

RESEARCH ARTICLE

Resource Partitioning in Sympatric Langurs and Macaques in Tropical Rainforests of the Central Western Ghats, South India

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In a competitive sympatric association, coexisting species may try to reduce interspecific interactions as well as competition for similar resources by several ecological and behavioral practices. We studied resource utilization of three sympatric primate species namely, lion-tailed macaques (*Macaca silenus*), bonnet macaques (*M. radiata*) and Hanuman langurs (*Semnopithecus entellus*) in a tropical rainforest of the central Western Ghats, south India. We studied resource use, tree-height use, foraging height, substrate use when consuming animal prey and interspecific interactions. The results revealed that across the year, there was very limited niche overlap in diet between each species-pair. Each primate species largely depended on different plant species or different plant parts and phenophases from shared plant species. Primate species used different heights for foraging, and the two macaque species searched different substrates when foraging on animal prey. We also recorded season-wise resource abundance for the resources shared by these three primate species. While there was low dietary overlap during the dry season (a period of relatively low resource abundance), there was high dietary overlap between the two macaque species during the wet season (a period of high resource abundance for the shared resources). We observed only a few interspecific interactions. None of these were agonistic, even during the period of high niche overlap. This suggests that the sympatric primate species in this region are characterized by little or no contest competition. Unlike in some other regions of the Western Ghats, the lack of interspecific feeding competition appears to allow these primates, especially the macaques, to remain sympatric year-round. *Am. J. Primatol.* 73:335–346, 2011. © 2010 Wiley-Liss, Inc.

Key words: lion-tailed macaque; bonnet macaque; Hanuman langur; niche overlap; interspecific interaction; coexistence

INTRODUCTION

The presence of two or more species of animals that travel, rest or feed together in the same location at a rate greater than predicted by chance is referred to as a polyspecific association. Mutual behavioral attraction, attraction to common resources or a location, or just “chance” may result in spatial associations between different animal species [Waser, 1984]. Polyspecific associations may be beneficial if they result in an increased efficiency in harvesting and defending resources [Cords, 2000] and detecting predators [Buzzard, 2010]. For example, groups of *Callimico goeldii* remained in proximity or in vocal contact with groups of *Saguinus fuscicollis* and *S. labiatus* during 7% of the day. When in association with *Saguinus* in wet season, *C. goeldii* spent 13% of time co-feeding as compared to only 2% in dry season. *Callimico* used the middle canopy 62% while in association as compared to 52% when they were a single species group [Porter, 2001]. Porter [2001] argued that *Callimico* received feeding and possibly predator detection advantages when part of a polyspecific association. However, in other cases,

species that are closely related or have largely similar food habits, such as consumption of fruits by lion-tailed macaques and bonnet macaques, may compete for resources [Sushma & Singh, 2006]. Under these conditions, we expected some form of niche separation. For example, based on a 16-month field investigation, when in polyspecific groups, *Cercopithecus diana* was found to feed and travel in the upper canopy in 88% scans, whereas *C. campbelli* and *C. petaurista* fed and traveled principally in the lower canopy. In contrast, at sites where *C. campbelli* and *C. petaurista* are present and *C. diana* is absent,

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the former species are found to increase their use of upper canopy from 12 to 29%. However, Buzzard [2010] argues that antipredatory calls by *C. diana* in response to sighting potential predators accorded important benefits to *C. campbelli* and *C. pataurista* and that this appears to outweigh the potential costs of reduced access to resources in the upper canopy. In several primate species, it has been argued that increased troop size resulting from a polyspecific association can increase the probability of detecting predators in all levels of the forest canopy [Terborgh, 1990].

Much attention has been paid during the last two decades to the ecological and behavioral processes that reduce competition between sympatric species. These processes result in resource partitioning or “niche specialization” or in mechanisms of coexistence based on a trade-off between resource exploitation and foraging efficiency [Houle et al., 2006]. Elton [1927] described niche as functional in terms of the role a species has in an ecosystem. In an ecosystem, the proportional use of shared resources by more than one species leads to food niche overlap between the species resulting in the potential for feeding competition if the particular resources shared are in limited supply [Kozłowski et al., 2008; La Morgia & Bassano, 2009; Mishra et al., 2004; Sushma & Singh, 2006; Vieira & Port, 2006]. Schreier et al. [2009] have illustrated eight possible processes by which sympatric species may minimize or avoid competition. These processes include use of different forest patches or foraging heights, specializing on different food resources or temporal differences in activity [Emmons, 1980; Gartlan & Struhsaker, 1972; Singh et al., 2000; Sushma & Singh, 2006; Terborgh, 1983; van Valkenburgh, 1996]. Such strategies of coexistence or avoidance have been observed in a wide variety of taxa. Lopez and Vaughan [2007] studied 15 species of frugivorous bats and observed that primarily *Carollia* consumed *Piper*, *Artibeus* consumed *Ficus* and *Cecropia*, and *Glossophaga* consumed *Vismia* resulting in niche separation. These results indicate that sympatric bat genera avoided feeding competition by exploiting a different tree species. Factors other than dietary overlap are also important for niche separation among primates such as the use of different parts of the tree canopy [Buzzard, 2006; Lahann, 2008; McGraw, 2000], using different substrates for consumption of animal prey [Nadjafzadeh & Heymann, 2008], interspecific encounters to reduce home range overlap [Sushma & Singh, 2006], use of different habitats or avoidance of overlap in ranging patterns of sympatric groups, and temporal shifts in activity patterns [Schreier et al., 2009].

