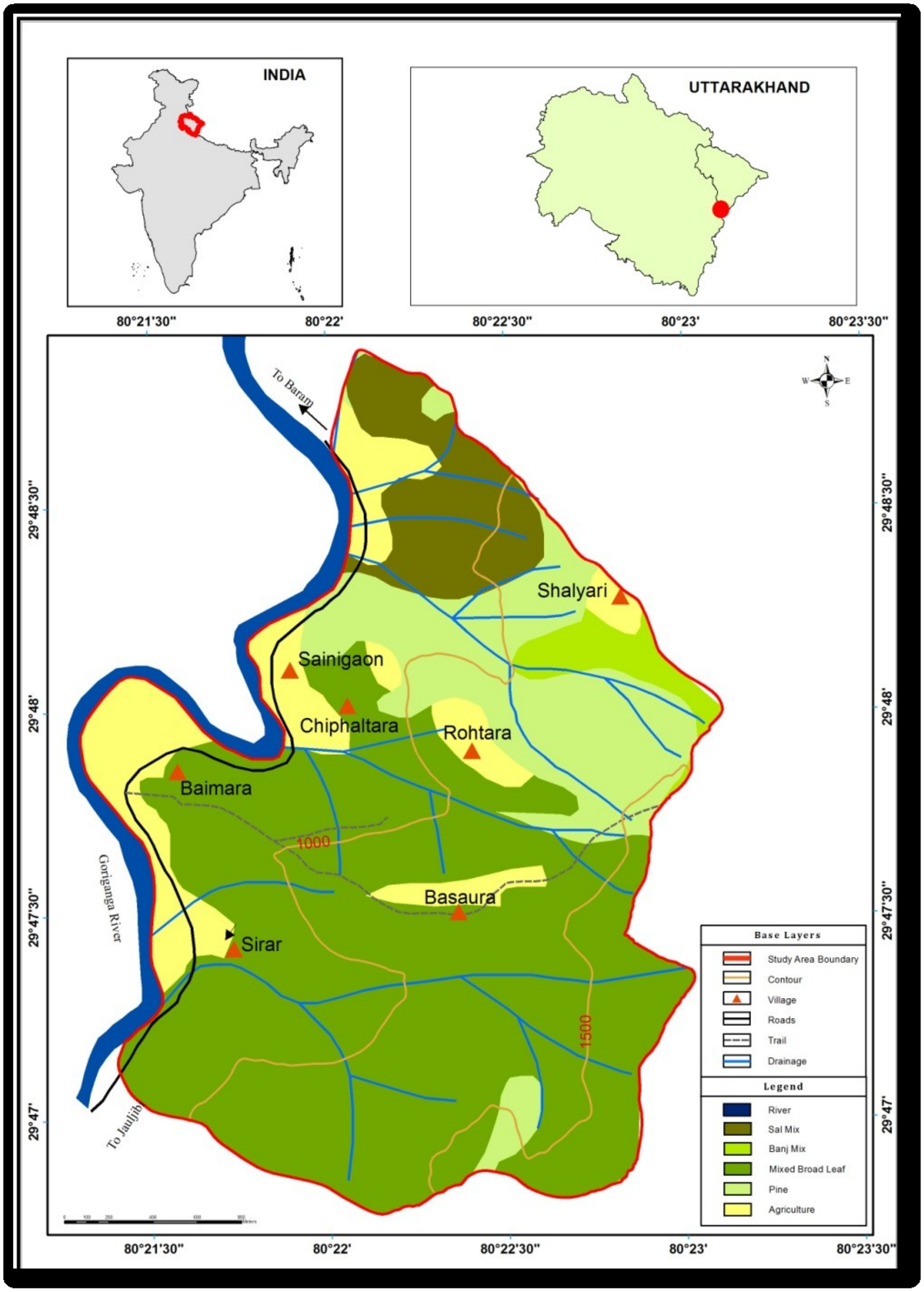

Figure 1. Map of the study area adjoining the Gori river in the Askot landscape where intensive follows of the Assamese and rhesus macaques were carried out.

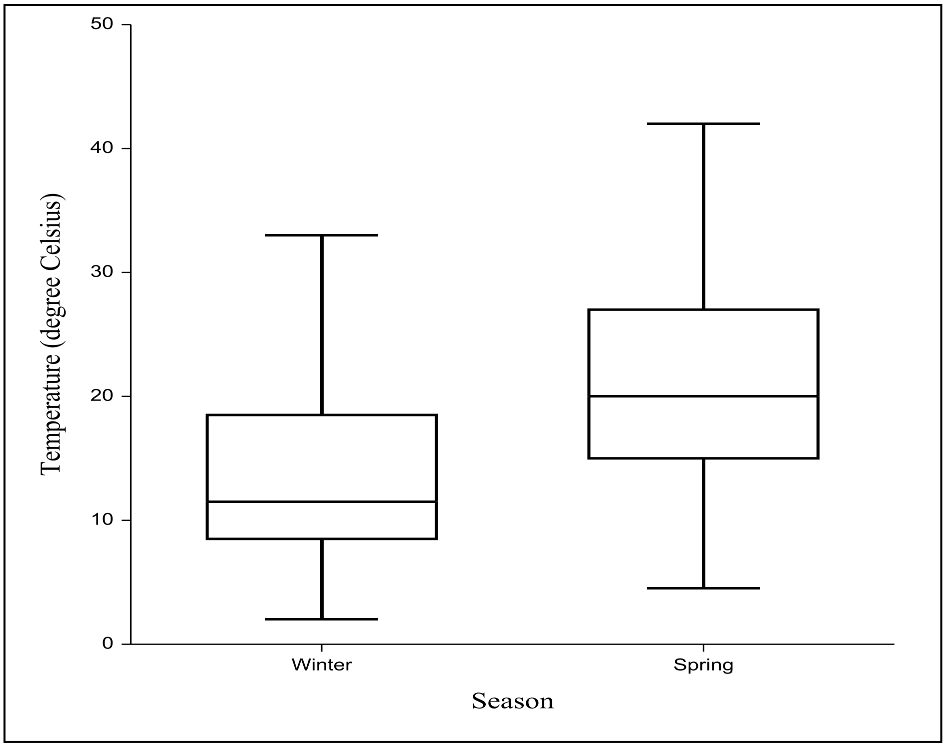

Figure 2. Box plot showing variation in temperature across winter and spring season. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The horizontal bar in the middle of the box represents the median value and the outliers are shown as whiskers. [Winter (n=1824), spring (n=1200)]

Apart from the Assamese and the rhesus macaques, other major mammalian species in the study area included Himalayan langur(*Semnopithecus schistaceus*), wild pig (*Sus scrofa*), barking deer (*Muntiacus muntjak*), goral (*Naemorhedus goral*), Himalayan serow (*Capricornis thar*), and leopard (*Panthera pardus*) (Plan and Division 2011). There were seven villages within the study area. Most of the people in these villages had marginal lands, not suffice enough for subsistence. Agricultural fields in the area were usually close to settlements. Main crops grown during the study period were wheat, masoor, barley, potato, onion, gram, pea, radish, cauliflower, and cabbage. The human settlements were fragmented in the whole area. State-owned NHPC has been working out a hydroelectric project on the Goriganga river in the area

Chapter 3

METHODS

3.1 Selection and habituation of the study troops

For the study period of five months, two troops each of Assamese (A1, A2) and the rhesus (R1, R2) macaques were selected (Table 1). The criteria for troop selection were their proximity to each other, age-sex characteristics of the troops, terrain features, and logistics. A1 was the biggest troop with troop size of 44 individuals, this troop primarily ranged along the roadside forest, occasionally venturing into the agriculture fields. Troop A2 was an all-male troop with six troop members; this troop was never seen near habitation and remained in the mixed broadleaf forest whenever it was located. Troop R1 with 35 individuals remained more to the lower regions in the area, whereas troop R2 with 22 individuals was most of the times sighted at the higher elevations in Chir pine forest. Initial days were spent following these troops in order to habituate them to my presence.

Table 1. Age-sex structure of the two study troops each of Assamese and rhesus macaques in the study area.

Species	Troop ID	Troop Size	Adult Males	Adult Females	Sub-adults	Juveniles	Infants
Assamese Macaque	A1	44	7	9	10	12	6
	A2	6	2	0	2	2	0
Rhesus Macaque	R1	35	4	7	9	11	4
	R2	22	3	5	6	6	2

Note: R1 and R2 troops had 2 and 1 infants respectively in March adding to the overall troop size

3.2 Troop follows

Attempts were made to follow each troop from morning till evening for five days in a row, continuously. Each such 'five-day follows' represented a session. However, there were instances when full day follows or continuous five-day follows were not possible due to rugged terrain, bad weather conditions, and elusive behaviour of the macaques. In such cases, when favorable conditions returned, the troop was located again and followed to complete the session. During the study period, a total of 14 such sessions were carried out, four for each troop, except for the troop A2 for whom, only winter sessions could be completed (Table 2). During spring season attempts were made to locate the troop on various occasions but these turned out to be unsuccessful. Due to time constraints, the fourth session of troops R1 and R2 had to cut down to four days. Among these four sessions per troop, two were completed until late February and were considered as winter sessions and the remaining two were carried out in March and April and were considered as spring sessions.

Table 2. Sampling schedule for the four macaque troops depicting all four sessions (date-wise) when full day follows were made

Observation Cycle (Session)	***1***	***1, 2***	***1, 2***	**3,4**	**4**
		Winter		**Spring**	
Troop ID	**December 2016**	**January 2017**	**February 2017**	**March 2017**	**April 2017**
A1	*12,13,14,15,16*	*21,22,23,24,25*		2,3,4,5,6 27,28,29,30,31	
A2		*30,31*	*1,2,3, 4,6,7,8,9*	Troop undetected	
R1	*25,28,29,30,31*		*11,12,13,14,15*	9,10,11,13,14 21	11,12,13
R2		*12,13,14*	*20,21* *22,23,24,25,26*	20,22,23,24	3,4,7,9,10

3.3 Data Collection

3.3.1 Time-activity budgets

Observations were made on the two troops at a distance of 5-100 m following Instantaneous scan sampling (Altmann 1974). A scan lasted for five minutes and was repeated every ten minutes. Nikon 8×40 binoculars were used to observe the macaques. The scans were done either from the left or right of the observer in a semicircular fashion to avoid repeat observations of the same individual. Age and sex of the scanned individuals (adult male, adult female, subadult, juvenile, and infant) along with their respective activity were noted down. As the troops were large and most of the times widely spread out, except for the A2 troop, all members could not be detected in a single scan. Therefore only the visible members of the troop were scanned for various activities, broadly clubbed into the five categories (Table 3).

Table 3. Operational definitions of behaviours

Behaviour	Operational definition
Feeding	Food handling, ingestion and active search for fallen seeds, small prey items or insects
Resting	Sleeping, sitting and period of inactivity
Moving	Locomotor behaviour that changed the spatial position of an individual
Social Interaction	Affiliative (touching, playing, allogrooming), Agonistic, Dominance-subordinate, and Sexual behaviours
Others	Autogrooming, vigilance, urinating, defecating, vocalizing, yawning and sneezing

Instantaneous scan sampling yielded a total of 11823 and 17772 scan samples over a time of 281.32 and 375.49 hours for Assamese and rhesus macaques respectively. The number of scan samples for adult males and adult females of Assamese and rhesus macaques were 2794 and 2329 respectively. Table 4 and Table 5 provide the summary of season-wise, species-wise and troop-wise scan samples and total contact hours for both the species.

Table 4. Sampling effort on the adults, subadults, and juveniles of the two macaque species

Species	Troop ID	Winter		Spring		Total	
		Total Contact Hours	Scan Samples	Total Contact Hours	Scan Samples	Total Contact Hours	Scan Samples
Assamese macaque	A1	96.83	3562	103.83	6413	200.66	9975
	A2	80.66	1848	Troop undetected		80.66	1848
Rhesus macaque	R1	107.58	4107	82.00	5645	189.58	9752
	R2	95.08	4736	90.83	3284	185.91	8020

Table 5. Sampling effort on the adults of the two macaque species

Species	Troop ID	Winter		Spring		Total	
		Total Contact Hours	Scan Samples	Total Contact Hours	Scan Samples	Total Contact Hours	Scan Samples
Assamese macaque	A1	96.83	863	103.83	1307	200.66	2170
	A2	80.66	624	Troop undetected		80.66	624
Rhesus macaque	R1	107.58	632	82.00	496	189.58	1128
	R2	95.08	719	90.83	482	185.91	1201

3.3.2 Diet

When during a scan an individual was seen feeding, the plant species and the plant parts eaten were noted down. Plant parts were categorized as leaf (young/mature), fruit and seed (ripe/semi-ripe), flower and bud (young/mature), stem and root (young/mature). For the plant species that could not be recognized in the field, a herbarium was made for later identification. These specimens were identified at the Wildlife Institute of India Herbarium. Whenever seen feeding, animal's feeding level, divided into 4 strata: Ground, lower (< 3 m) middle (3-5 m) and upper (>6 m) canopy layer was also noted down.

3.3.3 Movement, ranging and habitat use

Location of the troop was monitored at an average of 30 m distance interval by recording geographical coordinates of the approximate center of the troop with the help of a handheld GPS (Garmin etrex 10).Every time a GPS location was taken, habitat characteristics were noted down to analyze the habitat use by the two macaque species. Habitat of the area was broadly characterized into five categories- cliff (included bare or vegetated areas of steepest slope), mixed broadleaf forest (forested areas with very dense or moderately dense forest), open forest (open forest of various species e.g. *Pinus roxburghii*, *Shorea robusta*), scrub (Forest with small or stunted trees) and agriculture field (area in and around agriculture fields). To determine roosting site preferences of the two species, every evening, after the last scan of the day was over; characteristics of the roosting sites were noted down.

3.3.4 Conflict

Semi-structured interviews were conducted to gather information on the level of conflict with macaques and people's perception on both the macaque species. A total of 82 individuals from 33 households were interviewed from in and around the intensive study area. While interviewing, care was taken to involve members of different age and sex, occupation and landholdings. In each household, one individual or group of individuals were interviewed. Questions asked were related to crops planted, crop damage by macaques, seasonal losses from wildlife and their perception regarding macaques. The format of the interview has been presented in Appendix I.

