Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India

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Resource partitioning in a community of diurnal arboreal mammals consisting of the lion-tailed macaque *Macaca silenus*, bonnet macaque (BM) *Macaca radiata*, Nilgiri langur *Semnopithecus johnii*, and the Indian giant squirrel *Ratufa indica* of the Western Ghats, southern India, was studied. Differences in their diet, vertical stratification, food resource niche breadth, niche overlap, and behavioral interactions were examined. Resource partitioning was through differential habitat use, resource use, and vertical stratification. Of the four species, the BM was not a resident species and made frequent forays into evergreen forest from the adjacent deciduous forest during the flowering season of *Cullenia exarillata* and fruiting season of *Ficus microcarpa*. The macaques had narrower niches, and the langur and the squirrel had wider niches. Niche overlap was highest between the two macaques. Overlap among the study species was particularly pronounced during the flowering of *C. exarillata*. There was significant correlation between niche overlap and intolerance among the study species. Certain species pairs showed little or no mutual intolerance despite high overlap. Cooperative interactions such as alarm calls occurred more frequently among the resident species. Interaction matrices revealed an underlying pattern of interspecific dominance hierarchy, with the BM dominating over the other three species. Our study suggests that the BM do not coexist with the other three because of high overlap with its congener and low occurrence of cooperative interactions. *Key words:* bonnet macaque, Indian giant squirrel, interspecific interactions, lion-tailed macaque, niche breadth, niche overlap, Nilgiri langur, primates, resource partitioning. *[Behav Ecol 17:479–490 (2006)]*

The way species in a community share resources and interact has always interested ecologists. Interspecific interactions such as competition have implications for species survival and for the stability of the community. Two or more species, vying for a limited common resource, try to reduce the use of that resource by the other either through interference or exploitative competition (Miller, 1968). Competition leads to niche segregation where some resources are shared and others are used exclusively by species (Pianka, 1978). It is expected that closely related species would contend for the same limited resources, and therefore, fewer pairs of congeneric species will occur within a community at a given point in time (Pianka, 1978). In order to reduce the cost in competition, species use either different parts of a common resource or use resources at different time periods or through "preemption," where a resource is utilized earlier before it becomes available to the other (Terborgh, 1983). Niche segregation is also achieved through vertical partitioning of the common habitat (Emmons, 1980; Estrada and Coates-Estrada, 1985; Ungar, 1996). Coexistence of species is also determined by noncompetitive interactions resulting in interspecific associations such as mutualism (Odum, 1971). Many studies of mixed-species associations of primates and mixed foraging flocks are replete with examples of mutualism (see Heymann and Buchanan-Smith, 2000). There are instances where two competing species of primates coexist despite high niche overlap because of enhanced predator detection (Eckardt and Zuberbuhler, 2004).

In forest fragments, interspecific competition is thought to be an important factor regulating the relative abundance of species with overlapping niches (Kozakiewicz, 1993). Studies have also shown that density of a species increased when potential competitors were absent (Umapathy and Kumar, 2000).

Synecological studies are important because they identify key resources that support the entire community and assign conservation priorities to habitats especially for primate communities (Mittermeier and van Roosmalen, 1981). In this study, we focused on resource partitioning in sympatric lion-tailed macaque (LTM) *Macaca silenus*, Nilgiri langur (NL) *Semnopithecus johnii*, bonnet macaque (BM) *Macaca radiata*, and Indian giant squirrel (GS) *Ratufa indica* in the evergreen forests of the southern Western Ghats. These four mammals form the diurnal arboreal community along with two other species of squirrels viz Western Ghats striped squirrel *Funambulus tristriatus* and the dusky striped squirrel *Funambulus sublineatus* at the study site. These two species were not included in this study because of their small body size and rare sightings.

The Western Ghats pass through the states of Kerala, Karnataka, and Tamil Nadu in southern India (Pascal, 1988). These mountains are a home to many endemic species of flora and fauna. The diurnal arboreal mammalian community in the evergreen forests consists of primate fauna and three species of squirrels. In the southern Western Ghats, NL, LTM, BM, and Indian GS are sympatric (Kumar et al., 2002). In the central Western Ghats, three species of primates viz LTM, BM, and Hanuman langur (*Semnopithecus entellus*) are sympatric along with the Indian GS (Singh et al., 2000a). The effect of forest fragmentation on the arboreal mammal community was examined in an earlier study (Umapathy, 1998). With the exception of one study (Singh et al., 2000b), where differences in feeding heights, feeding by fruit size classes, and activity patterns were examined, the feeding niches of the arboreal mammal community and the way they partitioned resources are poorly understood.