Kumara and Singh [2004] observed that bonnet macaques (*M. radiata*), lion-tailed macaques (*M. silenus*) and Hanuman langurs (*Semnopithecus entellus*) are sympatric and permanent year round

residents in the rainforests of the central Western Ghats between the rivers Sharavathy and Aghanashini in the state of Karnataka. Given this pattern of year round residence, in this study, we examined resource availability, resource use and resource sharing among these three species. We predicted that under conditions in which food niche overlap among these sympatric primates is low and dietary overlap is greatest when shared resources are available in relatively high abundance, year-round coexistence is possible in response to low levels of feeding competition.

METHODS

Study Area

We conducted this study from March 2006 through June 2009 (40 consecutive months) in the northern limit of the evergreen forests of the plains and low elevations of the Western Ghats of South India [Pascal, 1988] in the Gerusoppa Forest Range (74°35'–74°47'E and 14°15'–14°25'N), Honnavara Forest Division in the state of Karnataka (Fig. 1). The total area of the Gerusoppa forest range is 208.1 km² and in that range, the “Gerusoppa beat” is 70.18 km². The main study area, Matnigadde village and associated forest area, was 25.18 km². The temperature ranged in this region between a maximum of 33°C in April and a minimum of 20°C in January. The area receives Monsoon rains that start from the last week of May and last to October. July is the rainiest month when the average rainfall is almost 3,000 mm with 80% average humidity. Total yearly rainfall is about 6,000 mm. Unlike some other areas of the Western Ghats, this region does not receive north-east Monsoons. Champion and Seth [2005] broadly classify this forest as “West Coast Tropical Evergreen Forest”. In this forest, there is an abundance of heliophilic or light tolerant species, which may be distinguished as *Persea macrantha*–*Diospyros* spp.–*Holigarna* spp. associations. The forest has a legal status as a “Reserve Forest” with interspersed revenue lands [Kumara & Singh, 2004].

Study Species

For this study, we selected one group each of lion-tailed macaques ($N = 21$) and Hanuman langurs ($N = 7$) and two groups of bonnet macaques (Group 1, $N = 11$ and Group 2, $N = 16$) ranging in the forests surrounding the village of Matnigadde. The four study groups' home ranges overlapped with each other, as well as with other groups of the three primate species in the study area. Approximately 70% of the 0.12 km² home range of Hanuman langurs overlapped with groups of two macaque species. There was approximately 40% overlap in the home ranges of lion-tailed macaques and bonnet macaques. These species had home ranges of 1.5 and