3.4 Analytical methods

3.4.1 Time-activity budget

After an initial exploration of the data, it was decided to exclude records for infants, juveniles, and subadults as they were not independent behavioural subjects. Percentages of the number of individuals engaged in each activity category among the total number of activities were used to construct the time-activity budgets. Separate activity budgets were constructed for males and females of four troops for winter and spring seasons respectively. Although when analyzing inter-specific differences data for two troops of each species was clubbed. Non-parametric Mann-Whitney U-Test (McDonald 2009) was performed to test for the differences in the activity budgets of the two species for the two seasons separately.

3.4.2 Diet

The number of feeding records for a food item was divided by the total records of feeding to get the percentage of a particular food item in the diet of two macaques. Food category composition was expressed as the percentage of different plant parts (leaf, flower, fruit, and stem) in the diet of the study troops for winter and spring months separately. Likewise, the percentage of different food types (tree, shrub, climber, agricultural crops) contributing to the diet of two macaque species was computed. Percentage of the time spent on the ground, low, middle and high canopy levels was also calculated.

G-test (McDonald 2009) was used to check for the differences in food category composition along with differences in the foraging heights between Assamese and rhesus macaques for both winter and spring season.

Niche breadth of the two macaque species was calculated using Levin's index (Hurlbert 1978, Krebs 1989)

$$B = \frac{1}{\sum Pj^2}$$

Where,

B = Levin's measure of niche breadth, and

Pj = Proportion of individuals found in or using resource state j

To standardize niche breadth to express it on a scale from 0 to 1.0, the following measure for standardized niche breadth (Hurlbert 1978) was used:

$$B_{A=} \frac{B-1}{N-1}$$

Where,

B_A = Levin's standardized niche breadth

B = Levin's niche breadth

N = Number of possible resource states

Food niche overlap between the two macaque species was calculated by Pianka's Index (Pianka 1973, Krebs 1989):

$$Ojk = \frac{\Sigma PijPik}{\sqrt{\Sigma Pij}^2 \Sigma Pik^2}$$

Where,

Ojk = Pianka's measure of niche overlap between species j and species k

pij = Proportion resource i is of the total resources used by species j

pik = Proportion resource i is of the total resources used by species k

n = Total number of resources states

Pianka's index varies between 0 (total separation) and 1 (total overlap)

3.4.3 Movement, ranging and habitat use

Location data of the four troops was imported to the software Arc GIS 9.3. Daily distance traveled was computed for the four troops for winter and spring season. Box plots were constructed to check for the variation in daily movement of all the four troops. Mean daily movement was calculated species-wise. Differences in the daily movement of two species were analyzed by Mann-Whitney U-test.

The conventional Minimum Convex Polygon (MCP) method has been used to determine the home ranges of the four troops of Assamese and rhesus macaques using ArcMap 9.3. In the case of troop A1, the adjusted MCP method was used. The area which fell outside its home range (due to terrain features in the 2-D image) was clipped to display only the actual home range.

Habitat use was expressed as the percentage of locations in each habitat type. Roosting sites were imported to Arc GIS to see their distribution in the study area. Characteristics of sleeping sites were explained based on the field observations. Average distance from human habitation was computed and compared for both the species. G-test was performed to see the differences in habitat use and in distance of both species from human habitation.

3.4.4 Co-occurrence of two macaque species

In order to analyze co-occurrence of the two macaque species, a null model analysis was used to test whether the observed patterns of locations of two macaque species were consistent with Diamond's assembly rules of non-random patterns of species co-occurrence (Cody and Diamond 1975). Location data of every single troop was overlaid on a 50x50 m grid size, the maximum area in which troop members were spread at a time. Using this data, a presence-absence matrix was created by assigning 1 to a grid if a particular species was 'present' and 0 if it was 'absent'. For the analysis, each grid was treated as a 'site' and each species was represented as a row.

Checkerboard score (C-score) was used to evaluate whether species co-occurrence patterns were segregated or aggregated in space (Stone and Roberts 1990). The number of checkerboard units (CU) for each species pair is calculated as:

$$CU = (r_i - S)(r_j - S)$$

Where, S = number of shared sites (sites containing both species) and

r_i and r_j = Row totals for species i and j.

The C-score is the average of all possible checkerboard pairs, calculated for all species that occur at least once in the matrix. The calculated C-score is then compared with 5,000 randomly generated 'pseudo-communities' using the sequential-swap randomization algorithm and fixed-fixed null model algorithms. In a competitively structured community, the C-score is expected to be significantly larger than expected by chance alone. Species that always occur together (complete aggregation) will have a C-score of zero. The greater the segregation in species, the larger the C-score will be. The C-score is based on the average co-occurrence of all species-pairs and therefore, relatively insensitive to noisy data (Gotelli 2000).

Null assemblages were created in EcoSim using a fixed-equiprobable model (SIM2), an algorithm robust to both type I and type II error (Gotelli 2000). In this model, row totals (= number of sites a species occupies) are held constant and sites are treated as equally suitable for species occupation. Standardized Effect Size (SES) values were calculated which reports the number of standard deviations the observed index is above or below the mean of the randomized assemblage to allow comparison among multiple tests (Gurevitch et al. 1992) It is calculated as

$$\frac{Iobs - Isim}{SDsim}$$

Where, I_{obs} and I_{sim} are the observed indexes and simulated index respectively and SD_{sim} is the standard deviation of the simulated index.

Assuming a normal distribution of deviations, approximately 95% of the SES values should fall between –1.96 and 1.96. Values larger than 1.96 indicates non-random species segregation, and values lower than –1.96 indicate non-random species aggregation (Wittman et al. 2010)

Along with determination of co-occurrence between species, same analysis was repeated to test the co-occurrence patterns between different troops.

3.4.5 Conflict

G-test was used to test for the differences between the level of crop losses by the two macaque species. Compiling the conflict data, broad comparisons on people's perception for the two macaque species were drawn.

Chapter 4

RESULTS

4.1 Time-activity budget

For the entire course of the study, feeding was the dominant activity for both Assamese macaque males (35%) and females (39%). This was followed by resting (28%) in males and social interaction (28%) in the case of females. Rhesus macaque males were primarily engaged in resting (41%) and females in feeding (36%). Males spent 28% of their time feeding and females spent 23% of their time resting. Time-activity budgets of males and females for the four study troops have been depicted across two seasons in Figures 3 and 4. Males of Assamese macaque troops spent more time in feeding where troop A1 spent slightly more time feeding in winter. Males of rhesus macaque troops spent maximum time in resting in both seasons; however time spent resting increased in spring. In case of females no major inter troop variations were observed.

Significant variations were found in the time-activity budget of Assamese and rhesus macaque males and females in both winter and spring seasons (Table 6 and Table 7). In winter Assamese macaques spent more time feeding and rhesus macaques in moving. For two seasons combined, Assamese macaques tended to interact more and rest less when compared to rhesus macaques (Mann Whitney U Test, $p<0.05$; Table 6, Figure 3). However considering only females of the species, they spent similar time in feeding and resting (Mann Whitney U Test, $p>0.05$) but the Assamese macaque females tended to engage more in social interactions and less in moving around when compared to rhesus macaque females (Mann Whitney U Test, $p<0.05$; Table 7, Figure 4).

Table 6. Time-activity budgets of the adult males of the two study macaque species in winter and spring along with the results of Mann-Whitney U test

Season	Species		Feeding	Resting	Social Interaction	Moving	Others
Winter	Assamese macaque	(%)	38	24	18	12	8
		No. of Scans	558	362	264	182	121
	Rhesus macaque	(%)	27	38	11	18	6
		No. of Scans	370	523	149	247	88
	n_1=10	Z	3.177	-3.744	2.798	-3.138	1.059
	n_2=10	p	<0.05	<0.05	<0.05	<0.05	0.28
Spring	Assamese macaque	(%)	34	31	16	13	6
		No. of Scans	437	403	213	172	82
	Rhesus macaque	(%)	28	43	8	17	4
		No. of Scans	280	422	75	164	37
	n_1=10	Z	-1.265	3.470	-3.023	1.151	-2.615
	n_2=9	p	0.20	<0.05	<0.05	0.13	<0.05

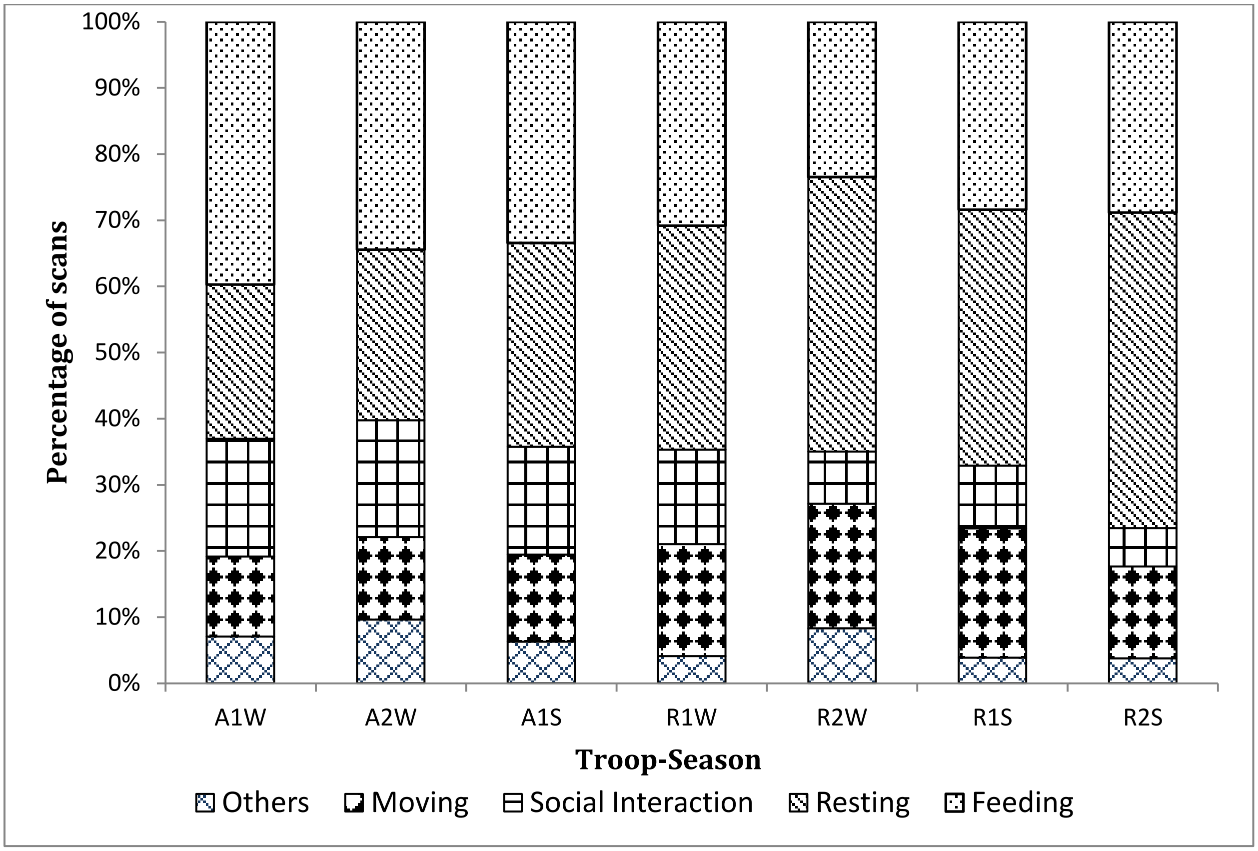

Figure 3. Time-activity budgets of the four macaque troop males (A1, A2, R1 and R2) during the winter (W) and spring (S) seasons

Table 7. Time-activity budgets of the adult females of the two study macaque species in winter and spring along with the results of Mann-Whitney U test

Season	Species		Feeding	Resting	Social Interaction	Moving	Others
Winter	Assamese macaque	(%)	39	18	28	11	4
		No. of Scans	370	176	265	101	41
	Rhesus macaque	(%)	35	24	18	19	4
		No. of Scans	704	495	358	392	80
	n_1=10	Z	0.264	-1.852	2.608	-3.138	0.189
	n_2=10	p	0.79	0.06	<0.05	<0.05	0.85
Spring	Assamese macaque	(%)	40	18	25	13	4
		No. of Scans	745	327	455	244	73
	Rhesus macaque	(%)	37	23	17	21	2
		No. of Scans	648	398	303	374	44
	n_1=10	Z	-0.939	1.511	-2.408	3.306	-1.144
	n_2=9	p	0.34	0.13	<0.05	<0.05	0.25