We examined differences in diet, height use patterns, dietary diversity, dietary overlap, and behavioral interactions
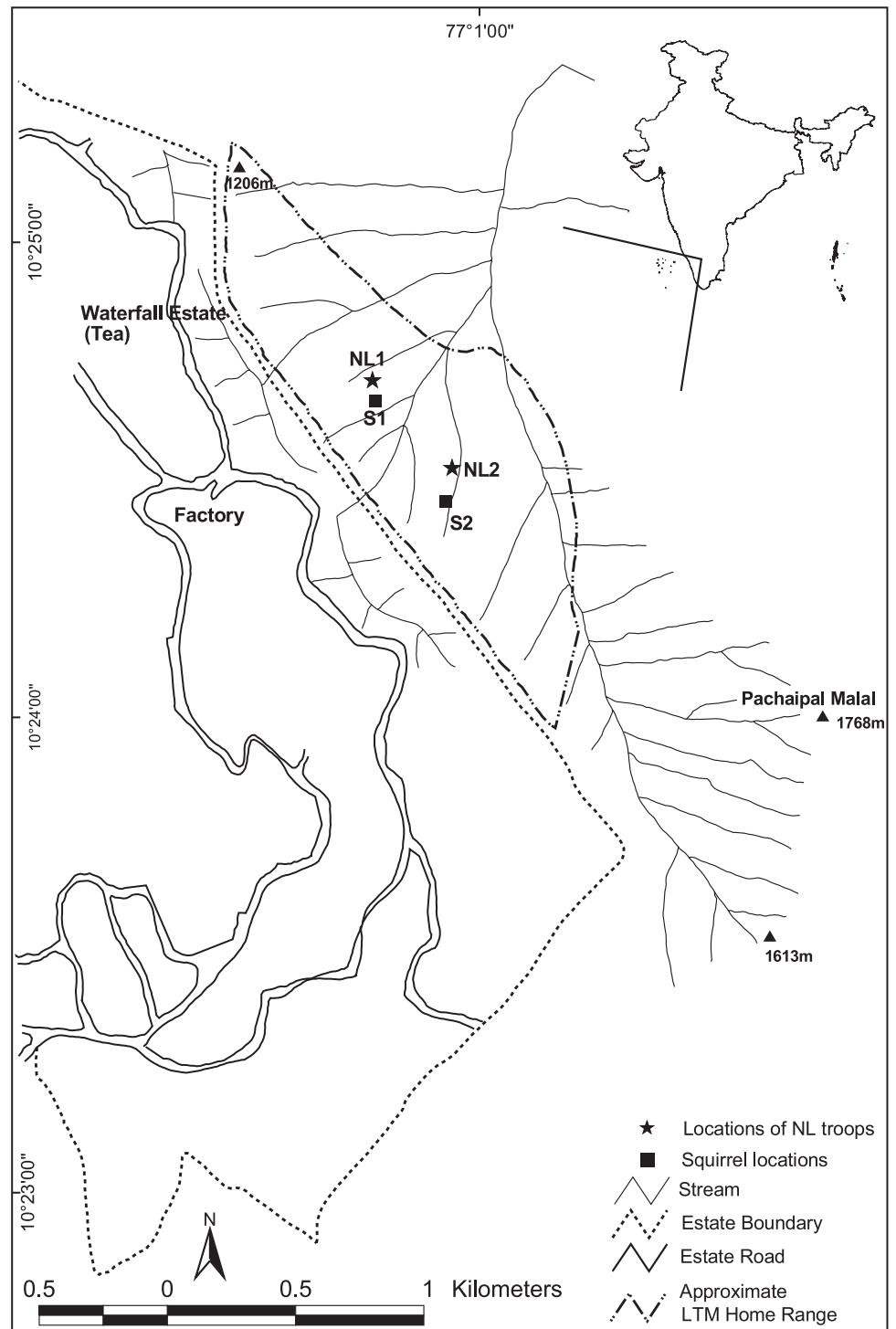
Figure 1
Study area map.

among the study species. On the niches of sympatric arboreal mammals, we hypothesize the following: (1) large niche overlap between the two congeneric macaque species, (2) large niche overlap between two predominantly folivorous species, the langur and the GS, and (3) large niche overlap between the LTM and the GS due to their frugivorous diet. In this study, we defined coexistence as constant use of the same habitat by two or more species. On the behavioral interactions among species pairs, we hypothesized that (1) no coexistence when large niche overlap and narrow niches result in greater number of intolerant interactions, (2) coexistence when large

niche overlap and broad niches result in fewer intolerant interactions, and (3) because the BM is a habitat generalist (Singh et al., 1997b), it would dominate over the habitat specialists in competition for food.

Study area

The study was carried out in an evergreen forest patch called Pachapal Malai shola, also known as Waterfall shola (10° 24′ 35.38″ N and 77° 0′ 31.34″ E) in Indira Gandhi Wildlife Sanctuary, in the Anaimalai hills of the Western Ghats (Figure 1).

Major forest types in the sanctuary include tropical dry thorn forests, tropical dry and moist deciduous forests, tropical wet evergreen forests and southern montane wet temperate forests (sholas), and montane wet grassland (Champion and Seth, 1968). The sanctuary receives rainfall both from the southwest (June–September) and northeast (October–January) monsoon. Most of the rainfall is from the southwest monsoon. The annual rainfall varies from 500 mm in the eastern parts to about 5000 mm at the ridge and on the western slopes. The study site was adjacent to a tea plantation on one side, and on the other side, it was contiguous with the deciduous forest in the sanctuary. The altitude of the study site ranged from 1200 to 1738 m. The tropical evergreen forest vegetation has been classified as a midelevation evergreen forest of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type (Pascal, 1988). The study site was isolated from other evergreen forest patches in the sanctuary. The area of the study site was about 3.5 km^2. The study period was divided into three seasons depending on the rainfall as—postmonsoon (October 2000–January 2001), dry (February–May 2001), and monsoon (June–October 2001).

Study species

The LTM is an endangered and endemic primate species of the Western Ghats and occurs only in the wet evergreen forests (Kumar, 1987). It is primarily frugivorous. It also feeds on flowers, nectar, and invertebrates (Kumar, 1987; Sushma, 2004; Umapathy, 1998). The macaque mostly lives in unimale groups with many females and their offspring (Kumar, 1987). Larger groups have more than one adult male. Average group size varies from 16.3 to 24.7 individuals in different areas (Kumar, 1995; Kumara and Singh, 2004; Ramachandran and Joseph, 2001; Singh et al., 2002). Its annual home range size is about 1.5 km^2 (Kumar, 1987).

The NL is an endemic folivorous primate of the Western Ghats and occurs in a variety of forest types such as tropical moist deciduous, riverine, wet evergreen, and montane wet temperate forests (Oates et al., 1980; Poirier, 1970). It lives primarily in unimale groups with many females and their young (Poirier, 1970), and the average group size is about 11 individuals (Singh et al., 1997b).

The BM is an omnivorous primate and feeds on fruits, seeds, flowers, insects, and young leaves (Ali, 1986). It occurs in a wide variety of forests throughout southern and central India and lives in multimale and multifemale groups (Roonwal and Mohnot, 1977). It mainly inhabits tropical dry thorn and dry and moist deciduous forests and is also commonly found in towns and villages. The average group size is about 29 individuals (Singh et al., 1997b). The home range size varies from 0.4 to 5 km^2 (Simonds, 1965; Sugiyama, 1971). The BM has not been studied in the tropical wet evergreen forests, and the present study is the first study to document its ecology and its interactions with the other species of arboreal mammals in this habitat. These three primates do not typically form mixed-species associations such as those found in South America and Africa. They are sympatric and randomly encounter each other at different times (Waser, 1982).

The Indian GS is a large, solitary, diurnal, arboreal squirrel (Ramachandran, 1988). It is widely distributed in peninsular India, occurring in the Western Ghats, the Eastern Ghats, and central India (Abdulali and Daniel, 1952). It primarily occurs in riverine, tropical moist deciduous, and wet evergreen forests (Abdulali and Daniel, 1952). The average home range in the moist deciduous forest is about 13.4 ha (Ramachandran, 1988), and in the wet evergreen forest, it is estimated to be about 1 ha (Borges, 1989). The Indian GS is a generalist herbivore and facultative frugivore, and its diet consists mainly of

Table 1

Age-sex structure of the study groups of LTM, NL, and BM

Age-sex	LTM (N = 19)	NL troop 1 (N = 7)	NL troop 2 (N = 12)	BM (N = 20)	GS (N = 2)
Adult male	1	1	1	3	1
Adult female	10	3	7	6	1
Subadult male	1	—	—	1	—
Juveniles	4	3	4	8	—
Infants	3	—	—	2	—

seeds during fruiting periods and young and mature leaves, flowers, pith, and bark during nonfruiting periods (Borges, 1992). In terms of diet, it is similar to the LTM and the NL (Umapathy, 1998; Umapathy and Kumar, 2000).