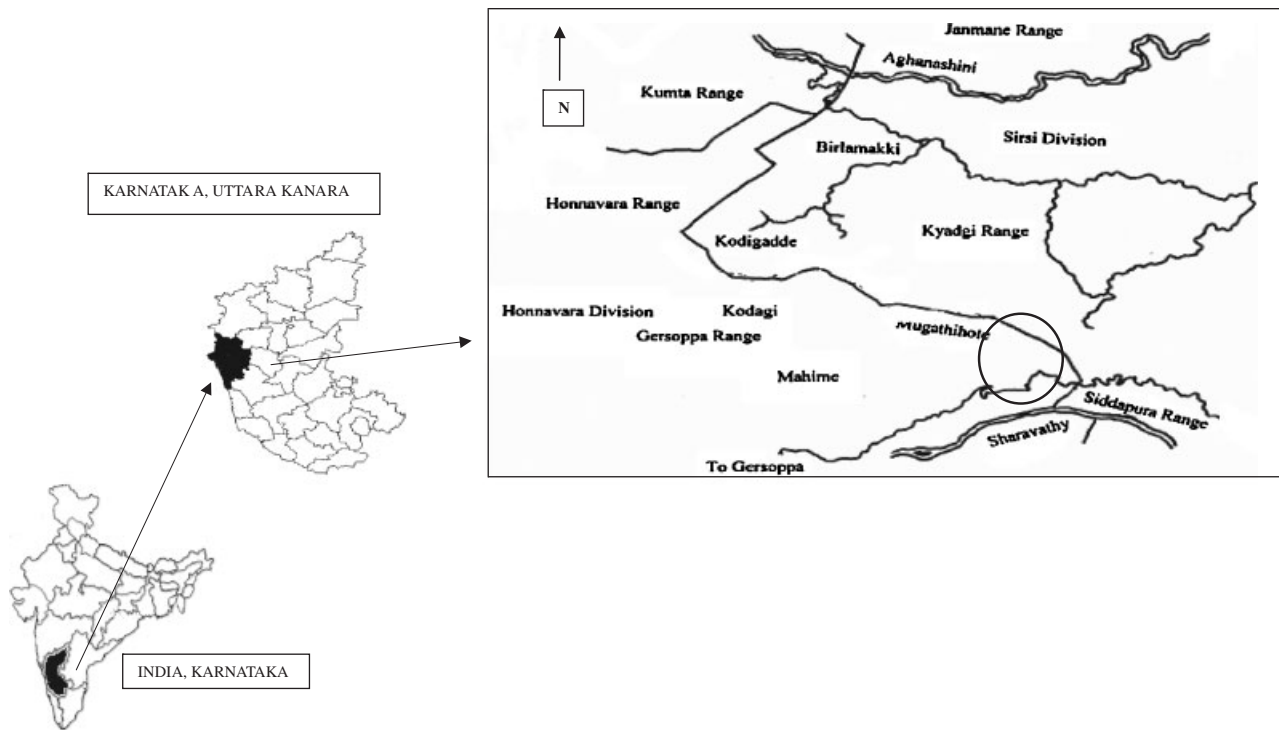


Fig. 1. Map of the study region. The circle in the map indicates the actual study area. Sharavathy and Aghnashini are rivers.

0.8 km² respectively. The lion-tailed macaque group was composed of two adult males, seven adult females and 12 immature individuals. Group 1 of the bonnet macaques contained two adult males, three adult females and six immatures, and group 2 included two adult males, five adult females and nine immatures. The Hanuman langur group contained one adult male, one adult female and five immature individuals.

Observation Protocol

We employed instantaneous scan sampling [Altmann, 1974; Lehner, 1996] to study the activity patterns of all visible individuals. We conducted a scan for a period of five minutes during which time each individual was observed. We collected the information through a pre-formatted data sheet recording Date, Study species, Group activity, Individual identity, Individual activity, Substrate used (only when the individual fed on insects), Place at which the individual was seen (i.e. in tree, on ground or in bamboo groove), Height at which the individual was present, Plant species (when the individual fed on plant food), Plant part eaten and Phenophase of the plant part. We recorded food items as whole leaf, petiole, leaf tip, mesocarp, seed, whole fruit, tendrils, bark and flower and their different phenophase as flush, young and mature for leaves and unripe, partially ripe and ripe for fruits. Other food items consumed such as pith and nectar also were recorded. We repeated the same procedure after a gap of 10 min (which gave overall four records

per individual/hour). We followed each species of primates for about five days every month from 0600 hr to 1800 hr. We collected a total of 8,422 scans (5,949 in the dry season and 2,493 in the wet season) on Hanuman langurs, 4,410 scans (3,053 in dry season and 1,357 in wet season) on lion-tailed macaques and 4,955 scans (3,338 in dry season and 1,617 in wet season) on bonnet macaques.

We collected data on interspecific interactions through ad libitum sampling. If groups of any two species came within 30 m of each other, we considered it as an intergroup encounter. The distance of 30 m was used because the study area was a dense rainforest and this was the unobstructed visual sighting distance we estimated a monkey could see. The same criterion (30 m) has been used to study interspecific interactions among primates in rainforests in other part of the Western Ghats [Sushma & Singh, 2006]. During an encounter, we recorded interactions as “intolerant” (fight, bark, displacement between two species) and “tolerant” (indifferent to the presence of each other).

Phenological Sampling

We carried out phenology sampling to record abundance of plant food resources. We laid 10 sample plots which were randomly distributed throughout the study area. All plots had a fixed width of 20 m but varied in length from 150 to 300 m covering a total length of 2,050 m. The total area sampled was 2.7, 5.1 and 25.0% of the home ranges of lion-tailed maca-

ques, bonnet macaques and Hanuman langurs respectively. We tag numbered all tree species having more than 30 cm CBH (circumference at breast height). However, for phenological data, we selected only those tree species that were used as plant food resources by primates. In total, we monitored more than 800 trees (the number of trees kept changing slightly due to natural calamities) of 71 species every month, and recorded the presence (+) and absence (–) of flush, young and mature leaves, flowers, ripe and unripe fruits.