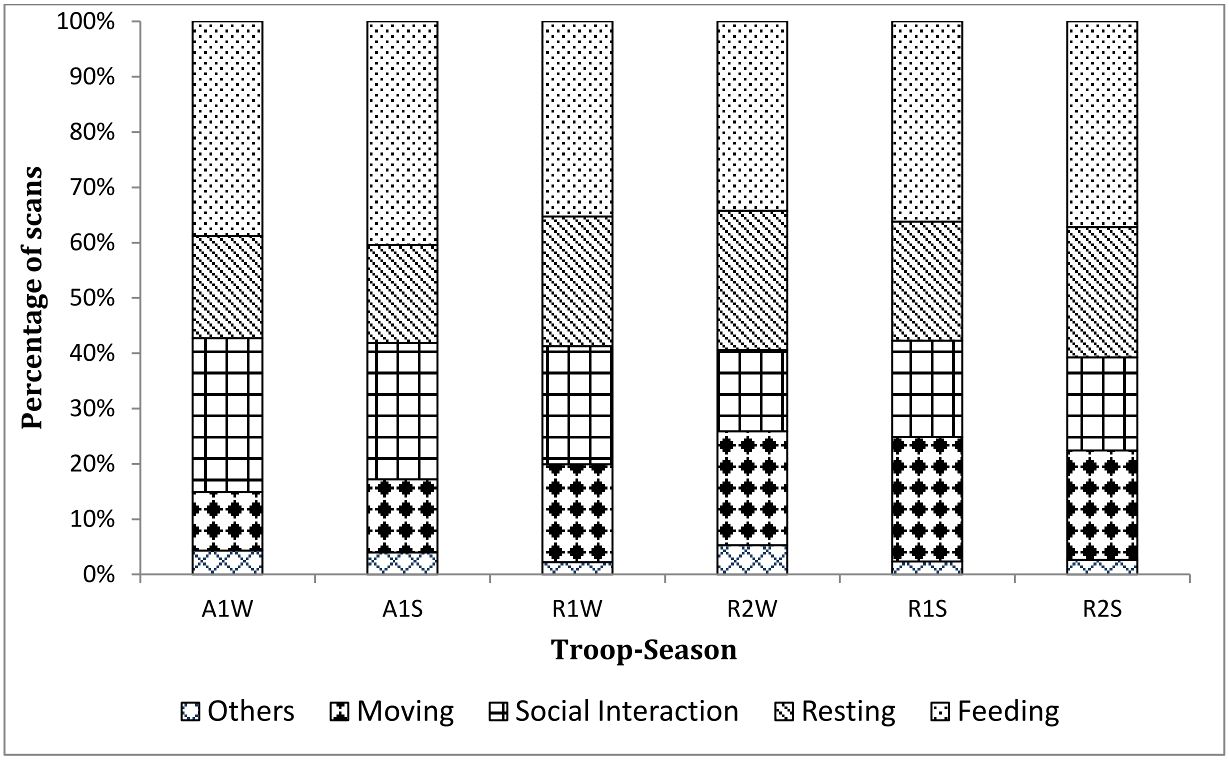

Figure 4. Time-activity budgets of the four macaque troop females (A1, A2, R1 and R2) during the winter (W) and spring (S) seasons

In the case of females, the two species differed significantly in social interaction and moving in both winter and spring seasons, although no significant differences were found between feeding and resting. In winter, Assamese macaque females spent more time in social interaction ($Z=2.608$, $p<0.05$, n_1, $n_2=10$) and rhesus macaque females in moving ($Z=-3.138$, $p<0.05$, n_1, $n_2=10$). In spring too, Assamese macaque females spent more time in social interaction ($Z=-2.408$, $p<0.05$, n_1, $n_2=9$) and rhesus macaque in moving ($Z=-3.306$, $p<0.05$, n_1, $n_2=9$).

4.2 Diet

4.2.1 Food items consumed by two primate species

A total of 84 plant species were consumed by two macaques over the entire study period (Appendix II) out of which Assamese macaque fed on 65 and rhesus macaque on 56 plant species. In total, 37 plant species were shared by both the macaques (44% of total plant species). In winter 69 food plants were consumed by the two macaque species, of which Assamese macaque and rhesus macaque ate 45 and 46 species, with 25 species (36%) in common. In spring a total of 54 food plants were consumed by the two species, of which 42 and 29 species were fed by Assamese macaque and rhesus macaque respectively, having 17 food items (31 %) in common. The plant species that accounted for >1% of total feeding scans, including agriculture crops and miscellaneous items were considered as the major food plants (Table 8). Within agriculture crops macaques predominantly fed on Wheat, Barley and masoor as these were the major crops planted in the study area. Major food items (26) contributed to a large proportion of the total diet (Assamese macaque: 88%; rhesus macaque: 89.5%). In winter only five plant species namely *Olea glandulifera*, *Maesa indica*, *Cayratia pedata*, *Ficus microcarpa* and *Bischofia javanica* formed 56.5% of the Assamese macaque's diet. In the case of rhesus macaque food items: *Ficus nervosa*, Agriculture crops, *Bauhinia variegata* and *Mucuna puriens* formed 63% of the total diet. In spring, six food items *Pyrus pashia*, *Mallotus philippensis*, *Urtica dioca*, Agriculture crops, *Quercus glauca* and *Woodfordia fruticosa* formed 74% of the total diet for the Assamese macaque. For the rhesus macaque, four food items with agricultural crops on the top, followed by *Mallotus philippensis*, *Pueraria tuberosa* and *Woodfordia fruticosa* formed 74.3% of the total food items. In winter, no major food plants were shared by the two species whereas in spring, both the macaques shared three major food items (agricultural crops, *Mallotus philippensis* and *Woodfordia fruticosa*).

Table 8. List of major food plants consumed by the study Assamese and rhesus macaque troops along with habit, parts eaten and phenological state

Family	Food items	Habit	Assamese macaque			Rhesus macaque		
			Parts eaten[a]	Phenological state[b]	(%F)[c]	Parts eaten[a]	Phenological state[b]	(%F)[c]
ACANTHACEAE	*Eranthemum pulchellum*	Shrub	F	M, Y	1.8			
ARACEAE	*Rhaphidophora glauca*	Liana	L, ST	M	1.4			
ASCLEPIADACEAE	*Hoya longifolia*	Climber	L, R	M	1.0			
CAESALPINIACEAE	*Bauhinia variegata*	Tree	B, F, ST	M	0.1	B, F, S	Y	5.7
CELASTRACEAE	*Elaeodendron glaucum*	Tree	S			S	R, SR	2.1
EUPHORBIACEAE	*Bischofia javanica*	Tree	FR	SR	1.6	FR	SR	0.4
	Mallotus philippensis	Tree	S, ST	Y	8.6	S, ST		12.7
FABACEAE	*Indigofera heterantha*	Shrub	F	M	0.7	F	Y, M	1.5
	Flemingia bracteata	Shrub	R, S			R	R, SR	1.5

Family	Food items	Habit	Assamese macaque			Rhesus macaque		
			Parts eaten[a]	Phenological state[b]	(%F)[c]	Parts eaten[a]	Phenological state[b]	(%F)[c]
	Mucuna puriens	Climbing shrub	S			S	R	2.7
	Pueraria tuberosa	Climber	F			F	Y, M	4.6
	Quercus glauca	Tree	L, F	Y, M	6.2	F	Y, M	0.9
LYTHRACEAE	*Woodfordia fruticosa*	Shrub	F	M	3.3	F	Y, M	2.1
MELIACEAE	*Toona ciliata*	Tree				L,ST	Y	1.8
MENISPERMACEAE	*Cocculus laurifolius*	Tree	L	Y	1.7			
MORACEAE	*Ficus hispida*	Tree	L, FR	R, SR	1.0			
	Ficus microcarpa	Climber	L	Y	5.1	L	Y	0.0
	Ficus nervosa	Tree	FR	R	0.2	FR	R, SR	14.6
	Ficus semicordata	Tree	FR, L	R, SR	1.1			
OLEACEAE	*Olea glandulifera*	Tree	L, FR	Y, M	7.9	L	Y, M	0.2
PRIMULACEAE	*Maesa indica*	shrub	LR, FR, F	R, SR	6.2	FR	Y	0.3
ROSACEAE	*Pyrus pashia*	Tree	F, FR	Y	13.9	F, FR	Y, M	0.5
URTICACEAE	*Urtica dioica*	Herb	L, F	M, Y	7.6	F	Y	0.2
VITACEAE	*Cayratia pedata*	Climber	L, FR	Y, M	4.8	FR	Y, M	0.1
		Herb,			7.7			29.5

Family	Food items	Habit	Assamese macaque			Rhesus macaque		
			Parts eaten[a]	Phenological state[b]	(%F)[c]	Parts eaten[a]	Phenological state[b]	(%F)[c]
	Agricultural crops: Wheat, Barley & Masoor (95%) Onion, Black gram, Potato, Tomato, Cabbage, Radish, Cauliflower & Malta orange (5%)	Shrub/ Tree						
	Miscellaneous	Insects, fungi, resin, unknown			7.3			8.1

Parts eaten[a]: L leaf, F flower, FR fruit, R root, B bud, S seed, ST stem **Phenological state**[b]: M mature, Y young, R ripe, SR semi-ripe **(%F)** [c] percentage of total feeding records

The food sources of the two macaque species included trees, herbs, shrubs, climbers, ferns, lianas, orchids, agricultural crops, insects, fungi and some unidentified items. For the two seasons combined trees (44.5%) and herbs/shrubs (23%) formed the dominant source of the Assamese macaque's diet whereas trees (44%) and farm crops (30%) were the dominant food sources contributing to the diet of the rhesus macaque (Fig. 5).

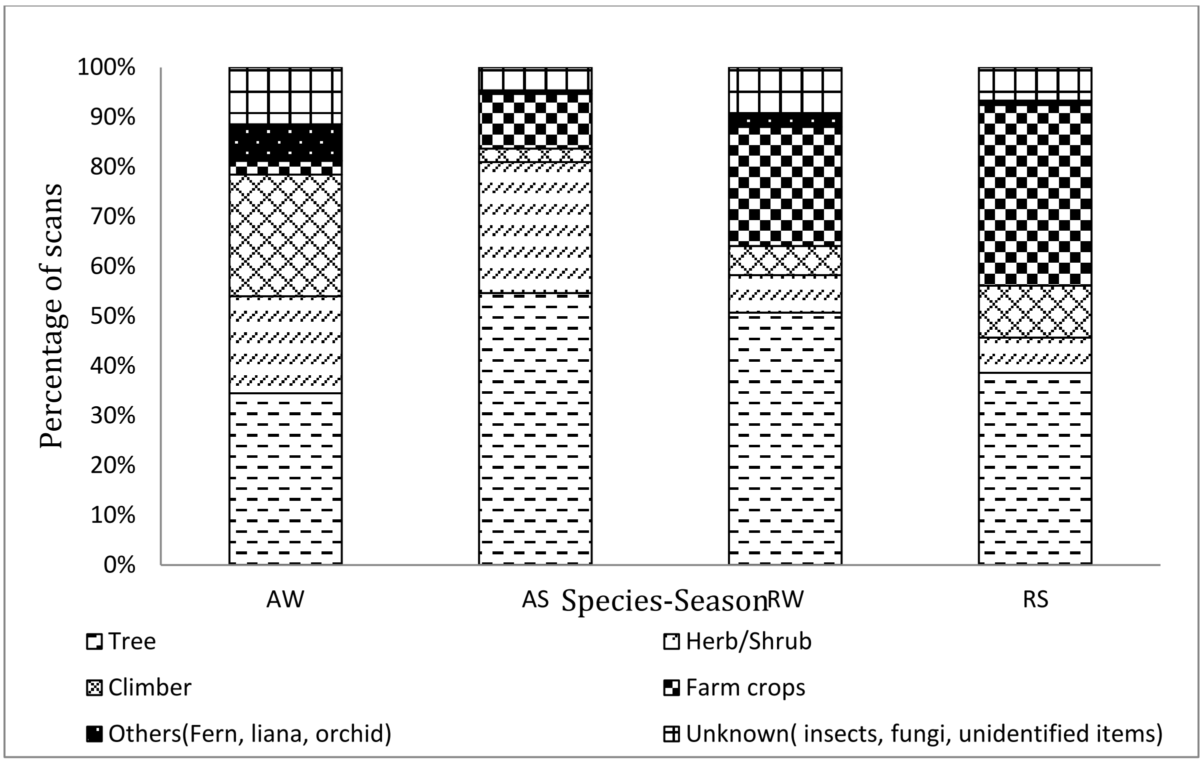

Figure 5. Percentage of different food sources for Assamese (A) and rhesus (R) macaques during the winter (W) and spring (S) seasons

4.2.2 Use of select plant parts

There was a marked inter-specific variation in consumption of different plant parts. The two macaque species differed significantly in the plant parts eaten both in winter ($G=1110.72$, $df=3$, $p<0.001$) and in spring ($G=359$, $df=3$, $p<0.001$). In winter, leaf (67%) was the dominant plant part in the Assamese macaque's diet that changed to flower and bud (51%) in spring. For rhesus macaques, fruit and seed remained the dominant plant parts for both winter (64%) and spring (47%). Two seasons combined, leaves constituted the major part of Assamese macaque's diet (43%), followed by fruit and seed (34%). Fruit and seed (57%) were the dominant plant part fed by rhesus macaques, followed by flower and bud (27%) (Figure 6)

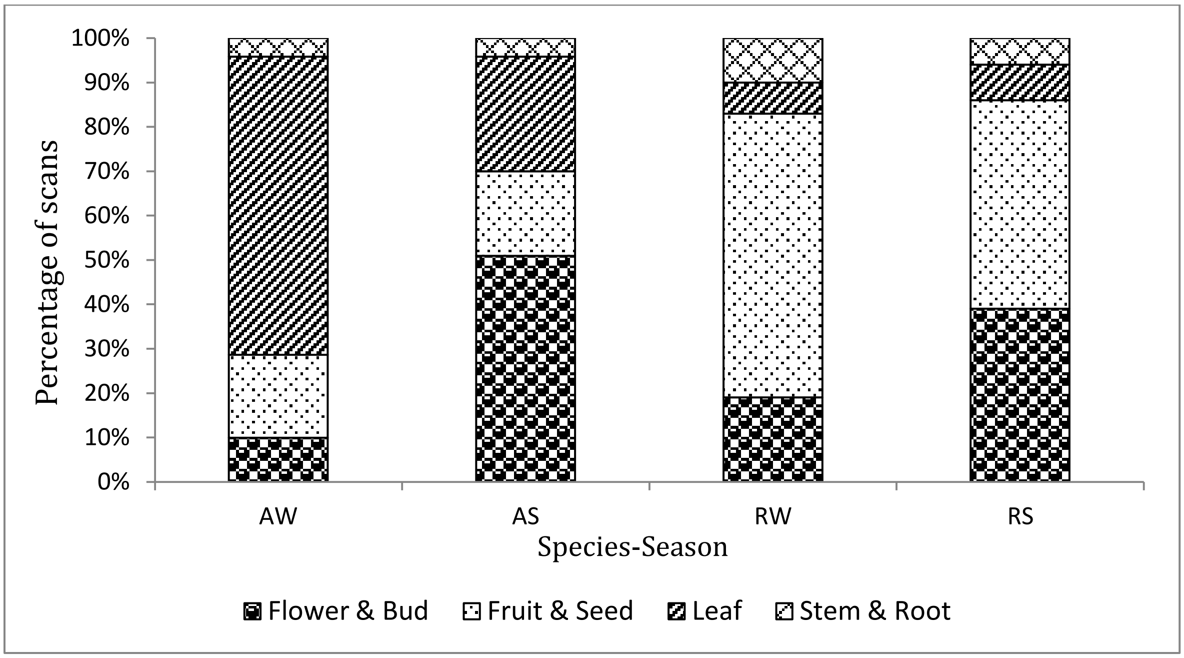

Figure 6. Percentage of different plant parts in the diet of Assamese (A) and rhesus (R) macaques during the winter (W) and spring (S) seasons

4.2.3 Niche breadth and overlap

The standardized niche breadth estimated using Levin's index was 0.22 for the Assamese and 0.11 for the rhesus macaque. It ranged from 0.2 in winter to 0.12 in spring for the Assamese macaque and 0.18 in winter to 0.12 in spring for the rhesus macaque respectively. The food niche overlap between two macaque species was 0.43. Niche overlap increased from 0.16 in winter to 0.51 in spring.