At the study site, Singh et al. (1997a) reported two groups of LTM, about 10 groups of NL and one group of BM. But during our study period, two groups of BMs periodically visited the study site from the adjoining deciduous forests. The number of GSs was not estimated through systematic census. However, from our searches along the forest trails, we encountered approximately about 20–25 individuals. One group each of LTM and BM, two groups of NLs, and two individual GSs were selected for the study. The study was carried out between January 2000 and November 2001. Only one observer was involved in the data collection. While other species were well habituated to the presence of humans, the BM groups were extremely shy of humans and required 7 months to select and habituate one of the groups. Group size and structure of the study species are given in Table 1. Home ranges of the study species were not examined. But we were able to delineate approximate home range of the LTM group based on the location of the group noted down during sampling. In the case of the langur and the squirrel, we have given locations of the study groups and individual squirrels on the map because they were too small to circumscribe on the map. In the case of the BM group, its home range in the evergreen forest completely overlapped with the LTM range. However, its home range use in the deciduous forest is not known as they could not be followed because of the steep terrain and the thorny ecotonal vegetation.

METHODS

Instantaneous sampling or scan sampling (Altmann, 1974) was used to gather information about group/individual activity. In the case of primates, group scans were taken on all visible members of the group for a period of 5 min at every 15-min interval. Indian GSs were sampled every 5 min. Each species was followed for about 5 days every month, and data were collected from dawn to dusk. Information recorded during scan sampling included date, time, individual (age-sex class), activity (resting, ranging, feeding on insects/fruits/flowers/leaves, social and self-directed activities), substratum used (only when the individual fed on insects), place at which the individual was seen (whether on ground or tree), animal height on a tree (visually estimated), plant species (when the individual fed on plant food), plant parts eaten, and its phenophase. Activity was recorded as follows:

Resting—When an individual showed passivity either sitting or sleeping. During feeding bouts, if the individual was inactive, it was recorded resting only if it lasted for more than 5 s (Struhsaker, 1975).

Ranging—Any movement between feeding trees or traveling. Movement within the same tree during feeding bouts was not recorded as ranging.

Feeding—When an individual ingested either plant food (fruits, leaves, flowers, etc.) or animal food (insects or any other live prey item).

Foraging—When an individual searched either for fruit or insect. Handling time for fruit or gnawing of seeds to feed on the endosperm as in the case of the squirrel was also recorded as foraging.

Social and self-directed behavior—Social behaviors such as grooming, play, agonistic interaction within the members of the group, and intergroup aggression were recorded under this category. Self-directed behavior included auto-grooming, self-play as in the case of infants, or exploring objects by infants.

Interspecific interactions among the study species were noted whenever two or more interacting species were present in the vicinity of each other within a radius of about 30 m. Data were collected on date, time, study species followed during the day, interacting species, activity of the study species before the encounter, activity of the study species during the encounter, activity of the interacting species during the encounter, distance between the interacting species (visually estimated), type of interaction (aggressive or affiliative), aggressor and the recipient, displacement (if any), species displaced, and duration of the interaction (time spent in proximity). Interactions were broadly classified as tolerant and intolerant.

Tolerant interactions—These included instances when the interacting species simply tolerated each other's presence in the vicinity without antagonism. It also included interspecific play or cooperative interactions like responding to each other's alarm calls.

Intolerant interactions—These included threats such as grunts, displacement of one species by the other, and chases. On one occasion, predation on an Indian GS by a LTM was observed. This was also recorded as an intolerant interaction.

Abundance and phenology of food trees

Between October 2000 and October 2001, 11 quadrats measuring 50×50–m plots were laid randomly in the study site, and food trees species of the four study species were marked. The tree species were chosen on the basis of previous studies and the present study (Kumar, 1987; Umapathy, 1998). The fruiting and flowering phenology of 337 trees of girth at breast height >10 cm, belonging to 43 species, was monitored once a month. Presence and absence of young leaves, mature leaves, and inflorescence were recorded. For fruits, the canopy was visually divided into four quadrants, and the number of fruits in each quadrant was roughly counted with the help of 10×35 Bushnell binoculars. Stages of ripeness were determined by fruit color and size. In a few species, for example, *Ficus exasperata* and *Meliosma pinnata*, fruit ripeness could not be determined with certainty. At the end of the study, vegetation sampling was carried out to estimate the density of important food trees. This sampling was carried out in 190 random circular plots of 5-m radius each. These plots were laid at a perpendicular distance of 10 m on either side of a randomly chosen trail and were spaced 50 m apart along the trail. Plant species were identified with the help of field guides (Gamble and Fischer, 1916–1935; Pascal and Ramesh, 1997). Leaf/fruit samples were collected and preserved for verification or identification by plant taxonomists. Except a few species whose specimens could not be collected, all plant species were identified to the species level.

Niche breadth

Levins' standardized measure of niche breadth (Hurlbert, 1978) was used to estimate the diversity of food resources in the diet of the study species. Food resources included food plant species, plant parts, and in the case of the macaques, insect prey. All arthropod prey items were treated as a single category. If the animal fed on two plant parts of a single species, it was considered as two distinct food resources. We chose this index because we wanted to emphasize the most frequently used food resources (Krebs, 1989).

Levins' standardized measure of niche breadth was calculated as follows:

$$B_A = \frac{B - 1}{n - 1},$$

where B_A is Levins' standardized niche breadth, B is Levins' measure of niche breadth, and n is the number of resource states. Levins' measure of breadth is

$$B = \frac{1}{\sum p_i^2},$$

where p_i is the proportion of food resource category i in the diet of the animal species. Niche breadth values are standardized on a scale from 0 to 1 (Hurlbert, 1978).