We collected the plant parts dropped by the animals to ascertain the edible part of the item and its phenophase. We identified the plant species with the help of field guides [Gamble-Fischer, 1916–1935; Pascal & Ramesh, 1997]. In most cases, we preserved sample plant parts including leaf, flower and fruit for confirmation of identification by plant taxonomists of the Department of Forest Biology, College of Forestry, Sirsi, who had worked in the same forest. We identified most of the plants to the species level.

We recorded different substrates including leaf litter, dead branch, vine, moss, dead log, dry leaf, tree hole, bark, foliage, trunk and dead tree trunk when primates fed on fauna. We recorded animal height and foraging height through visual estimation and categorized these heights into different classes (0: Ground; 1: 1–5 m; 2: 6–10 m; 3: 11–15 m; 4: >16 m). The categories were based on the vegetation height of the study area as most of the trees had an average height of >20 m [Pascal, 1988] but most foraging by all primates occurred up to a height of 15 m or less. Accordingly, the height categories were divided as ground, low stratum (ground up to one quarter of the vegetation), lower middle stratum and higher middle stratum (the middle half of the vegetation) and canopy (the highest quarter of the vegetation) [Ren et al., 2001].

Data Analysis

Out of a total 40 months of the study period which included laying of transects, selection of study groups and initial vegetation sampling, the scan sampling data on primates were collected from November 2006 to December 2008. The data for 25 months were pooled to analyze annual and seasonal (November–April as dry season and May–October as wet season) resource use and partitioning.

We used Morisita measure of niche overlap [Krebs, 1989] to determine food niche overlap in species-pairs. We considered the major food items as those which were observed to be consumed by a primate species in at least 1% of the feeding scans. We considered each food item with its phenophase as a “resource”. For example, if a primate species fed on both “unripe” and “ripe” fruits of a particular tree species, it was considered as two resources since

these were available at different times. Consumption of partially ripe fruits was considered separately in feeding scans, but in the proportion of resource abundance, it was merged with unripe fruits. All faunal items consumed by the monkeys were scored as insect.

We used the data on proportion of each food resources used by a species to calculate Morisita measure of niche overlap as follows:

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

where C is Morisita’s index of niche overlap between species j and k ; p_{ij} is the proportion of resource i in 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 ; N_j and N_k are the total number of individuals of each species in sample,

$$\sum n_{ij} = N_j, \quad \sum n_{ik} = N_k$$

In this measure, the value of C ranges between zero and one, indicating no niche overlap to complete niche overlap. We used χ^2 test of proportion [Gibbons & Chakraborty, 1992] to test for the significance of difference for height at which an animal foraged. The χ^2 test of proportion was used to test for differences in utilization of various substrates by macaques feeding on insects.

RESULTS

Overall, the diet (based on percent feeding scans) of macaques was composed primarily of fruits, flowers and insects, and the diet of Hanuman langurs was composed primarily of leaves. Of the 4,410 scans on lion-tailed macaques, feeding was observed to occur in 667 and 268 scans during dry and wet seasons respectively. Of the 4,955 scans on bonnet macaques, feeding was observed to occur in 846 and 339 scans during dry and wet seasons respectively. Of the 8,422 scans on Hanuman langurs, feeding was observed to occur in 1,685 and 789 scans during dry and wet seasons respectively.

Resource Partitioning

Use of selective plant species by primates

The plant species that accounted for 1% of each species feeding time, including trees, shrubs and climbers, were considered as the major food plants (Table I). Hanuman langur mainly used plant species including *Chionanthus malabarica*, *Knema attenuata* and *P. macrantha* in the dry season and *Archidendron monadelphum*, *Cassine glauca*, *Hydnocarpus*

TABLE I. Plant Species Used Over the Year and in Dry and Wet Seasons for Selective Resources by the Primate Species