4.2.4 Feeding heights

Feeding height categories used by the two macaque species in winter and spring seasons are shown in Figure 7. In most of the scans, both the species were observed either on the ground or 3-5 m above ground. However, the difference among the species for feeding heights was significant both in winter ($G= 231.3$, $df= 3$, $p < 0.001$) and spring ($G=187.2$, df= 3, p <0.001). Assamese macaques spent more time at the middle level (winter 41%; spring 40%). Rhesus macaques, on the other hand, fed primarily on the ground (winter 46%; spring 50%).

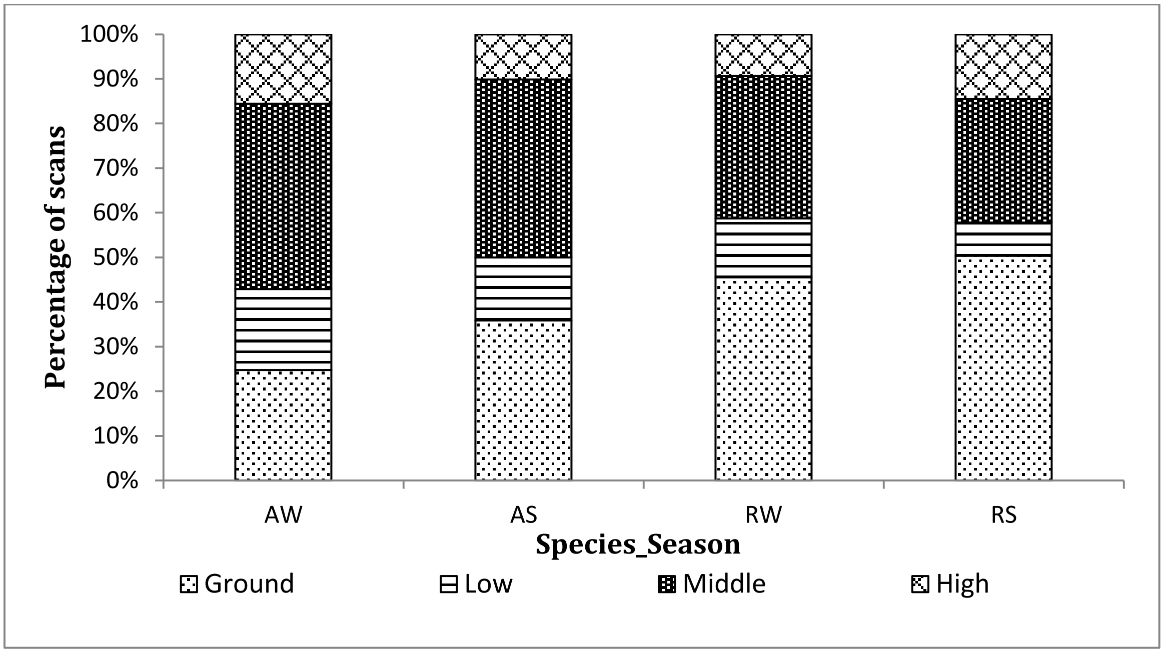

Figure 7. Percentage of individual (adult, subadult, juvenile and infant) Assamese (A) and rhesus (R) macaques observed at various substratum heights during the winter (W) and spring (S) season (Low <3 m, Mid 3-5, High >5 m)

4.3 Spatial use

4.3.1 Day range

Assamese macaque had a mean day range of 0.62±0.06 km in winter, and 1.15±0.11 km in spring whereas the mean day range of rhesus macaques varied from 1.25±0.18 km in winter to 1.30±0.12 in spring. There was a significant difference between day ranges of the two species in winter ($Z= -2.60$, $p=0.009$, n_1, $n_2=10$). In spring, however, no significant differences were found between day ranges of the two species ($Z=0.53$, $p=0.595$, $n_1=10$, $n_2=9$). Figure 8 depicts variation in the day range of the study Assamese and rhesus macaque troops for winter and spring seasons.

4.3.2 Home range

The winter, spring and overall home ranges of the study troops, have been presented in Figure 9, 10 and 11. Troop A1 with the maximum number of individuals had the biggest home range which overlapped with the home ranges of other three troops. Troop A2 with only six individuals had smallest home range overlapping partially with troop A1. Home ranges of troops R1 and R2 were situated in between the two Assamese macaque troops. Home ranges were larger in the winter whereas home range area reduced as spring approached (Table 10). The area of overlap between home ranges of the two species is given in Table 11.

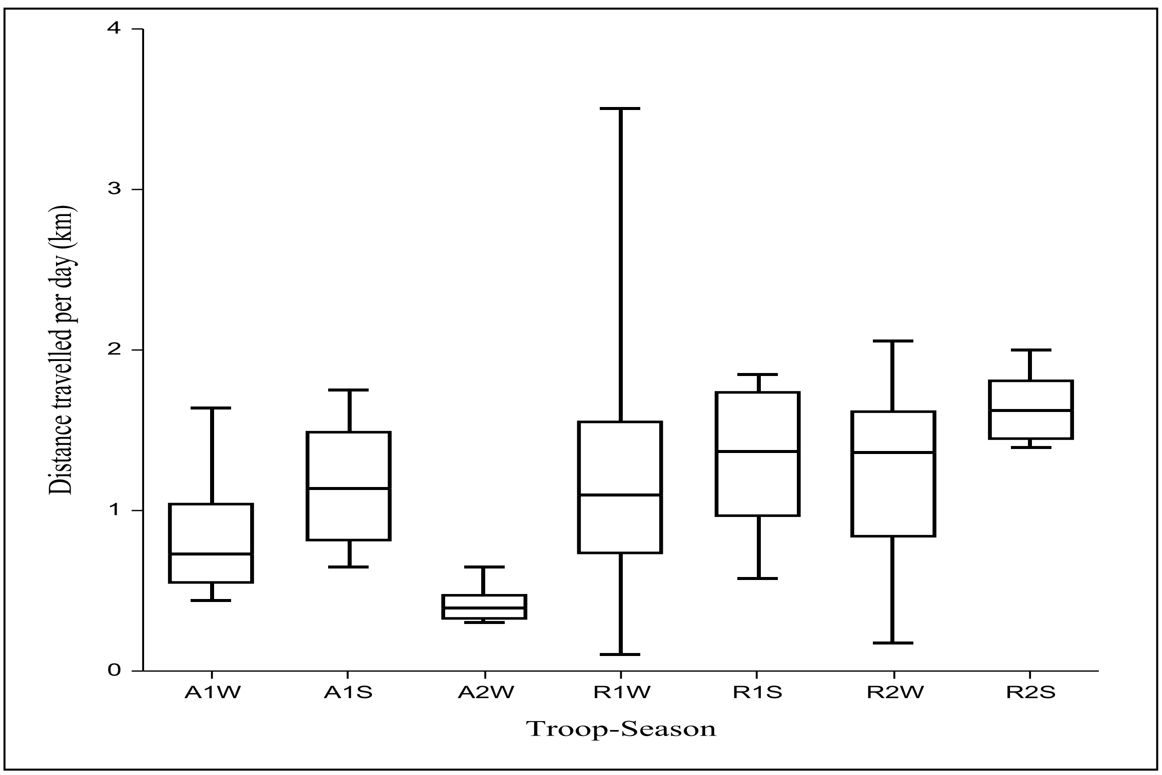

Figure 8. Box plot showing variation in the day range of the study Assamese and rhesus macaque troops, A1, A2, R1 and R2 during the winter (W) and spring (S) seasons. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The horizontal bar in the middle of the box represents the median value while the outliers are shown as whiskers.

Table 9. Home range area in ha (100% MCP) of the Assamese and rhesus macaque troops

Study troop	Fixes	Winter home range	Fixes	Spring home range	Fixes	Overall home range
A1*	147	**176**	166	**134**	313	**237**
A2	108	**26**	Troop not detected		108	**26**
R1	175	**118**	129	**98**	304	**131**
R2	157	**102**	139	**57**	296	**130**

* Adjusted MCP method has been used in case of troop A1

Table 10. Home range area overlaps (ha) between the Assamese and rhesus macaques study troops along with percentage overlap in parenthesis

		A2	R1	R2
Winter	A1	7.1(3.5)	88.6(30)	28.6(10)
	R1	No overlap		13.8(6)
Spring	A1	Undetermined*	38.5(16.5)	33.4(17)
	R1	Undetermined		22(14)
Overall	A1	7.1(3)	109(30)	65.6(18)
	R1	No overlap		28.5(11)

* Troop A2 could not be detected in spring and therefore, home range overlap could not be determined

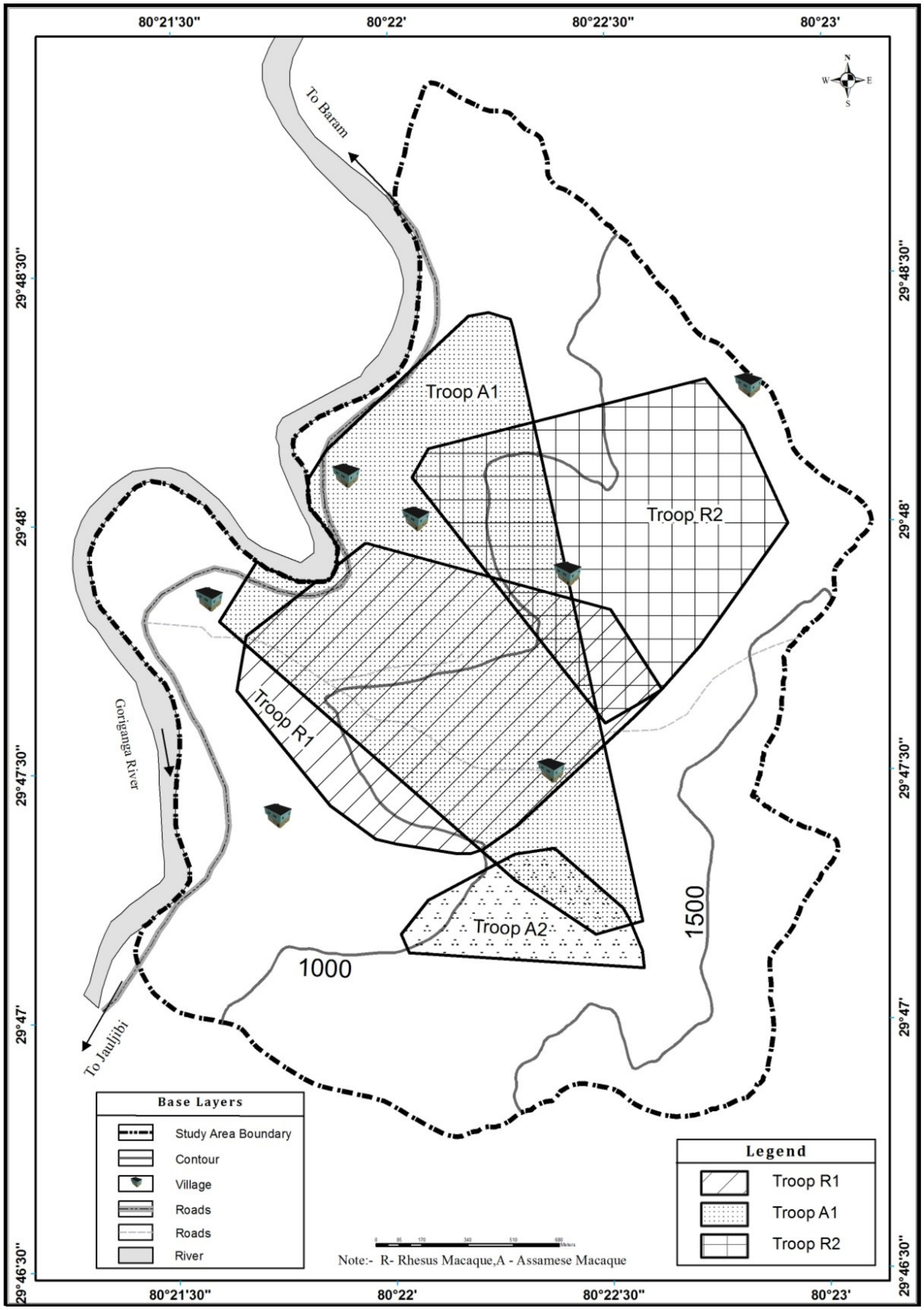

Figure 9. Winter home range of the study Assamese and rhesus macaque troops, calculated using the Minimum Convex Polygon method