Niche overlap

Morisita measure of niche overlap (Krebs, 1989) was used to estimate niche overlap among the four species. Overlap between the species was estimated for food resources and substrates used for insect foraging. This index was used as it is believed to be bias free at all sample sizes and also when there is a large number of resource states (Smith and Zaret, 1982).

$$C = \frac{2\sum_i^n p_{ij} p_{ik}}{\sum_i^n p_{ij}[(n_{ij} - 1)/(N_j - 1)] + \sum_i^n p_{ik}[(n_{ik} - 1)/(N_k - 1)]},$$

where C is Morisita's index of niche overlap between species j and k, p_{ij} is the proportion of resource i in of the total resources used by species j, p_{ik} is the proportion of resource i in the total resources used by species k, n_{ij} is the number of individuals of species j that use resource category i; n_{ik} is the number of individuals of species k that use resource category i, and N_j and N_k are the total number of individuals of each species in sample, where $\sum_{i=1}^n n_{ij} = N_j$, $\sum_{i=1}^n n_{ik} = N_k$.

Analyses

One-way analysis of variance (ANOVA) was used to test for significance of difference in height in the canopy at which individuals were present with Tukey's (honestly significant difference [HSD]) test used for post hoc comparisons (Sheskin, 2000). Chi-square goodness of fit test was used to test for differences in frequencies of different food items in the diet within each season (Sheskin, 2000). It was also used to test for differences in frequencies of interactions during feeding and nonfeeding periods. Interactions among the study animals were analyzed pairwise. Chi-square test for proportion (Gibbons, 1971) was used to test for differences in proportion of interactions in three seasons. Based on the total duration of proximity and number of interactions between a species pair, interaction rate was calculated per hour. Direction of aggression or displacement (aggressor and recipient) in each intolerant interaction was used to determine interspecific hierarchy (Waser and Case, 1981). Proportion of intolerant interactions per unit time (I/T) was computed by dividing intolerant interaction rate by total interaction rate. Mantel's correlation coefficient using Excel 2003 Pop Tools was used to determine correlation between niche overlap and I/T among the six species pairs. Abundances of flowers and fruit were

Table 2
Occurrence of food items in the scans of the four study species in three seasons

Food items	Postmonsoon				Dry				Monsoon			
	LTM	BM	NL	GS	LTM	BM	NL	GS	LTM	BM	NL	GS
Fruit	195 (36.79)	9 (7.2)	209 (38.14)	282 (58.50)	359 (63.53)	287 (79.28)	189 (48.09)	54 (38.84)	429 (81.25)	205 (91.92)	317 (51.04)	281 (67.22)
Flower	219 (41.32)	95 (76)	117 (21.35)	87 (18.04)	73 (12.92)	26 (7.18)	113 (28.75)	29 (20.86)	—	—	17 (2.73)	—
Leaf	—	—	222 (40.51)	106 (22)	—	16 (4.41)	91 (23.15)	56 (40.28)	—	—	287 (46.21)	83 (19.85)
Insects	116 (21.88)	21 (16.8)	—	—	133 (23.53)	33 (9.11)	—	—	99 (18.75)	18 (8.07)	—	—
Pith	—	—	—	—	—	—	—	—	—	—	—	53 (12.67)
Bark	—	—	—	3 (0.62)	—	—	—	5 (3.59)	—	—	—	5 (1.19)
χ^2	32.87**	104.28**	35.88**	146.02**	241.58**	570.45**	40.36**	9.75**	—	171.90**	263.75**	220.83**

Percent values are given in the parentheses.
** $p < .01$.

analyzed in two different ways. In the case of flowers, abundance of flowering trees of a particular food plant species per hectare was estimated by multiplying the average number of sampled trees in flower in a season with the density of that species. In the case of fruit, average number of fruits produced by the sampled trees in a season was multiplied with the density of the species to obtain fruit crop per hectare. Shared food plant resources, which had ≥4% contribution to the annual diet of at least two of the study species, were considered as important shared resources.

RESULTS

Number of scan records on the NL, the LTM, the BM, and the Indian GS was 4641 (422 h), 5651 (456 h), 1767 (140 h), and 3128 (394 h), respectively. During postmonsoon, the two macaques had higher proportion of flower in their diets, and the langur spent higher proportion of time feeding on leaves (Table 2). Fruits dominated the diet of the squirrel during this season. During dry season, all three primates had higher proportion of fruit in their diets, and the squirrel spent higher percent of time feeding on leaves. During monsoon, fruits constituted a major part of the diet of all the four study species.

Niche breadth

The LTM had the narrowest niche breadth (0.17), and NL had the broadest niche breadth (0.35). For BM, the niche breadth represents the dietary niche in the study site. Therefore, its actual diet niche is expected to be wider. There was distinct seasonal variation in the niche breadths of these animals (Table 3). The LTM had the narrowest niche breadth during postmonsoon, and during dry and monsoon seasons it was similar (Table 3). NL also had the narrowest niche breadth during postmonsoon, but it used the highest number of food resources in this season. The BM had the broadest niche during monsoon, and in the dry season it was narrowest. GS had narrowest and broadest niche during dry and postmonsoon seasons, respectively.

Niche overlap

Niche overlap was highest between the macaques, followed by NL-GS, and least between BM-GS pair (Table 4). There was seasonal difference in overlap among the species pairs where highest overlap was in LTM-BM pair in monsoon and postmonsoon seasons, and in the dry season, it was highest in NL-GS pair. There were also seasonal differences in overlap within each species pair. The macaques had the highest overlap in postmonsoon (0.78), and it was least in monsoon. The LTM-NL pair showed least overlap in monsoon, and it was highest in the dry season. The LTM-GS pair showed higher niche overlap in postmonsoon than in dry and monsoon seasons. The NL-GS pair attained highest niche overlap values during the dry season and least during monsoon. The niche overlap value was least in BM-NL pair.

Shared resources and their abundance

Important shared food plant resources were flowers and fruits of *C. exarillata* (family: Bombacaceae), fruits of *Ficus microcarpa* and *F. exasperata* (family: Moraceae), and *M. pinnata* (family: Sabiaceae). *C. exarillata* was a common species in the study area with a density of about 59.6 trees/ha (Table 5). This is a mass cauliflorous flowering species, and each flower is tubular, about 4- to 4.5-cm long, and cream in color (Ganesh and Davidar, 1997). It flowered at the beginning of postmonsoon (October 2000) and continued till early dry season (February 2001), and it flowered again at the end of monsoon season (October 2001). These flowers were abundant only during postmonsoon season. All the four species ate these flowers during postmonsoon and dry seasons. The base of the sepals was eaten for nectar, and the anthers and stigma were dropped. The macaques relied heavily on this resource mainly during the postmonsoon season (Table 5). The NL and the GS spent less and nearly equal amount of time feeding on these flowers in postmonsoon and dry seasons.