Hanuman langur		Lion-tailed macaque		Bonnet macaque	
Plant species used	Family	Plant species used	Family	Plant species used	Family
<i>Archidendron monadelphum</i> ^a	Fabaceae	<i>Aglaia roxburghii</i>	Meliaceae	<i>A. roxburghii</i>	Meliaceae
<i>Callicarpa tomentosa</i>	Verbenaceae	<i>Caryota urens</i>	Arecaceae	<i>C. urens</i>	Arecaceae
<i>Cassine glauca</i>	Celastraceae	<i>C. glauca</i>	Celastraceae	<i>Cayratia auriculata</i>	Vitaceae
<i>Chionanthus malabarica</i>	Oleaceae	<i>Cayratia auriculata</i>	Vitaceae	<i>Chionanthus malabarica</i>	Oleaceae
Climber	–	Climber	–	<i>Cleidion spiciflorum</i>	Euphorbeaceae
<i>Dillenia pentagyna</i> ^a	Dilleniaceae	<i>Diospyros crumenata</i>	Ebenaceae	Climber	–
<i>Dimocarpus longan</i>	Sapindaceae	<i>Diospyros pruriens</i>	Ebenaceae	<i>Diospyros crumenata</i>	Ebenaceae
<i>Hydnocarpus penitandra</i> ^a	Flacourtiaceae	<i>Dipterocarpus indicus</i>	Dipterocarpaceae	<i>Diospyros pruriens</i>	Ebenaceae
<i>Knema attenuata</i>	Myristicaceae	<i>Drypetes venusta</i> ^a	Euphorbeaceae	<i>Ficus callosa</i>	Moraceae
<i>Litsea floribunda</i>	Lauraceae	<i>Ficus callosa</i>	Moraceae	<i>Ficus nervosa</i>	Moraceae
<i>Litsea laevigata</i>	Lauraceae	<i>Garcinia gummigutta</i>	Clusiaceae	<i>Ficus racemosa</i>	Moraceae
<i>Litsea stocksii</i>	Lauraceae	<i>Holigarna grahamii</i>	Anacardiaceae	<i>Ficus tsjakela</i> ^a	Moraceae
<i>Mangifera indica</i>	Anacardiaceae	<i>Knema attenuata</i>	Myristicaceae	<i>Garcinia gummigutta</i>	Moraceae
<i>Ochlandra radii</i> ^a	Poaceae	<i>Litsea stocksii</i>	Lauraceae	<i>Holigarna grahamii</i>	Clusiaceae
<i>Olea dioica</i> ^a	Oleaceae	<i>Macaranga peltata</i>	Euphorbiaceae	<i>Hopea ponga</i>	Anacardiaceae
<i>Persea macrantha</i>	Lauraceae	<i>Mangifera indica</i>	Anacardiaceae	<i>Knema attenuata</i>	Dipterocarpaceae
<i>Piper nigrum</i> ^a	Piperaceae	<i>Persea macrantha</i>	Lauraceae	<i>Litsea floribunda</i>	Myristicaceae
<i>Pothos scandens</i>	Araceae	<i>Syzygium cumini</i>	Myrtaceae	<i>Madhuca nerifolia</i>	Lauraceae
<i>Syzygium gardneri</i>	Myrtaceae	<i>Syzygium gardneri</i>	Myrtaceae	<i>Mimusops elengi</i> ^a	Sapotaceae
<i>Tabernaemontana heyneana</i> ^a	Apocynaceae			Paddy ^a	Poaceae
Unidentified				<i>Persea macrantha</i>	Lauraceae
<i>Vitex altissima</i> ^a	Verbenaceae			<i>Polyalthia fragrans</i>	Annonaceae
<i>Vitis canarensis</i> ^a	Vitaceae			<i>Syzygium gardneri</i>	Myrtaceae
<i>Xantolis tomentosa</i> ^a	Sapotaceae			<i>Trewia nudiflora</i>	Euphorbeaceae
<i>Carallia brachiata</i> ^a	Rhizophoraceae				
<i>Psychotria nigra</i> ^a	Rubiaceae				
<i>Canthium angustifolium</i> ^a	Rubiaceae				
<i>Elaeocarpus serratus</i> ^a	Elaeocarpaceae				

^aPlant species used exclusively by study species.

pentandra, *Litsea floribunda*, *L. stocksii*, *Mangifera indica*, *Ochlandra redii*, *Pothos scandens*, *Tabernaemontana heyneana*, *Vitex altissima*, *Vitis canarensis* only in the wet season. Lion-tailed macaque used *Drypetes venusta* and *Holigarna grahamii* only in the dry season and *Aglaia roxburghii*, *C. glauca*, *Cayratia auriculata*, *Diospyros pruriens*, *Ficus callosa*, *L. stocksii*, *Macaranga peltata*, *M. indica* and *Syzygium cumini* only in the wet season. Bonnet macaques used *Caryota urens*, *C. malabarica*, *Cleidion spiciflorum*, *Diospyros crumenata*, *Ficus nervosa*, *Ficus tsjakela*, *H. grahamii*, *Hopea ponga*, *Madhuca neriifolia*, *Mimusops elengi* and rice paddies only in the dry season and *A. roxburghii*, *D. pruriens*, *Ficus racemosa*, *Garcinia gummigutta*, *K. attenuata*, *L. floribunda*, *Syzygium gardneri* and *Trewia nudiflora* only in the wet season. In Table I, the plant species indicated by asterisk were exclusively used by each of the primate species. In the case of Hanuman langurs, plant species used exclusively, including *Olea dioica* and *Dimocarpus longan*, contributed to almost 50% of the total feeding time. The major item used exclusively by bonnet macaques was rice paddies constituting about 9% of the total feeding time. Lion-tailed macaque used *D. venusta* exclusively as one of their major food items, which contributed more than 20% of their total feeding time throughout the year.