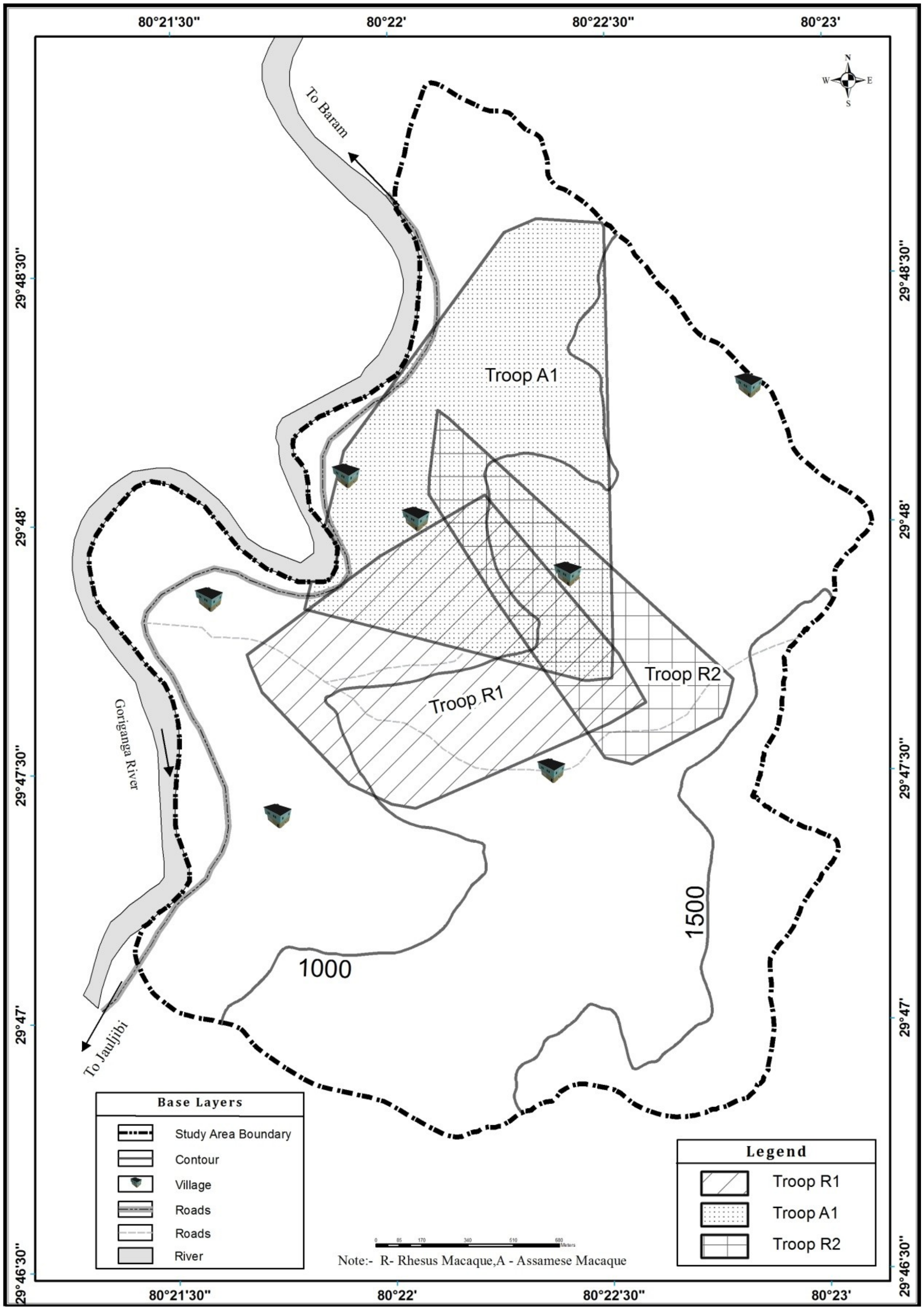

Figure 10. Spring home range of the study Assamese and rhesus macaque troops, calculated using the Minimum Convex Polygon method

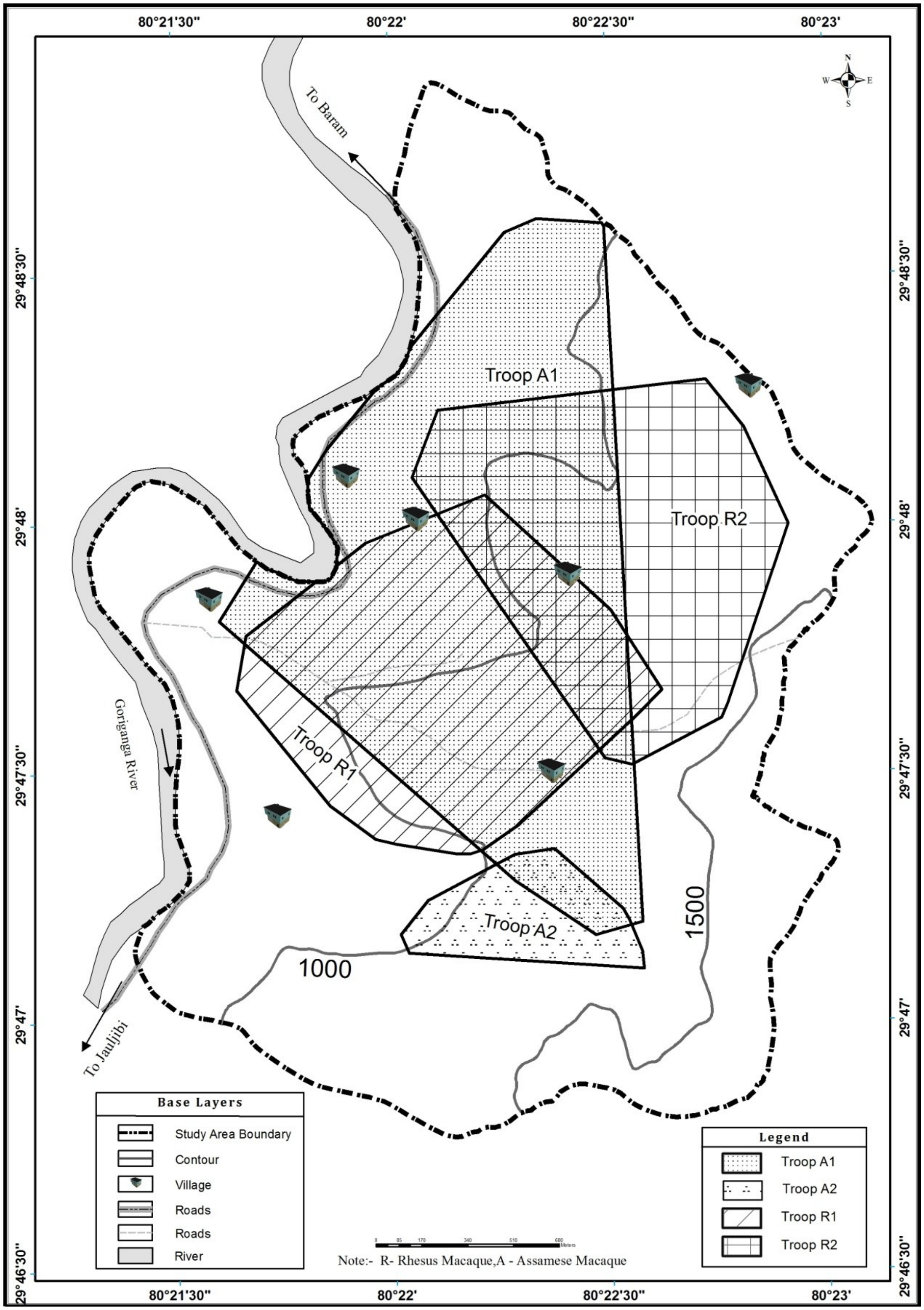

Figure 11. Overall home range of the study Assamese and rhesus macaque troops, calculated using the Minimum Convex Polygon method

4.3.3 Co-occurrence of the two macaque species

The observed C-score for Assamese and rhesus macaque pairs was greater than simulated C-score (Table 12) for both winter and spring seasons, which indicated that the two species are segregated in space, more so in winters – a period of resource crunch. Two macaque species appeared to be non-randomly distributed, which according to Diamond's assembly rules imply competitive interactions between these species leading to non-random co-occurrence patterns.

The SES values for all troop pairs, when compared between the two seasons, were greater for winter as compared to spring. It indicates more competition and therefore greater segregation in winter as opposed to a lesser segregation in spring. A comparison between SES values between and within the species indicates that inter-specific segregation is greater than intra-specific segregation.

Table 11. Results of co-occurrence analysis (50x50m grid) showing the observed and simulated C-Score Index, along with corresponding p-values for species and troop pairs

		C-Score Index			
Season	**Species/Troop code**	**Observed**	**Simulated**	**p-value**	**SES**
Winter	All macaques	4126.8	4131.5	0.53	-0.04
	A-R	**14873**	**12880.9**	**0.00**	**2.70**
	A1-A2	1656	3134.1	0.00	-6.47
	A1-R1	5810	5355.5	0.14	1.28
	A1-R2	6264	5393.3	0.00	2.63
	A2-R1	3108	2592.4	0.00	2.49
	A2-R2	3024	2468.6	0.00	2.61
	R1-R2	4899	4510.1	0.14	1.28
Spring*	All macaques	6573.6	6877.6	0.12	-1.18
	A-R	**11920**	**11686.4**	**0.44**	**0.29**
	A1-R1	6880	6855.8	0.55	0.05
	A1-R2	5625	5871.7	0.36	-0.51
	R1-R2	5625	5864.7	0.36	-0.49

*Co-occurrence analysis couldn't be carried out for troop pairsA1-A2, A2-R1 and A2-R2 because locations for troop A2 were not available for the spring season (as troop remained undetected in spring).

4.3.4 Habitat preference

The overall habitat categories used by the two macaque species are shown in Figure 12. In most location records, Assamese macaques were seen either in the mixed broadleaf forest (51%) or on the cliffs (36%), whereas rhesus macaques were either seen in the open forest (42%) or in agricultural fields (23%). Significant interspecific variation was found in the use of different habitat types (G=943, df=4, p <0.001).

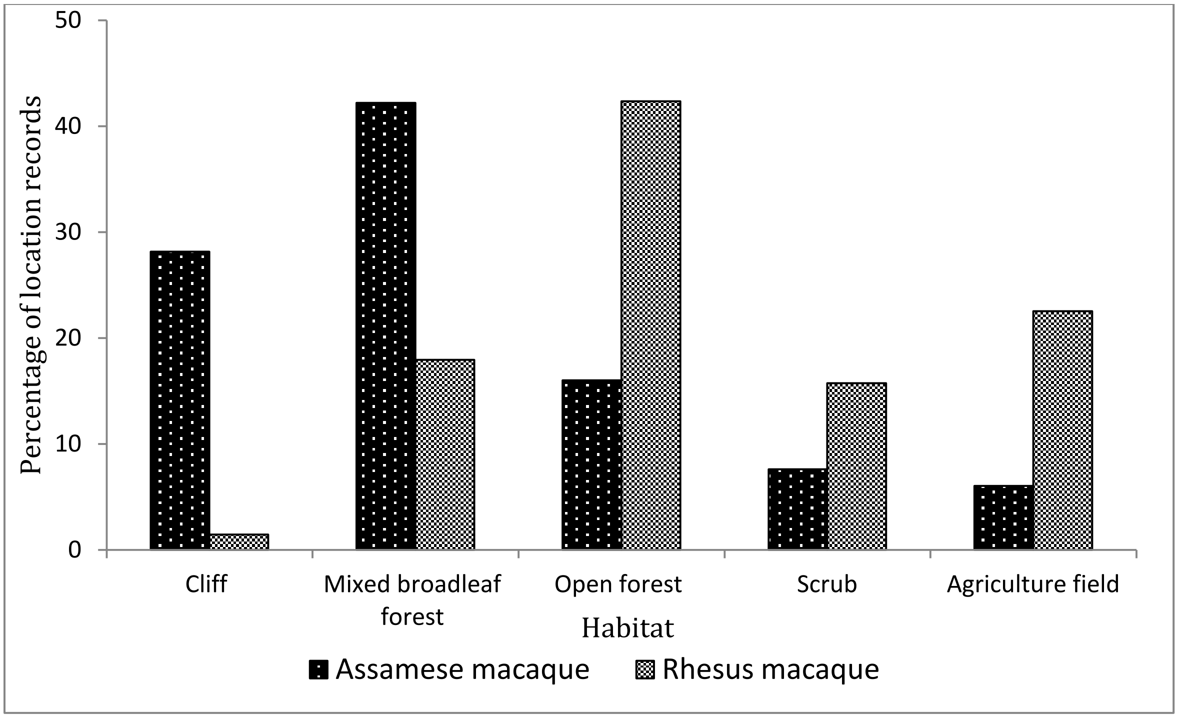

Figure 12. Percentage of location records in different habitat types for the Assamese and rhesus macaques

4.3.5 Roosting sites

A total of 13 roosting sites were located from 30 full day's troop follow for the Assamese macaque. Three of these sites were shared by both A1 and A2 troops. Out of these 13 sites, 12 were steep cliffs, both bare and rocky or with short scattered vegetation. It was only on two occasions that A2 troop was seen using a huge tree of *Olea glandulifera.* Out of these 13 sites, five sites were situated along the road, closer to human habitations, and the rest of them were in the dense mixed broadleaf forest. Troop A1 used a single cliff for four days continuously. Likewise, troop A2 used another cliff for three consecutive days.

In contrast to Assamese macaques, Rhesus macaques preferred to roost mostly on big trees of *Shorea robusta*, *Pinus roxburghii*, *Engelhardtia spicata*, *Bischofia javanica, Toona ciliata* or *Quercus glauca*. Sometimes they roosted on *Bauhinia variegata* and *B. vahlii* species with big leaves that would conceal them. Though rarely, they also used cliff to roost (three times during this study). A total of 30 sites, most of them near cultivated land were located from 37 full day follows and no single roosting site was used for two consecutive days.

Roosting sites of Assamese macaques were located at an average distance of 421±34.8 m from human habitation, while the average distance of Rhesus macaque's roosting sites from human habitation was 274±27.4 m. A significant difference was found between the distances of roosting sites of two macaque species from human habitation ($Z= 3.581$, $p <0.05$, $n_1=30$, $n_2=37$).