Fruit of *C. exarillata* is a large spiny capsule, about 13 cm in diameter, which contains a few large seeds. The seeds were eaten by the study species except BM. However, it was an important fruit resource only for LTM and GS. NL feed only on old dehisced fruits. LTM and GS, on the other hand, were observed to rip open the fruit while feeding. Fruits were present in the three seasons. Seeds of *C. exarillata* constituted about 20% of the annual fruit diet of LTM. Although, LTM fed on the fruit in the three seasons, it spent highest percent of time feeding on it during monsoon (Table 5). GS fed on its fruit only during monsoon and dry seasons. It constituted only 7.12% of the squirrel's annual diet. NL fed on the seeds of *C. exarillata* only in the dry season. It represented only

Table 3

Niche breadth (Levins' standardized measure) of the study species during the three seasons

	a. LTM				b. NL				c. BM				d. Indian GS			
	Postmonsoon	Dry	Monsoon	Overall	Postmonsoon	Dry	Monsoon	Overall	Postmonsoon	Dry	Monsoon	Overall	Postmonsoon	Dry	Monsoon	Overall
No. of food plant species eaten	26	26	21	41	44	32	41	64	2	7	6	12	16	13	21	30
No. of plant parts eaten	5	5	3	5	7	7	7	8	2	4	3	5	7	6	6	8
No. of food resources	27	28	22	45	64	43	59	98	3	10	7	15	15	19	27	50
Niche breadth	0.16	0.25	0.24	0.17	0.20	0.39	0.36	0.35	0.31	0.13	0.40	0.19	0.59	0.26	0.41	0.29

Table 4

Overall niche overlap among the six species pairs and niche overlap during the three seasons

Species pairs	Overall	Postmonsoon	Dry	Monsoon
LTM-BM	0.56	0.78	0.54	0.35
LTM-NL	0.25	0.32	0.44	0.02
LTM-GS	0.22	0.36	0.17	0.18
BM-NL	0.13	0.25	0.12	0.11
BM-GS	0.08	0.31	0.02	0.01
NL-GS	0.41	0.47	0.60	0.12

1% of feeding scans during this season and therefore ranked as a minor food resource for NL.

All the four study species ate ripe fruits of *F. microcarpa*, however, GS feeding on the fruit was not captured in the scan samples. The macaques fed heavily on its fruit, LTM fed on the fruit in 16% of scans and it served as a major resource. LTM fed on its fruit in all the three seasons. This fruit was fed most often during dry season (Table 5). BM fed on the fruit only in monsoon and dry seasons. This resource occurred 53% of the plant diet in BM. In monsoon and dry seasons, it ranked as a major food resource occurring in about 73 and 47% of the scans, respectively. NL fed on its fruit only during dry season, occurring in about 2% of feeding scans and therefore ranked as a minor food resource.

Only NL and GS fed on fruits of *F. exasperata* and *M. pinnata*. Fruits of *F. exasperata* were available throughout the year. This resource constituted about 4% of the annual diet of NL. Although fruit crop per hectare was marginally more in dry season, the langurs fed on the fruit only during monsoon and postmonsoon. GS fed on its fruit during monsoon and postmonsoon, and it constituted about 5% of the annual diet.

Fruits of *M. pinnata* were available in postmonsoon and monsoon. NL consumed the fruit only in postmonsoon. In this season, NL fed on the fruit in about 19% of the feeding scans. Out of the total feeding scans, only in 7% of the scans NL fed on the fruit. GS fed on its fruit in postmonsoon and monsoon, and it contributed to 7% of the diet.

Vertical stratification

The macaques were present at higher strata in the canopy than the NL and GS (Figure 2a). Height at which these ani-

mals were present varied significantly (ANOVA: $F = 240.67$, df $= 3$, $p < .01$). Post hoc comparisons (Tukey's HSD test) revealed that all species pairs except NL and GS had significant differences in mean height use. BM was present at a higher level in the canopy than the other three species, GS and NL used lower heights. While feeding, BM used greater heights in the canopy than the other study animals (Figure 2b; $F = 220.40$, df $= 3$, $p < .01$). Post hoc comparisons revealed that the study species differed significantly in their height during feeding activities. NL occupied the least height while feeding.

Interspecific interactions

We observed 346 interspecific interactions, 144, 97, and 105 occurred in postmonsoon, monsoon, and dry seasons, respectively. Interactions between species were influenced by feeding activity ($\chi^2 = 104.32$, df $= 1$, $p < .01$). Intolerant interactions occurred mainly during feeding, while tolerant interactions occurred equally in both feeding and nonfeeding periods (Table 6). Except for the LTM-NL pair, the rest of the species pairs had significantly different number of interactions in the three seasons (Table 7). Among the six species pairs, the LTM-GS and NL-GS interacted at a higher rate than other pairs (Table 7). I/T ratio was highest between the two macaques. LTM-GS showed similar rate of intolerant interactions as the macaques, but their I/T ratio differed. LTM-GS and LTM-NL pairs had similar I/T ratios. Certain species pairs, for example, BM-GS and NL-GS, did not show any intolerance toward each other. However, among the six species pairs, there was a significant correlation between niche overlap and I/T ratio (Mantel's $r = .52$, $p < .05$). Intolerant interactions were significantly influenced by seasons ($\chi^2 = 7.69$, df $= 2$, $p < .05$), with highest numbers in postmonsoon (Table 8). Because three of the species pairs—LTM-BM, LTM-GS, and LTM-NL—showed mutual intolerance, abundance of three important shared resources viz flowers and fruits of *C. exarillata* and fruits of *F. microcarpa* were compared with the proportion of intolerant interactions (Figure 3). The other two food resources (fruits of *F. exasperata* and *M. pinnata*) were not considered for the comparison because only NL and GS, which showed no intolerance, fed on them. A clear direct relationship was only seen between abundance of flowers of *C. exarillata* and the occurrence of intolerant interactions (Figure 3a). However, in the case of *F. microcarpa*, though it had a large fruit crop especially in postmonsoon,

Table 5

Availability of five important shared resources and percent of feeding scans of the four study animals on each of these resources

Resource	Postmonsoon					Dry					Monsoon				
	Availability	LTM	NL	BM	GS	Availability	LTM	NL	BM	GS	Availability	LTM	NL	BM	GS
Cullenia exarillata flower (59.64 trees/ha)	47.22 trees/ha	46%	13%	90%	16%	7.46 trees/ha	13%	15%	6%	16%	5.96 trees/ha	0	0	0	0
Cullenia exarillata fruit	UF-0; RF-186[a]	7%	0	0	0	UF-1908; RF-0	5%	1%	0	17%	UF-3025; RF-289	34%	0	0	12%
Ficus microcarpa (2.68 trees/ha)	UF-506; RF-975	3%	0	0	0	UF-632; RF-599	25%	2%	73%	0	UF-89; RF-178	18%	0	47%	0
Ficus exasperata (0.25 trees/ha)	10	0	3%	0	7%	93	0	0	0	0	66	0	8%	0	5%
Meliosma pinnata (12.06 trees/ha)	8234	0	19%	0	10%	0	0	0	0	0	572	0	0	0	5%

Density of each plant species is given within the parentheses.