Use of Common Resources by the Three Primate Species and Their Abundance

Overall shared use of resources and resource availability

Five plant species including *P. macrantha*, *K. attenuata*, *H. grahamii*, *S. gardneri* and climbers were used by all primate species (Table II). However, all the three primate species shared only the ripe whole fruit of *S. gardneri* (Table III) over the year. Among species-pairs, ripe mesocarp of *P. macrantha* and the whole fruit of *S. gardneri* were shared by Hanuman langurs and lion-tailed macaques; ripe whole fruit of *S. gardneri* was also shared by Hanuman langurs and bonnet macaques and other than insects, whole ripe fruits of *S. gardneri* and climbers, ripe mesocarp of *G. gummigutta* and ripe aril of *A. roxburghii* were shared by lion-tailed macaques and bonnet macaques over the year (Table III). Ripe fruits and flowers of *K. attenuata* had the highest annual abundance followed by ripe fruits of *G. gummigutta* and *H. grahamii* (Fig. 2). These abundant resources were found in the diet of each of the sympatric primate species.

Shared use of resources and resource availability in the dry season

In the dry season, all three primate species jointly fed on three plant species including

TABLE II. Plant Species Used by Different Species-Pairs Over the Year and in Dry and Wet Seasons

Overall/seasons	Hanuman langur and Lion-tailed macaque	Hanuman langur and Bonnet macaque	Lion-tailed macaque and Bonnet macaque
Overall	<i>Persea macrantha</i> <i>Knema attenuata</i> <i>Syzygium gardneri</i> <i>Holigarna grahamii</i> Climber	<i>Hopea ponga</i> <i>Persea macrantha</i> <i>Knema attenuata</i> <i>Syzygium gardneri</i> <i>Holigarna grahamii</i> Climber	<i>Persea macrantha</i> <i>Knema attenuata</i> <i>Syzygium gardneri</i> <i>Garcinia gummigutta</i> <i>Holigarna grahamii</i> Climber <i>Aglaia roxburghii</i> <i>Diospyros pruriens</i> <i>Caryota urens</i> <i>Diospyros crumenata</i> <i>Caryota urens</i>
Dry Season	<i>Persea macrantha</i> <i>Knema attenuata</i> <i>Syzygium gardneri</i> <i>Holigarna grahamii</i> Climber	Unidentified <i>Persea macrantha</i> <i>Holigarna grahamii</i> <i>Chionanthus malabarica</i> Climber <i>Modhuca neriifolia</i>	<i>Diospyros crumenata</i> <i>Caryota urens</i> <i>Diospyros crumenata</i> <i>Persea macrantha</i> <i>Holigarna grahamii</i> Climber
Wet Season	<i>Knema attenuata</i> <i>Syzygium gardneri</i> <i>Cassine glauca</i> Climber <i>Mangifera indica</i> <i>Litsea stocksii</i>	<i>Knema attenuata</i> <i>Syzygium gardneri</i> Climber <i>Litsea floribunda</i>	<i>Persea macrantha</i> <i>Knema attenuata</i> <i>Ficus callosa</i> <i>Syzygium gardneri</i> <i>Garcinia gummigutta</i> Climber <i>Aglaia roxburghii</i> <i>Cayratia auriculata</i> <i>Diospyros pruriens</i>

Bold indicates shared plant species by all three primate species over the year.

TABLE III. Shared Resources as Percent of Total Diet from Shared Plant Species by Three Primates Over the Year and in Dry and Wet Seasons