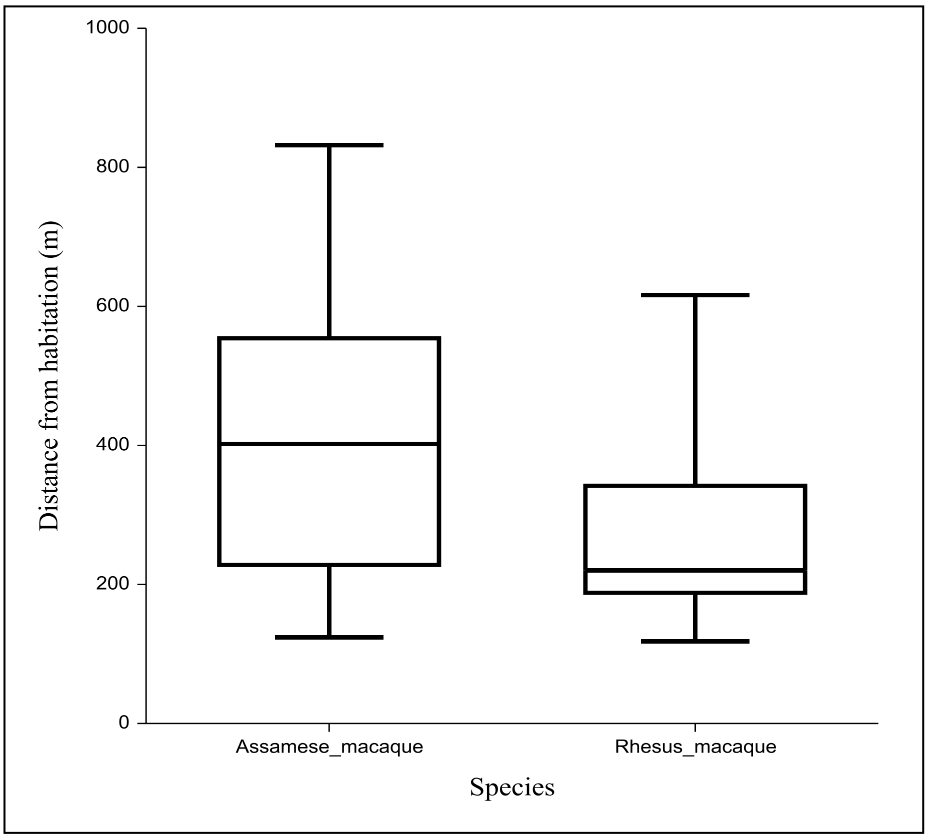

Figure 13. Box plots showing the distance of the study Assamese and Rhesus macaque troops from human habitation. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The horizontal bar in the middle of the box represents the median value while the outliers are shown as whiskers. (n_1=30, n_2=37)

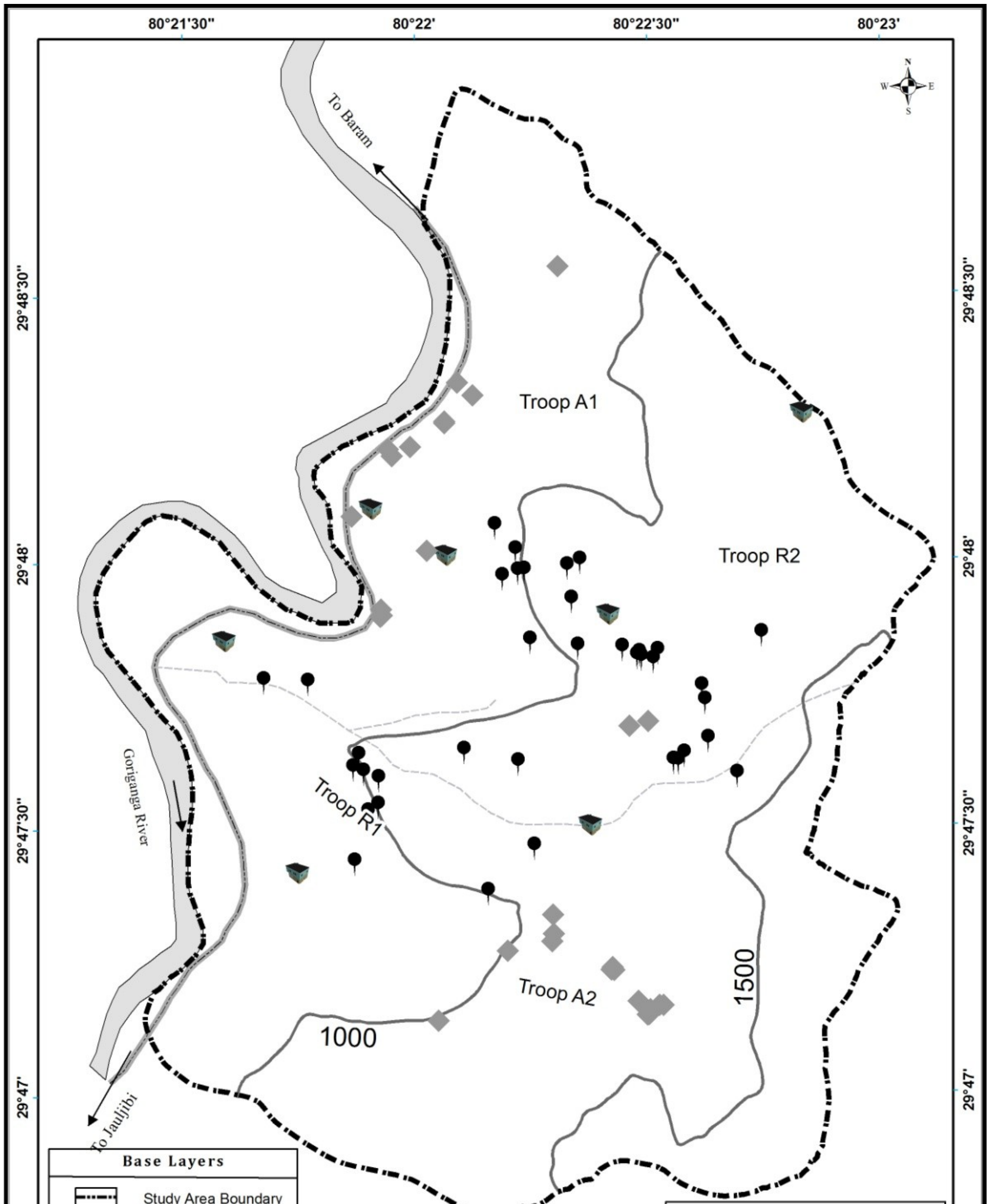

Figure 14. Location of the roosting sites of Assamese and rhesus macaque troops in the study area

4.4 People's perception

Of the total households interviewed (n=33), 74% of the people mentioned wildlife to be a major cause for crop loss. Rhesus macaque, wild pig and Assamese macaque were the main species that caused maximum damage. When the comparison was limited to macaques, 15% and 85% of the people mentioned Assamese and rhesus macaques to be very serious pests (Figure 15). The seriousness of crop damage by two macaque species varied significantly (G=30.51, df=4, $p<0.001$). Average loss by the two macaque species was reported to be 25% in case of the Assamese and 49% for rhesus macaque. In the case of Assamese macaque, a majority of the local people (42%) reported that the species visits their fields seasonally, around the time when crops mature. For rhesus macaque, a majority (67%) of people reported that it visits their fields regularly, every second or third day.

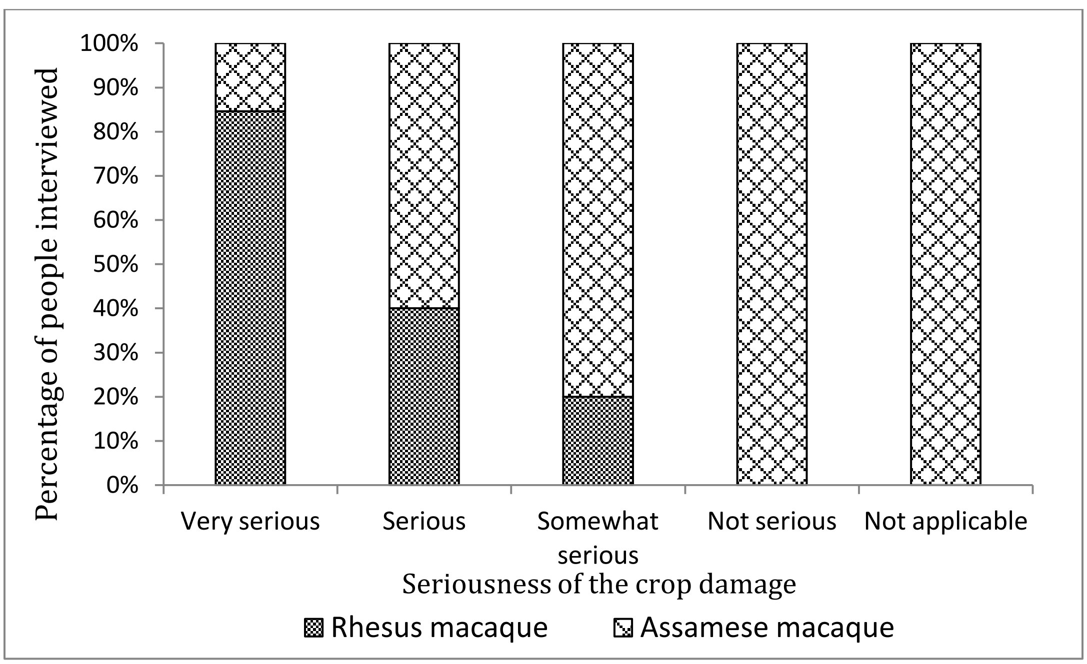

Figure 15. People's perception of the extent of crop damage caused by the Assamese and rhesus macaques in the study area

When asked about their viewpoint as to how they see these species, a majority of people reacted negatively (64% in case of Assamese and 58% in case of rhesus macaques). Negative feelings ranged from calling these monkeys pests, "enemy" or "monsters" whereas some people who reacted positively referred to them as "God" or saw them as being part of nature.

About 94% of the people agreed that the population of rhesus macaques has increased whereas 64% of people claimed the same for the Assamese. Approximately 39% of the villagers said that keeping dogs and throwing stones at macaques to chase them away were the best strategies to avoid crop losses. About 30% of them favoured the option of killing them while 24% of them suggested that taking them away to some other place or sterilizing them would be the best options.

Chapter 5

DISCUSSION

5.1 Time-activity budget

Time spent on various activities by the two species followed patterns observed in previous studies, where feeding and resting were dominant behaviours for Assamese and rhesus macaques respectively (Sarkar et al. 2012, Jaman and Huffman 2013). Activity budgets of the two species in the study site varied significantly. In winter, Assamese macaque males spent more time in feeding and social interaction whereas, rhesus macaques spent more time in resting and moving. This trend was opposite to that found in limestone habitats of China, where rhesus macaques spent more time on feeding and less time resting compared to the Assamese macaques (Zhou et al. 2014), this difference may simply be the result of differential resource distribution in both the landscapes. More time spent feeding by Assamese macaques in the present study can be explained by their folivorous nature. Animals need to diversify food resources when consuming leaves to obtain the best complement of nutrients (Westoby 1978), which requires more feeding time as seen in howler monkeys (*Alouatta palliate*) (Dunn et al. 2010). Time spent moving is determined primarily by the distribution of food in the habitat (Sarkar et al. 2012). Leaves are abundant and evenly distributed food resources, whereas fruit tends to be more patchily distributed (Richard 1985). Because of patchy distribution of desirable fruiting trees, spider monkeys (*Ateles belzebuth*) were found to travel great distances daily to satisfy their dietary needs (Suarez 2006). Likewise, frugivorous rhesus macaques had to travel more to locate the fruit trees distributed in patches. Greater time spent ranging by rhesus macaques can also be attributed to human disturbances as was the case for lion-tailed macaque (*Macaca silenus*) in Anaimalai region of the Western Ghats (Menon and Poirier 1996). In the study area, rhesus macaques spent a large proportion of their daytime in raiding crops, and in the process, would be chased away by the local people constantly, resulting in higher movement. The greater time spent on locomotion would imply greater energy costs (Sarkar 2002) and this could be the reason rhesus macaques had to spend more time resting to make up for such energy losses.

The two species did not differ in their feeding and resting behaviours in spring, which could be due to an increase in resource abundance. Assamese macaques, though primarily leaf-eating monkeys, would eat fruit and flowers when available (Chalise 2003). During spring, Assamese macaques in the study area also switched their diet to include fruits and flowers; this commonality in the diet may be a reason for there being no significant differences in feeding during this season. As there was an increase in temperature during spring, both the macaque species would start feeding since early morning and then would rest equivalently in the daytime heat, the probable reason for not obtaining any significant difference in the resting activity during spring.

Comparing time-activity budgets of females, the two species differed in social interaction and moving in both the seasons. Female Assamese macaques spent more time in social interaction while rhesus macaque females spent more time moving. The differences in social behaviour for both the sexes can partly be explained by differences in their reproductive parameters. Having an average gestation period of 5.5 months, conceptions in the case of Assamese macaques occur between October and February (Fürtbauer et al. 2010) but between October and December in the case of rhesus macaques (Johnsingh and Manjrekar 2012). This is in accordance with field observations, wherein rhesus macaques had already conceived before December and were seen with infants during late March while no newborns were seen with Assamese macaques until the end of the study; their mating continued until late winter. As Assamese macaques were sexually active for a longer duration during the study period, this could be one of the reasons for more social interaction in Assamese macaques, as compared to that in the rhesus macaque.