[a] UF, unripe fruit/ha; RF, ripe fruit/ha.
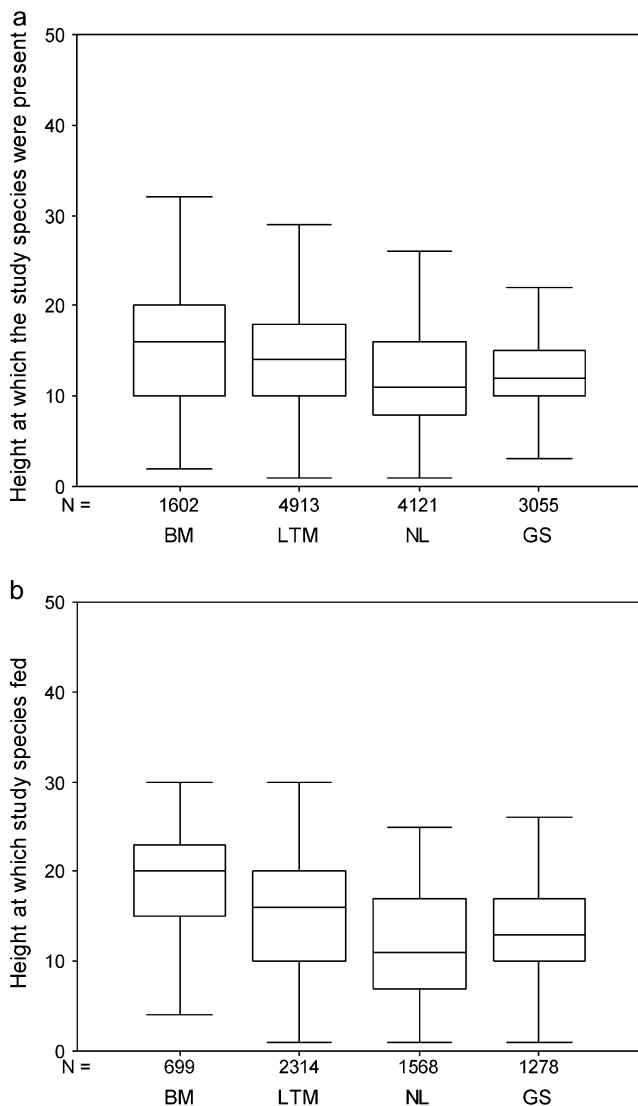
Figure 2
Height at which the four study species were present during all activities (a) and during feeding activities (b). The boxes represent the median and quartiles, and the outliers are given by the vertical brackets.

the study species sparsely fed on it. Displacement was similar in LTM-BM, LTM-NL, and LTM-GS, but overt aggression such as threats and chases was highest in LTM-BM pair (Table 8). Responses to alarm calls of other species occurred more frequently among pairs with resident species than pairs with BM. LTM-GS responded more to each other's alarm calls than other species pair. Only BM showed intolerance toward LTM

Table 6

Occurrence of tolerant and intolerant interactions during feeding and nonfeeding periods

Interactions	Feeding period	Nonfeeding period	Total
Tolerant	137	131	268 (77.45%)
Intolerant	69	9	78 (22.54%)
Total	206	140	346 ($\chi^2 = 104.32$, df = 1, $p < .01$)

(Figure 4). Out of 31 agonistic interactions observed, in 25 instances, BM directed aggression toward LTM. Among the resident species, LTM showed intolerance toward the other two species (NL and GS; Figure 4).

DISCUSSION

Only macaques fed on insects. LTM spent higher percent of time feeding on insects than BM. This difference is mainly due to former's dependence on insects for protein (Kumar, 1987). Fruit flesh contains a high concentration of simple sugars, but poor in protein, although leguminous seeds have higher content of protein than fruit flesh (Milton, 1983; Waterman, 1984). Frugivorous primates have to either depend on foliage or invertebrates for protein. Fruits, which the LTM feeds on, are rich in sugars and polysaccharides but poor in protein (Kumar, 1987). The diet of LTM lacks foliage component and leguminous seeds and, therefore, it depends on invertebrates for protein. In fact, it is more insectivorous than other macaques (Kumar, 1987). BM presents quite a different picture. Its diet in the deciduous forest has higher proportion of leaves (about 18%) and a negligible amount of insects (1%) (Singh, 1999). It also feeds on leguminous seeds of *Prosopis* sp. and *Tamarindus indica* (Cooper M, personal communication). In the present study, foliage constituted a small proportion and insects constituted high proportion of its diet. This study reports greater proportion of fruits in the diet of BM than in reports from previous studies (Singh, 1999). Availability of figs and flowers of *C. exarillata* largely determined the presence of the bonnet group at the study site. It appears that feeding on insects was probably only an interstitial activity for BM in the wet evergreen forest. NL in contrast with the previous studies (Oates et al., 1980; Sunderraj, 1998) can be described as a facultative frugivore because of its ability to capitalize on resources such as fruits whenever they were available (Sushma, 2004). Such foraging pattern is reported in *Alouatta seniculus*, which is otherwise a folivorous primate (Guillotin et al., 1994). NL was frugivorous during monsoon and dry seasons, when they fed primarily on seeds and unripe fruits and predominantly folivorous during postmonsoon.