Overall/season	Hanuman langur	Lion-tailed macaque	Bonnet macaque
Overall	<i>P. macrantha</i> -mesocarp-ripe ^a (2.84) <i>K. attenuata</i> -petiole-mature <i>S. gardneri</i> -wholefruit-ripe ^{a,b} (4.22) Climber-wholeleaf-flush Climber-wholeleaf-young Climber-wholeleaf-mature	<i>P. macrantha</i> -mesocarp-ripe ^a (3.70) <i>S. gardneri</i>-wholefruit-ripe^a (6.00) <i>P. macrantha</i> -inflorescence <i>K. attenuata</i> -inflorescence <i>H. grahamii</i> -mesocarp-ripe Climber-seed-ripe Climber-wholefruit-ripe (1.53) <i>C. urens</i> -mesocarp-ripe <i>D. crumenata</i> -mesocarp-ripe <i>D. crumenata</i> -mesocarp-ripe <i>G. gummigutta</i>-mesocarp-ripe (7.14) <i>A. roxburghii</i> -mesocarp-ripe <i>A. roxburghii</i>-aril-ripe (5.11) Different insect (21.97)	<i>S. gardneri</i>-wholefruit-ripe^b (2.09) Climber-wholefruit-ripe (4.82) <i>H. ponga</i> -inflorescence <i>P. macrantha</i> -mesocarp-ripe <i>K. attenuata</i> -aril-ripe <i>H. grahamii</i> -hypocarp-unripe <i>H. grahamii</i> -mesocarp-ripe Climber-mesocarp-ripe Climber-inflorescence <i>G. gummigutta</i>-mesocarp-ripe (1.99) <i>A. roxburghii</i>-aril-ripe (4.71) <i>C. urens</i> -pith <i>C. urens</i> -mesocarp-ripe <i>A. roxburghii</i> -mesocarp-ripe <i>D. pruriens</i> -mesocarp-ripe Different insect (14.87) Climber-wholefruit-ripe (1.88) <i>P. macrantha</i> -wholeleaf-flush ^b (1.35) <i>C. macrantha</i> -mesocarp-ripe <i>H. grahamii</i> -mesocarp-ripe <i>H. grahamii</i> -hypocarp-unripe Climber-inflorescence <i>M. nerifolia</i> -inflorescence <i>D. crumenata</i>-mesocarp-ripe (1.35) <i>C. urens</i> -pith <i>C. urens</i> -mesocarp-ripe Different insect (13.73) <i>S. gardneri</i> -wholefruit-unripe ^b (2.81) <i>S. gardneri</i>-wholefruit-ripe (6.25) Climber-wholefruit-ripe (10.00) <i>K. attenuata</i>-aril-ripe (6.25) Climber-mesocarp-ripe Climber-inflorescence Climber-wholefruit-unripe <i>K. attenuata</i> -aril-ripe <i>L. floribunda</i> -inflorescence <i>P. macrantha</i>-inflorescence (1.25) <i>G. gummigutta</i>-mesocarp-ripe (5.94) <i>D. pruriens</i>-mesocarp-ripe (1.25) <i>A. roxburghii</i>-aril-ripe (14.06) <i>C. auriculata</i>-mesocarp-ripe (2.19) <i>F. callosa</i> -mesocarp-unripe <i>A. roxburghii</i> -mesocarp-ripe <i>D. pruriens</i> -mesocarp-ripe Different insect (12.50)
Dry Season	<i>P. macrantha</i> -mesocarp-unripe <i>P. macrantha</i> -mesocarp-ripe ^a (3.47) <i>K. attenuata</i> -wholeleaf-young <i>K. attenuata</i> -petiole-mature <i>S. gardneri</i> -wholefruit-ripe ^a (4.52) Climber-wholeleaf-flush Climber-wholeleaf-young Climber-wholeleaf-mature Unidentified-wholeleaf-young Unidentified-petiole-mature <i>C. malabarica</i> -wholeleaf-flush ^b (2.63) Climber-wholeleaf-flush Climber-wholeleaf-young <i>M. indica</i> -mesocarp-ripe <i>L. stocksii</i> -wholefruit-ripe <i>S. gardneri</i> -wholefruit-unripe ^b (1.49) <i>C. glauca</i> -mesocarp-ripe <i>L. floribunda</i> -wholefruit-ripe	<i>P. macrantha</i> -mesocarp-ripe ^a (4.97) <i>S. gardneri</i> -wholefruit-ripe ^a (3.60) <i>K. attenuata</i> -inflorescence <i>H. grahamii</i> -mesocarp-ripe Climber-seed-ripe Climber-wholefruit-ripe (1.20) <i>C. urens</i> -mesocarp-ripe <i>D. crumenata</i>-mesocarp-ripe (15.61) <i>D. crumenata</i> -mesocarp-ripe Different insect (22.64) <i>K. attenuata</i> -inflorescence <i>S. gardneri</i>-wholefruit-ripe (10.16) Climber-wholefruit-ripe (1.95) <i>K. attenuata</i>-aril-ripe (1.17) <i>C. glauca</i> -seed-ripe Climber-mesocarp-ripe Climber-wholefruit-ripe <i>M. indica</i> -mesocarp-ripe <i>L. stocksii</i> -wholefruit-unripe <i>P. macrantha</i>-inflorescence (1.17) <i>G. gummigutta</i>-mesocarp-ripe (16.41) <i>A. roxburghii</i> -mesocarp-ripe <i>D. pruriens</i> -mesocarp-unripe <i>D. pruriens</i>-mesocarp-ripe (1.17) <i>F. callosa</i> -wholefruit-ripe <i>A. roxburghii</i> -aril-ripe <i>A. roxburghii</i>-aril-ripe (15.63) <i>C. auriculata</i>-mesocarp-ripe (1.17) Different insect (15.63)	
Wet Season			

Bold indicates shared resources by lion-tailed macaques and bonnet macaques. Values in parentheses indicate percent of the resource in the total diet of a species. Parape, Partially ripe.

^aShared resources by Hanuman langurs and lion-tailed macaques.

^bShared resources by Hanuman langurs and bonnet macaques.