5.2 Diet

Assuming food to be a limited resource, diet is a commodity over which species most likely compete (Ganzhorn 1999). Physiological and behavioural adaptations evolve within species living in sympatry which results in maintaining a particular kind of diet, varying it in accordance with the seasonal cycle of food availability (Hladik 2011). The current study found significant differences between diets of the two species. Although both species shared 37 (44%) of their dietary spectrum (84 food items), the major food items shared were few. This degree of overlap is higher than the value of 11% reported for the two species in limestone habitats in China (Zhou et al. 2014). But it is similar to those reported for other sympatric primate species: 42% for northern pig-tailed macaque (*Macaca leonina*) and rhesus macaque in Bangladesh (Feeroz 2012), 43% for western red colobus (*Procolobus badius*) and mantled guereza (*Colobus guereza*) in Uganda (Chapman and Pavelka 2005) and 40% for Mentawai langur (*Presbytis potenziani*) and pig-tailed langur (*Simias concolor*) in Indonesia (Hadi et al. 2012). The dietary preferences showed major differences in winter, a period of resource scarcity. This small degree of dietary overlap in winter was also reflected by the relatively low value of Pianka's index (0.16), indicating very little overlap. In spring, the season of flowering and fruiting of many species, however, niche overlap increased to 0.51, indicating a partial overlap. It was in spring when both species shared their major diet (fruits of *Mallotus philippensis*, flowers of *Woodfordia fruticosa* and agricultural crops). The results clearly indicated a higher niche overlap in periods of high fruit availability. This trend, where niche overlap increases with increase in food resources, is consistent with that shown by many other sympatric primates (Chapman 1987, Stevenson et al. 2000, Yamagiwa and Basabose 2006, Marshall et al. 2009, Singh et al. 2011). But these patterns are not universal and sometimes there may be higher diet overlap in the periods of low fruit availability. For example, overlap indices between jointly foraging tamarins (*Saguinus* spp.) were very high during times of greatest scarcity presumably because both species were forced to resort to the common food resources (Peres 1996). Similarly, the dietary overlap between Assamese and rhesus macaque increased in the dry season, as fruit scarcity in the dry season forced rhesus macaque to consume leaves along with the Assamese macaque, resulting in more niche overlap (Zhou et al. 2014). In the former cases, due to food abundance, even with high niche overlap, there is still less feeding competition (Wahungu 1998, Goulson and Darvill 2007). This fact is well supported by our field observations; during spring season among a total of seven interspecific encounters, only one encounter resulted in aggression.

The Assamese macaque, more of a forest-dwelling species, often supplements its diet with crops when available (Cooper 1989). In our study, agricultural crops constituted only 7.7% of the diet of the Assamese macaque while 80% of its diet came from trees, herbs, shrubs and climbers. A major part of the rhesus macaque's diet in rural areas is constituted by agriculture crops (Feeroz 2012). In our study area too, along with trees, agricultural crops (30%) were the major food source for rhesus macaques. The number of food species that these macaques utilize explains the difference in niche breadth of these species. Assamese macaque has a greater niche breadth because it primarily feeds on leaves, consumption of which has been positively related to diet diversity (Dunn et al. 2010). The rhesus macaque, on the other hand, is a frugivore, and was observed in the present study to spend most of its time in and around agricultural fields, resulting in a smaller niche breadth of 0.11. The folivorous and frugivorous nature of Assamese and rhesus macaques has been already reported (Zhou et al. 2011, Huang et al. 2015). Dietary differences like these have been observed among other sympatric primate species as well (Dunbar and Dunbar 1974, MacKinnon and MacKinnon 1980, Hadi et al. 2012). For example, in French Guiana, Guiana spider monkey (*Ateles paniscus*) is almost exclusively frugivorous, Venezuelan red howler (*Alouatta seniculus*) is frugivorous-folivorous and tufted capuchin (*Cehus apella*) partially insectivorous; thus, the overall specific diet spectra are well separated (Guillotin et al. 1994). These differences in diet choice play a vital role in niche segregation and reduced competition among sympatric species.

Assamese macaques spend their maximum time feeding at the middle canopy layer opposed to rhesus macaques, primarily restricted to the ground. These variations in substratum used may largely be related to food preferences. In this study, young leaves constituted a major part of the Assamese macaque's diet, which it finds in the forest, mostly from trees or climbers at the middle level (3-5m) above ground. Rhesus macaques depend largely on agricultural crops and this could be the reason for the maximum number of their feeding locations being on the ground. Such vertical separation has also been observed in lion-tailed macaques, bonnet macaques (*Macaca radiata*) and Hanuman langurs (*Semnopithecus entellus*) in the Western Ghats (Singh et al. 2011) as well as in many other sympatric primates. (Lahann 2008, Feeroz 2011, 2012, Hadi et al. 2012).

5.3 Space use

Daily and seasonal home ranges are key measures of space use. Day range (daily distance traveled) is an important measure for understanding relationships between animal distributions and food resources and is associated with the energetic requirements and foraging habits of an animal. Folivorous species will have shorter day ranges compared to frugivorous species (Carbone et al. 2005), which was the case in the present study as well. Assamese macaques tended to move less in both the seasons when compared to rhesus macaques. It is possibly because of food distribution that Assamese macaques, being predominantly folivorous, moved less when compared to rhesus macaques, who had to travel more to locate fruit patches and to take chances to raid crops while moving from one village to another. Many species often travel less and rest more during periods of fruit scarcity, presumably to save energy (Stevenson et al. 2000). For both the species, therefore, daily movement was less in winter and more in the spring season when the abundance of fruit trees increased.

Home ranges of troops A1, R1 and R2 overlapped partially. The home range of troop A2 only overlapped with troop A1 but not with any of the rhesus macaque troops, primarily because it never came near villages, where the rhesus macaques predominantly resided. The home range of troop A1, with maximum troop members, was largest while the home range of troop A2 with only six troop members was the smallest. Similarly, the rhesus macaque troop R1, with a larger number of individuals, had a larger home range, as compared to troop R2. This inter-troop variation in home range size can be explained by differences in troop size, a finding reported in other macaque species as well (Southwick et al. 1996, Kumar et al. 2007).

Although certain levels of range overlap existed between the two macaque species, they were rarely observed at close quarters. Therefore, a direct competition for food sources seemed rare, as indicated by the rare occurrence of more than one species in the same food patch together. Co-occurrence analysis also indicated non-random spatial segregation of the two macaque species. The results of the study were in accord with those obtained for stump-tailed macaque (*Macaca arctoides)*, northern pig-tailed macaque and rhesus macaque co-occurring in Hollongapar Gibbon Wildlife Sanctuary, Assam (Sharma 2012).

Assamese macaques were predominantly located in mixed broadleaf forest and cliffs while rhesus macaques were dominantly seen in open forest and around agricultural fields. Such differential habitat choice might be an important mechanism to reduce interspecific competition (Schoener 1974, Ganzhorn 1989). Habitat selection as a major axis for niche separation has been seen in mouse lemurs (*Microcebus* spp.) in Madagascar (Rakotondravony and Radespiel 2009). Roosting sites are major components in segregation of species in horizontal space (Dunbar and Dunbar 1974). Showing an impressive flexibility in their sleeping habits, primates complement their successful radiation into dissimilar ecological niches (Anderson 1984). In the present study, there was a clear difference in roosting sites favoured by the two species. Assamese macaques typically preferred rocky cliffs also reported by other researchers (Chalise 2003) whereas rhesus macaques preferred roosting on big trees and sometimes on lianas like *Bahunia vahlii* with big leaves to conceal them. In addition to influencing the occurrence and group sizes of primates, sleeping sites can constrain day range and home range of a primate (Anderson 1984). It can be concluded that using different habitats along with evolving to use different roosting sites is one of the factors that contributes to niche segregation in congeneric species.

5.4 Conflict

Foraging on crops is integral to the ecology of primates inhabiting the forest-agriculture ecotone (Naughton-treves et al. 1998). Comparing two macaque species, it was found that rhesus macaques caused higher losses when compared to Assamese macaques. Rhesus macaques are generally perceived as pests and referred as weed species over its entire distribution (Richard et al. 1989). Assamese macaques, though a non-weed species, has been reported to raid crops occasionally (Richard et al. 1989). Field observations also showed that rhesus macaques would go to cultivated lands almost every day, especially in winter when there were few fruiting plants. One troop of Assamese macaque also visited the fields but their visits were more frequent in spring when the crops matured. A study done in Nepal, however, reported Assamese macaques to be the most frequent crop-raider (Chalise 2003).

Humans have contradictory views about non-human primates, some perceive them as sacred, and for others, they are mythical creatures of great cunning and deviousness (Lee and Priston 2005). Even minimal experience of crop-raiding leads to an attribution of the blame on macaques (Chalise and Johnson 2001; Saraswat et al. 2015). In the study area, questionnaire surveys revealed that maximum people had negative feelings regarding both the macaque species, reason for this being the losses incurred by the locals due to crop damage by the macaques. According to the local people, there was nothing they could do except keeping a guard dog or throwing stones at the macaques, but whatever they did, they still were unable to escape the absolute losses that they suffered.

Discussions with the locals revealed that rhesus macaques had always been a pest in the area whereas it was only recently that the Assamese macaques have started entering the fields. The population of rhesus macaques was also reported to have increased in recent years while most people were ignorant about the trend in the population of the Assamese macaque. The conflict between humans and non-human primates is increasing with the spread of agriculture and human activity in areas that previously sustained non-human primates alone (Lee and Priston 2005). The majority of people agreed that habitat destruction and anthropogenic disturbances were the main reasons for the increase in human-macaque conflict. On the whole, the limited surveys done in and around the study area indicated a high level of potential conflict with macaques. The conflict was reported more with rhesus macaques when compared to the Assamese macaques, consistent with our field observations.

5.5 Conclusions

Ecological theory predicts that closely related species should be highly competitive as they occupy similar niches (Pianka 2007). Therefore, in situations where closely related species live in sympatry, one would expect prominent differences in ecology and behaviour of those species. Prominent ecological and behavioural differences were observed between sympatric Assamese and rhesus macaques in the Askot landscape of Uttarakhand state. Niche partitioning was seen along all three axes examined in this study: activity pattern, diet, and space. The two species differed either in the choice of food plants or in the plant parts they consumed. Differences were also seen in the foraging heights of the two species. Both macaques had different habitat- and sleeping site preferences. Distinction in their diet and habitat use was also reflected in their activity patterns, daily movement, and home range size. Although niche overlap increased during spring, the two species continued to coexist because of the abundance of food resources in the spring season. Interviews with the local people revealed that both macaques were in conflict with them although conflict with the Assamese macaque was relatively low when compared to that with the rhesus macaque. A more detailed survey on the human-macaque conflict across the landscape will help in better understanding of the conflict issue.

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APPENDIX I

Questionnaire form for accessing the extent of human macaque conflict in the area

Questionnaire form One: Assessing crop damage by wildlife including macaques (Interviews of individuals/groups of local people)

Name of the village:

GPS location: Lat: Lon: Alt:

Name of people interviewed:

Particulars of people interviewed (GB/Hunters/Agriculturalist/Government employee…)

1. Do you encounter any problems with crops? (Disease/insects and other small pests/rodents/damage by wildlife/drought/frost)
   Yes/No

2. How serious are these problems? (For each interview, rank as 1, 2, 3… where 1 is the most important)

Disease	Insects/Pests	Rodents	Drought	Frost	Wildlife	Other

3. How serious is the problem of crop damage by the following wildlife species?

Species	Not applicable	Not serious	Somewhat serious	Serious	Very serious
Wild pig					
Rhesus macaque					
Assamese macaque					

4. Agriculture land holdings per household: (a) Crop fields________ (b) Fruit orchards_______ (c) Others_______

5. Average production of main crops (quintals/kg per season) ____________

6. Average income/season from agriculture (INR) ____________

7. Is wildlife damage considerable (Yes/No) _____________

	Percentage of crop loss
Assamese macaque	
Rhesus macaque	

8. If macaque damage crops…

	Rhesus Macaque	Assamese macaque
Main crops affected?		
How often(i) Everyday, (ii) once in a week, (iii) once in a month		
At what time are they seen in the field? Morning/ Afternoon/ Evening/ No specific time)		
Which season of the year?		
When was the last time macaques damaged your crop?		
How serious are the damage in yield and economic terms Negligible/Low/High:		

9. Any other conflict

	Attacks	Bite	Property damage	Other
Rhesus macaque				
Assamese macaque				

10. Have you been attacked (Yes/No)? How many times?

Questionnaire 2: Assessing the attitudes of people towards macaques in the area

(Interviews of individuals/groups of local people)

1. How do you consider the macaques?

	Representation of God	Agricultural pest	Part of nature as I am	As an animal that humans should take care of	Any other view
Rhesus					
Assamese					

	Rhesus macaque	Assamese macaque
2. Were these macaques always an agricultural pest and therefore a nuisance?		
3. If not, since when has the conflict become intolerable?		
4. Have the numbers of macaques increased/ decreased?		
5. Since when (a) last five years (b) last 10 years		

6. If increased, why has this occurred?

	Forest cover has increased near the village	Forest Department does not permit killing of macaques	Forest cover has decreased, so macaques come into fields	I do not know why	Any other view
Rhesus macaque					
Assamese macaque					

7. If decreased, why has this occurred?

	Forest cover has reduced near the village	Forest Department permit killing of macaques	Habitat quality has decreased	I do not know why	Any other view
Rhesus macaque					
Assamese macaque					

8. A. What kind of practices are used to stop macaques from raiding crop fields?

B. What technique do you think is best among these (rank 1, 2…)

	Local people/ dogs chase away them	Plant crops that they don't eat	People shoot/injure /trap macaques	Colours, firecrackers, drums…	No practice helps, but the compensation from the Forest Department helps
Rhesus macaque					
Assamese macaque					

9. Wild animals that cause crop damage are pests and should all be shot? Agree/disagree/don't know

10. Favourite animal

11. Taboos/Folklore

APPENDIX II

List of all food items consumed by the Assamese and rhesus macaque study troops during the winter and spring seasons in decreasing order of their use

(Note: [a]Parts eaten: L leaf, F flower, FR fruit, R root, B bud, S seed, ST stem **[b] Phenological state**: M mature, Y young, R ripe, SR semi-ripe **[c] (%F)**: percentage of total feeding records)