Niche breadth

LTM and NL had the least and most diverse diets, respectively. BM was similar to LTM, and GS was similar to NL in their diet niche breadth. NL and GS were generalists being able to feed on a wide variety of resources. Availability of food resources largely determined their niche breadths in the three seasons. The diet of NL was more diverse in monsoon and dry season than in postmonsoon. It concentrated feeding on a few species even when it used maximum number of food resources (Table 3b) in postmonsoon. This indicates selectivity on the part of the animal. In general, availability of important food resources was low in the dry season (Sushma, 2004). During periods of low food abundance, animals either increase searching time or reduce selectivity of food items (Emlen, 1973; Pyke et al., 1977; Schoener, 1971). The mode of foraging, reducing selectivity during periods of low food availability, and thereby having a more diverse diet is reported in other species of primates (Guillotin et al., 1994). The foraging strategy adopted by NL by increasing its dietary breadth follows the principles of optimal foraging theory. In the case of GS, dietary diversity was highest in postmonsoon, when fruit abundance was more, and least in dry season, when fruit abundance was low. There was an increase in the consumption of leaves in the dry season (Table 3d). In LTM, the diet niche was narrowest in postmonsoon. In this season, it concentrated feeding on flowers of *C. exarillata*. In the other two seasons,

Table 7

Total number of interactions during the three seasons

| Species pairs | Duration of interactions (in h) | Postmonsoon | Dry | Monsoon | χ^2 (df = 2) | All interactions (N = 346) | | | |
						Tolerant	Intolerant	I/T[a]	Total
LTM-BM	28.33	32	28	8	63.90[b]	37 (1.30)[c]	31 (1.09)[c]	0.45	68 (2.41)[c]
LTM-NL	31.45	24	24	26	3.73	52 (1.65)	22 (0.70)	0.30	74 (2.35)
LTM-GS	18.66	26	11	25	83.95[b]	39 (2.09)	23 (1.23)	0.36	62 (3.44)
BM-NL	25.75	19	13	8	34.15[b]	38 (1.47)	2 (0.08)	0.05	40 (1.55)
BM-GS	11.88	12	13	8	29.48[b]	33 (2.77)	0	0	33 (2.77)
NL-GS	22.05	31	16	22	86.61[b]	69 (3.12)	0	0	69 (3.13)
Total		144	105	97		37	31		

[a] Prop, intolerance per unit time.
[b] Significant at 0.01.
[c] Interactions per hour are given within parentheses.

time was evenly spent on the food resources. BM used only three food resources in postmonsoon. In this season, BM mainly fed on flowers of *C. exarillata*.

Niche overlap

LTM-BM and NL-GS pairs had high overlap in their feeding niche. This was expected as these species pairs had similar resource needs. In this study, niche overlap between species pairs was higher during postmonsoon and dry seasons than during monsoon. This was mediated by flowers of *C. exarillata*, which was superabundant during postmonsoon and dry seasons. It is the most common flowering tree species and the flowers also last for a long period. High niche overlap mediated by most abundant food items are known to influence arboreal mammal communities (Guillotin et al., 1994; Struhsaker, 1978; Terborgh, 1983). Another tree species that contributed to high overlap between macaques was *F. microcarpa*. The macaques were avid fig eaters, and this species was responsible for their niche overlap in monsoon and dry seasons. Interestingly, only the macaques exploited this fruit intensively. Unlike fruit and flower of *C. exarillata*, fruit of *F. microcarpa* was an ephemeral resource that lasted only 7–10 days (personal observation). It also occurred in low density at the study site (Table 5). Therefore, it was a key food resource for macaques when the overall food availability in the forest was low. The niche overlap in NL-GS pair was high in postmonsoon and monsoon due to fruits of *M. pinnata* and *F. exasperata*. Another important food resource, flowers of *C. exarillata*, caused niche overlap in the dry season.

Vertical stratification

Many authors have noted that vertical stratification is one of the important modes of niche separation among sympatric
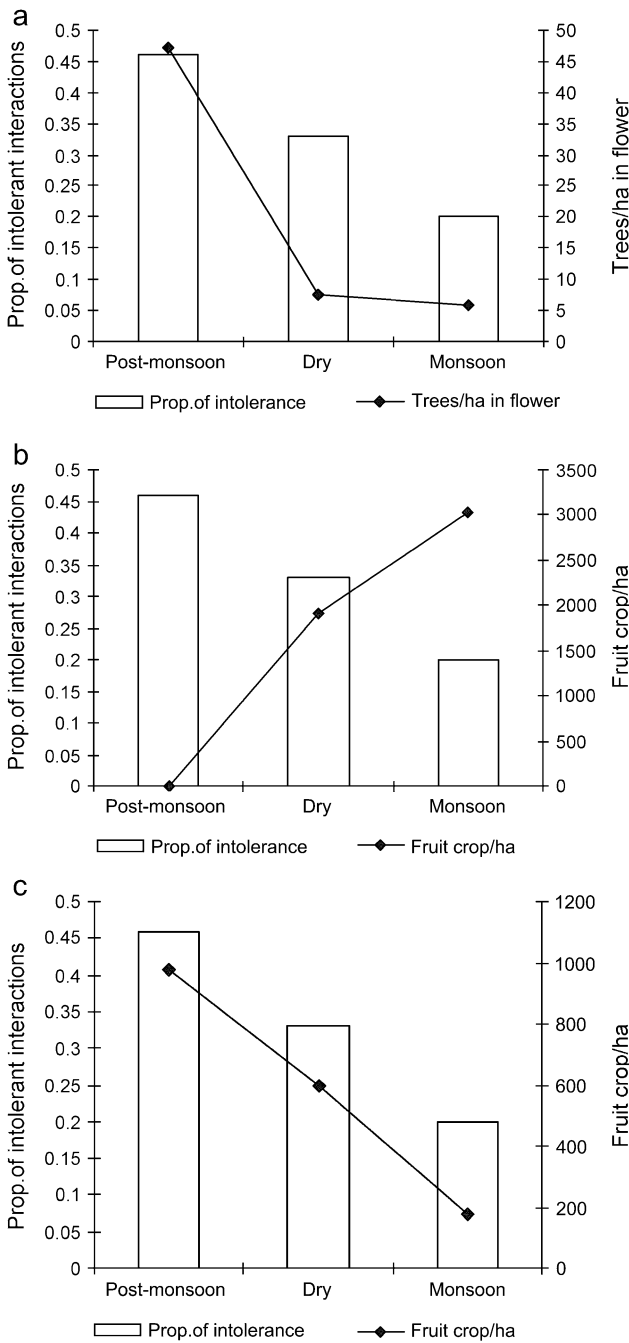
arboreal mammals (Emmons, 1980; Estrada and Coates-Estrada, 1985; Gartlan and Struhsaker, 1972; MacKinnon JR and MacKinnon KS, 1978; Ungar, 1996). We found a clear pattern of vertical stratification among the four study species. Although tree height classes were equally available to all the four species and they were seen at all height classes, each of them differed significantly in their use of vertical space in the forest canopy. The two macaques occupied greater heights in the canopy than NL and GS because the former used mainly large food tree species such as *F. microcarpa* and *C. exarillata* and the latter used understorey trees. Emergent trees in evergreen forests are tall and have large crown diameter. They are also fully exposed to sun and are thus likely to be more productive (Terborgh, 1983). In this study, BM used greater heights in the canopy than LTM. However, in the deciduous forests, BM occupies a lower stratum in the forest than the sympatric hanuman langur (*S. entellus*), and it spends considerable amount of time on the ground (Singh, 1999). Change in use of vertical space with habitat type is known from other primate studies as well (Mittermeier and van Roosmalen, 1981; Terborgh, 1983). NL and GS fed on leaves from 10- to 15-m tall trees. Folivory on understorey trees in shade exceeds those on leaves of tall trees exposed to sun because the latter have tough leaves and contain high levels of secondary compounds than the former (Lowman, 1985; Lowman and Box, 1983). In the case of the squirrel, another possible explanation for occupying the understory is avoidance of aerial predators.

Interspecific interactions

Aggressive interactions between species are quite common in primates, although it may be an ineffective means of excluding competitors if the contested resource is a large fruiting tree (Waser, 1987). In situations when groups find it difficult

Table 8

Intolerant interactions during the three seasons

| Species pairs | Intolerant interactions | | | | | | |
	Postmonsoon	Dry	Monsoon	Total	Alarm calls	Displacement	Overt aggressive interactions
LTM-BM	15	16	0	31	4	19	12
LTM-NL	12	8	4	22	10	20	2
LTM-GS	7	4	12	23	20	20	3
BM-NL	2	0	0	2	3	2	0
BM-GS	0	0	0	0	4	0	0
NL-GS	0	0	0	0	12	0	0
Total	36	16	26	78			

Figure 3
Proportion of intolerant interactions among the study species and
(a) no. of *Cullenia exarillata* trees/ha in flower, (b) *C. exarillata*
fruit crop/ha, and (c) *Ficus microcarpa* fruit crop/ha.

Figure 4
Matrices of tolerance-intolerance between LTM and bonnet and
among the coexisting species pairs.

to locate food patches and defend food patches, routing competitors from the shared food resource will become an ineffective means of increasing one's share of food (Waser and Case, 1981). In this study, majority of the aggressive interactions occurred during feeding, and intolerance was high only in two macaques and LTM-GS pair. Intolerant interactions were largely influenced by niche overlap among species pairs. *F. microcarpa* was an important ephemeral resource for the macaques only in monsoon and dry seasons. This meant that the macaques could not have economically defended it. Moreover, apart from the macaques, there were many other consumers on the fruits, such as several species of birds (personal

observation). During postmonsoon, figs were available; however, LTM and BM spent less time feeding on it and more time feeding on flowers of *C. exarillata*. The energy-rich food resource in flowers of *C. exarillata* was responsible for higher proportion of intolerance among competing species pairs. It appears that the availability of flowers of *C. exarillata* in the postmonsoon and dry seasons largely determined the occurrence of intolerant interactions among the study species. Like figs, the flowers of *C. exarillata* are eaten by a number of birds and other mammals (Ganesh and Davidar, 1997). The macaques shared similar food niches and vertical strata and, therefore, exhibited interference competition. In NL-GS pair, niche overlap was high, but no intolerance was exhibited. One explanation for this lies in their broad feeding niche. Both species had diverse diets and showed ability to switch to alternative food items such as leaves, pith, and bark in periods of low fruit availability. This might have reduced the competition for shared food resources in the species pair.

There are many subtle associations among species in nature leading to coexistence. Coexistence might be favored when two or more species together access a difficult resource successfully, while individually, they cannot access the same resource (Cody, 1971; Struhsaker, 1981; Terborgh, 1983). Species associations have enhanced ability to detect predators, thereby, reduce the risk of being preyed on (Gartlan and Struhsaker, 1972; Gautier-Hion et al., 1983; Terborgh, 1983). The study species usually tolerated the presence of another in its vicinity. There were instances when one responded to each other's alarm calls. Cooperative interactions such as alarm calls are reported from studies of mixed-species associations in primates (Eckardt and Zuberbuhler, 2004; Gautier-Hion et al., 1983; Oates and Whitesides, 1990). In this study, each species responded to other's alarm calls. In LTM-GS pair, alarm calls were made most often. We reason that GS being solitary and alert to aerial predators (Ramachandran, 1988) makes alarm calls, which benefits LTM. The LTM gains from the calls of the squirrel presumably because group dispersion is high and each individual space themselves apart while foraging on insects. Except for LTM, the other species are habitat generalists (Singh et al., 1997b; Umapathy and Kumar, 2000). The NL and the GS were resident species of the study site. The interaction matrices of species pairs indicated interspecific dominance hierarchy, with BM dominating all other species. LTM dominated NL and GS, and between NL and GS, there was no evidence of hierarchy. Body size is not an important

factor among LTM, NL, and BM because NL is largest and the two macaques have more or less the same body size (Rowe, 1996). The number of adult males is probably an important factor because the BM had three adult males, and LTM and NL had only one adult male in their groups. We feel that another reason for the dominance of BM over LTM could be due to food provisioning by humans for BM. The BM study group was part of a contiguous population interspersed with commensal populations. Our explanation also finds support from the fact that members of commensal macaque groups show higher curiosity, exploration, and dominance over their forest counterparts (Singh, 1969). BM exhibited the least cooperative interactions, large niche overlap, high intolerance, and dominance over LTM. This highlights the tenuous nature of association exhibited by BM where coexistence may not be favored.

Some generalizations on resource use and coexistence can be made from the results of the present study. (1) If two closely related species have high niche overlap and narrow niche breadth, they are less likely to coexist. This was the case with the two macaques. (2) If two species have a high niche overlap but also have a large niche breadth, they may reduce competition by feeding on a large variety of items, and hence, could coexist. This was the case with NL and GS. (3) If two species have a low niche overlap and are separated in space, they could coexist on a regular basis. This was the case with LTM and NL.

Niche differentiation among the resident arboreal mammals in the study was mediated through their use of food resources and the available habitat. Such differentiation has resulted in nested niches, with the niche of LTM included within in the niche of NL and GS, which are generalists. Often, in such communities, species with the nested niche controls the preferred resource (Colwell and Fuentes, 1975). It means that specialist species dominate over the preferred food resource and supplant generalists that use alternate food resources. In other parts of the Western Ghats, BM is resident and sympatric with LTM (Kumara and Singh, 2004). It will be important to investigate resource partitioning when the combination of resident sympatric species is changed to LTM, BM, and Hanuman langur in the evergreen forest.

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