Species: Assamese macaque		**Season: Winter**			
Family	**Food items**	**Habit**	**[a]Parts eaten**	**[b]Phenological State**	**[c](%F)**
OLEACEAE	*Olea glandulifera*	Tree	L, FR	Y, M	19.1
PRIMULACEAE	*Maesa indica*	shrub	L, FR, F	R, SR	12.0
VITACEAE	*Cayratia pedata*	Climber	L, FR	Y, M	11.9
	Miscellaneous				11.3
MORACEAE	*Ficus microcarpa*	Climber	L	Y	9.5
EUPHORBIACEAE	*Bischofia javanica*	Tree	FR	SR	4.1
ARACEAE	*Rhaphidophora glauca*	Liana	L	R, SR	3.5
	Agri crops				2.8
EUPHORBIACEAE	*Mallotus philippensis*	Tree	S, ST	Y	2.7
ASCLEPIADACEAE	*Hoya longifolia*	Climber	L, R	R	2.4
ACANTHACEAE	*Goldfussia dalhausiana*	Herb	F	M, Y	2.1
FABACEAE	*Milletia auriculata*	Shrub	L, F	Y, M	2.0
ORCHIDACEAE	*Rhynchostylis retusa*	Orchid	LT	Y	1.9
MORACEAE	*Ficus hispida*	Tree	L, F	R, SR	1.9
MORACEAE	*Ficus semicordata*	Tree	FR, L	R, SR	1.8
URTICACEAE	*Urtica dioica*	Herb	L, F	M, Y	1.2
MORACEAE	*Ficus clavata*	Tree	L, F	Y, M	1.1
FABACEAE	*Ougeinia oojeinensis*	Tree	L	M, Y	1.1
ACANTHACEAE	*Eranthemum pulchellum*	Shrub	F	M, Y	0.8
TILIACEAE	*Grewia oppositifolia*	Tree	L, F	R, SR	0.8
DIOSCORIACEAE	*Dioscorea deltoidea*	Climber	L	Y, M	0.7

Species: Assamese macaque		Season: Winter			
Family	**Food items**	**Habit**	**[a]Parts eaten**	**[b]Phenological State**	**[c](%F)**
ASCLEPIADACEAE	*Cryptolepis buchanani*	Climber	L, F	Y	0.6
FABACEAE	*Mucuna nigricans*	Climber	L, S	M	0.5
MORACEAE	*Ficus nerifolia*	Tree	F, L	M, Y	0.4
RUBIACEAE	*Randia tetrasperma*	Shrub	L	Y	0.4
ROSACEAE	*Rubus ellipticus*	Shrub	ST	Y	0.4
APOCYNACEAE	*Trachelospermum axillare*	liana	L	Y, M	0.4
ORCHIDACEAE	*Bulbophyllum affine*	Orchid	L, R	M, Y	0.3
ROSACEAE	*Pyrus pashia*	Tree	F, FR	Y	0.3
SMILACACEAE	*Smilax zeylanica*	Climber	S	Y, M	0.3
VITACEAE	*Vitis jacquemontii*	Climber	L	M, Y	0.2
BRASSICACEAE	*Cardamine macrophylla*	Herb	F	R, SR	0.2
ORCHIDACEAE	*Luisia zeylanica*	Orchid	L	Y	0.2
RUTACEAE	*Murraya paniculata*	Tree	FR	R	0.2
ANACARDIACEAE	*Spondias pinnata*	Tree	FR	R	0.2
MYRSINACEAE	*Ardisia solanacea*	Shrub	FR	R, SR	0.1
VERBENACEAE	*Callicarpa arborea*	Tree	FR	R, SR	0.1
LEEACEAE	*Leea asiatica*	Tree	ST	Y	0.1
ARACEAE	*Pothos cathcartii*	Climber	Leaf	R	0.1
VITACEAE	*Tetrastigma obtectum*	Climber	L	Y, M	0.1
LEGUMINOSAE	*Atylosia scarabaeoides*	Climber	S	R	0.1
CAESALPINIACEAE	*Bahuhinia vahlii*	Liana	S	R, SR	0.1
BERBERIDACEAE	*Berberis asiatica*	Shrub	F	M, Y	0.1
MORACEAE	*Ficus nervosa*	Tree	FR	R	0.1
MALPIGHIACEAE	*Hiptage benghalensis*	Liana	F	Y	0.1
LOMARIOPSIDACEAE	*Nephrolepis cordifolia*	Fern	S	M	0.1
LYTHRACEAE	*Woodfordia fruticosa*	Shrub	F	M	0.1

Species :Rhesus macaque		Season: Winter			
Family	**Food items**	**Habit**	**Parts eaten**	**Phenological state**	**%F**
MORACEAE	*Ficus nervosa*	Tree	FR	R, SR	26.5
	Agri crops				23.9
	Miscellaneous				9.2
CAESALPINIACEAE	*Bahunia varigata*	Tree	B, F, ST	Y	8.0
FABACEAE	*Mucuna puriens*	Climber	S	R	4.9
PINACEAE	*Pinus roxburghii*	Tree	S	R, SR	3.9
CELASTRACEAE	*Elaeodendron glaucum*	Tree	S	R, SR	3.3
FABACEAE	*Indigofera heterantha*	Shrub	F	Y, M	2.8
FABACEAE	*Flemingia bracteata*	Shrub	R	R, SR	2.3
EUPHORBIACEAE	*Mallotus philippensis*	Tree	S, ST		2.3
EUPHORBIACEAE	*Macaranga pustulata*	Tree	S	R, SR	1.9
ACANTHACEAE	*Goldfussia dalhausiana*	Herb	F	Y, M	1.2
ORCHIDACEAE	*Luisia zeylanica*	Orchid	L	Y, M	1.2
ORCHIDACEAE	*Rhynchostylis retusa*	Orchid	L	Y	1.1
EUPHORBIACEAE	*Bischofia javanica*	Tree	FR	SR	0.7
CAESALPINIACEAE	*Bahuhinia vahlii*	Liana	S	Y	0.5
MORACEAE	*Ficus religiosa*	Tree	FR	Y, M	0.5
EUPHORBIACEAE	*Antidesma acidum*	Tree	L	Y, M	0.5
EUPHORBIACEAE	*Macaranga indica*	Tree		Y, M	0.4
ERICACEAE	*Rhododendron arboreum*	Tree	F	M	0.4
MORACEAE	*Ficus clavata*	Tree	FR	Y, M	0.4
FABACEAE	*Mucuna nigricans*	Climber	L, S	M	0.4
MALVACEAE	*Urena lobata*	Shrub	S	M	0.4
URTICACEAE	*Urtica dioica*	Herb	F	Y	0.3
BERBERIDACEAE	*Berberis asiatica*	Shrub	F	Y, M	0.3
ASCLEPIADACEAE	*Hoya longifolia*	Climber			0.3
OLEACEAE	*Olea glandulifera*	Tree	L	Y, M	0.3
ROSACEAE	*Pyrus pashia*	Tree	F, FR	Y, M	0.3
DIPTEROCARPACEAE	*Shorea robusta*	Tree	R	Y	0.3

Species :Rhesus macaque		Season: Winter			
Family	Food items	Habit	Parts eaten	Phenological state	%F
FABACEAE	*Ougeinia oojeinensis*	Tree	L		0.2
ANACARDIACEAE	*Lannea coromondolica*	Tree		Y	0.2
MYRTACEAE	*Syzygium cumini*	Tree	L	Y, M	0.2
MYRSINACEAE	*Ardisia solanacea*	Shrub	FR	R, SR	0.1
LEGUMINOSAE	*Atylosia scarabaeoides*	Climber	S	R	0.1
DIOSCORIACEAE	*Dioscorea deltoidea*	Climber	L	Y, M	0.1
MORACEAE	*Ficus auriculata*	Tree	S	M	0.1
TILIACEAE	*Grewia oppositifolia*	Tree	FR	R, SR	0.1
PRIMULACEAE	*Maesa indica*	shrub	FR	Y	0.1
MIMOSACEAE	*Mimosa himalayana*	shrub	L	Y, M	0.1
ANACARDIACEAE	*Spondias pinnata*	Tree	FR	R	0.1

Species: Assamese macaque		**Season: Spring**			
Family	**Food items**	**Habit**	**Parts eaten**	**Phenological state**	**%F**
ROSACEAE	*Pyrus pashia*	Tree	F, FR	Y	23.1
EUPHORBIACEAE	*Mallotus philippensis*	Tree	S,ST	Y	12.5
URTICACEAE	*Urtica dioica*	Herb	L, F	M, Y	11.9
	Agri crops				11.0
FABACEAE	*Quercus glauca*	Tree	L, F	Y, M	10.4
LYTHRACEAE	*Woodfordia fruticosa*	Shrub	F	M	5.5
	Miscellaneous(Insects, fungi, resin, unknown)				4.7
MENISPERMACEAE	*Cocculus laurifolius*	Tree	L	Y	2.8
ACANTHACEAE	*Eranthemum pulchellum*	Shrub	F	M, Y	2.5
PRIMULACEAE	*Maesa indica*	shrub	L, FR, F	R, SR	2.4
MORACEAE	*Ficus microcarpa*	Climber	L	Y	2.1
EUPHORBIACEAE	*Macaranga pustulata*	Shrub/small tree	ST	Y	1.4
CAESALPINIACEAE	*Caesalpinia decapetala*	shrub/climber	F	M, Y	1.2
FABACEAE	*Indigofera heterantha*	Shrub	F		1.1
EUPHORBIACEAE	*Macaranga indica*	Tree	ST	Y	0.7
MORACEAE	*Ficus semicordata*	Tree	FR, L	R, SR	0.7
ARALIACEAE	*Schefflera venulosa*	Climber	L	M	0.6
LOMARIOPSIDACEAE	*Nephrolepis cordifolia*	Fern	S		0.5
OLEACEAE	*Olea glandulifera*	Tree	L, FR	Y, M	0.5
POLYGONACEAE	*Polygonum sp.*	Herb	L	Y, M	0.5
MORACEAE	*Ficus clavata*	Shrub/small tree	L, FR	Y, M	0.4
ROSACEAE	*Rubus ellipticus*	Shrub	ST		0.4
MORACEAE	*Ficus hispida*	Tree	L, FR	R, SR	0.4
MORACEAE	*Ficus sp.*	Tree	FR		0.3
URTICACEAE	*Oreocnide frutescens*	Shrub	FR		0.3
MYRSINACEAE	*Ardisia solanacea*	Shrub/small tree	FR	R, SR	0.3
MORACEAE	*Ficus nervosa*	Tree	FR	R	0.2
LINACEAE	*Reinwardtia indica*	Shrub	F		0.2
PINACEAE	*Pinus roxburghii*	Tree	S, FR		0.2
FABACEAE	*Milletia auriculata*	Shrub	L, F	Y, M	0.2

Species: Assamese macaque		Season: Spring			
Family	Food items	Habit	Parts eaten	Phenological state	%F
PIPERACEAE	*Peperonia heyneana*	Herb	L		0.2
CAESALPINIACEAE	*Bahunia varigata*	Tree	B, F		0.1
SAPOTACEAE	*Diploknema buryracea*	Tree	FR		0.1
MORACEAE	*Ficus auriculata*	Tree	S		0.1
LEEACEAE	*Leea asiatica*	Shrub/small tree	ST	Y	0.1
ARECACEAE	*Phoenix acaulis*	Tree	FR		0.1
DIPTEROCARPACEAE	*Shorea robusta*	Tree	R		0.1
CAESALPINIACEAE	*Bahuhinia vahlii*	liana	S	R, SR	0.1

Species: Rhesus macaque		**Season: Spring**			
Family	**Food items**	**Habit**	**Parts eaten**	**Phenological state**	**%F**
	Agri crops	Herb, Shrub, Tree			36.3
EUPHORBIACEAE	*Mallotus philippensis*	Tree	S,ST,F		23.1
FABACEAE	*Pueraria tuberosa*	Climber	F	Y, M	10.2
	Miscellaneous				6.7
LYTHRACEAE	*Woodfordia fruticosa*	Shrub	F	Y, M	4.7
MELIACEAE	*Toona ciliata*	Tree	L	Y	3.9
CAESALPINIACEAE	*Bahunia varigata*	Tree	B, F, S	Y	2.9
FABACEAE	*Quercus glauca*	Tree	F	Y, M	2.1
CAESALPINIACEAE	*Caesalpinia decapetala*	shrub/climber	F	Y, M	1.5
PINACEAE	*Pinus roxburghii*	Tree	S	R, SR	1.5
FLACOURTIACEAE	*Xylosma longifolium*	Tree	S	R, SR	1.2
ROSACEAE	*Pyrus pashia*	Tree	F, FR	Y, M	0.9
CELASTRACEAE	*Elaeodendron glaucum*	Tree	S	R, SR	0.7
MORACEAE	*Ficus religiosa*	Tree	FR	Y, M	0.6
MORACEAE	*Ficus auriculata*	Tree	S	M	0.5
SAPOTACEAE	*Diploknema buryracea*	Tree	FR	R, SR	0.5
FABACEAE	*Flemingia bracteata*	Shrub	R	R, SR	0.4
ORCHIDACEAE	*Luisia zeylanica*	Orchid	L	Y, M	0.4
ORCHIDACEAE	*Coelogyne cristata*	Orchid	L	Y	0.3
MYRICACEAE	*Myrica esculenta*	Tree	FR	Y, M	0.2
ROSACEAE	*Rubus ellipticus*	Shrub	ST	Y	0.2
DIPTEROCARPACEAE	*Shorea robusta*	Tree	R	Y	0.2
FABACEAE	*Vicia sativa*	Herb	F, S	Y, M	0.2
VITACEAE	*Cayratia pedata*	Climber	FR	Y, M	0.2
LEEACEAE	*Leea asiatica*	Shrub/small tree	ST	Y	0.2
MORACEAE	*Ficus clavata*	Shrub/small tree	FR	Y, M	0.1
CAESALPINIACEAE	*Bahunhiia vahlii*	liana	FR,S	Y	0.1

Plate 1 Assamese and rhesus macaques in their habitat

Rhesus macaques resting on a steep slope below an agricultural field

Assamese macaques allogrooming in their typical habitat

Plate 2: Field work

Observing a rhesus macaque troop feeding on fruits of *Ficus nervosa*

Projecting the location of an Assamese macaque troop on one of their roosting sites along the road

Plate 3: Feeding by Assamese and rhesus macaques

A juvenile Assamese macaque feeding on flowers of *Pyrus pashia*

A juvenile rhesus macaque feeding on fruits of *Ficus nervosa*

Plate 4: Resting and grooming activities of the two study macaque species

Resting and grooming activities of the Assamese macaque

Resting and grooming activities of the Rhesus macaque

Plate 5 Roosting sites of the two study macaque species

Assamese macaques roosting on a rocky cliff

Rhesus macaques roosting on *Pinus roxburghii*

Plate 6 Crop-feeding by the two study macaque species

Assamese macaque female feeding on wheat in an agricultural field

A male and female rhesus macaque feeding on *Colocasia* in an agriculture field