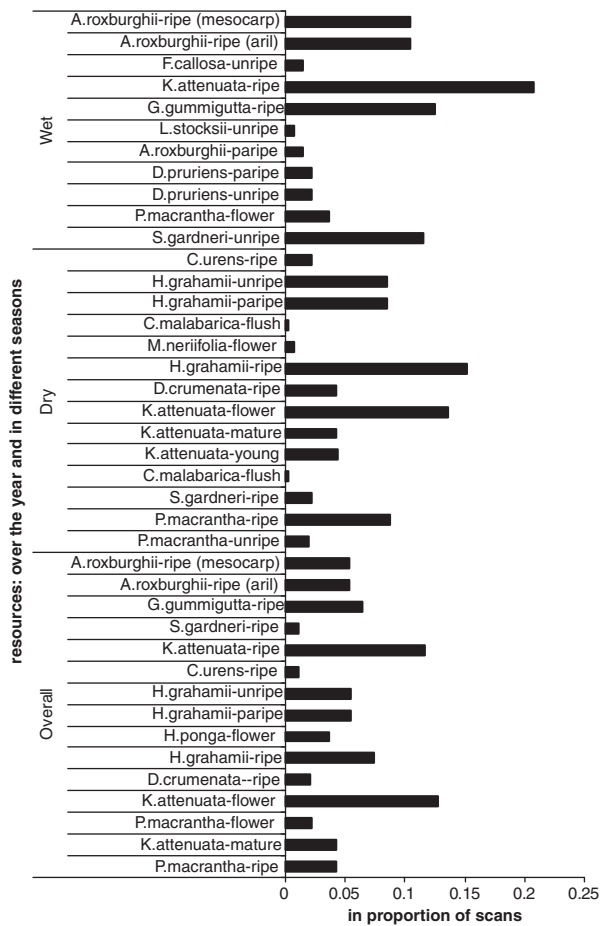


Fig. 2. Abundance of plant food resources indicated by their occurrence in proportion of scans over the year and in dry and wet seasons (paripe, partially ripe).

P. macrantha, *H. grahamii* and one climber (Table II). Other plants were not jointly exploited in dry season by all three primate species (Table III). For example, the ripe mesocarp of *P. macrantha* and the whole fruit of *S. gardneri* were shared by Hanuman langurs and lion-tailed macaques. Hanuman langurs and bonnet macaques shared only the flush of whole leaves of *C. malabarica*. Excluding insects, the ripe whole fruit of one climber and the partially ripe mesocarp of *D. crumenata* were shared by lion-tailed macaques and bonnet macaques. The abundance of food accounting for more than 1% dietary scans in the dry season indicates that ripe fruits of *H. grahamii* and flowers of *K. attenuata* were the most abundant resources, followed by ripe and partially ripe fruits of *H. grahamii* and ripe fruits of *P. macrantha* (Fig. 2).

Shared use of resources and resource availability in the wet season

Only three plant species including *K. attenuata*, *S. gardneri* and climbers were shared by all three primate species in the wet season (Table II). During

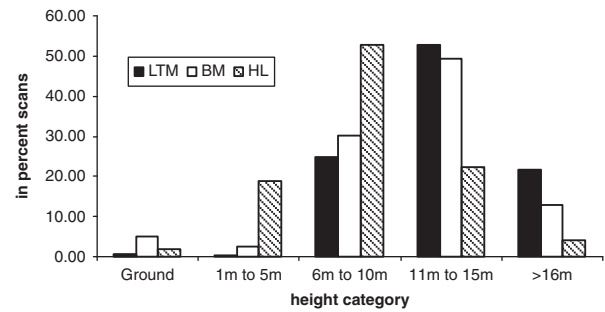


Fig. 3. Height categories at which primate species were observed to forage in percent scans.

this period of the year, Hanuman langurs and bonnet macaques only shared the unripe whole fruit of *S. gardneri* (Table III). Lion-tailed macaques and bonnet macaques shared resources including the ripe whole fruit of *S. gardneri* and climbers, the ripe aril of *K. attenuata* and *A. roxburghii*, the ripe mesocarp of *G. gummigutta* and *C. auriculata*, the partially ripe mesocarp of *D. pruriens*, inflorescence of *P. macrantha* and insects. The abundance of resources used by all three primate species in wet season showed that ripe fruits of *K. attenuata* had the highest abundance, followed by the unripe fruits of *S. gardneri*, ripe fruits of *G. gummigutta*, ripe mesocarp and the ripe aril of *A. roxburghii* (Fig. 2). Lion-tailed macaques and bonnet macaques shared the greatest number of resources. Most of the resources that they shared in wet season were abundant in the study area. Overall, these data suggest that each study species used many resources seasonally; however, only a few of these species were jointly exploited by all primate species.

Niche Overlap

The food niche overlap between Hanuman langurs and lion-tailed macaques was 0.034, 0 and 0.039 during the dry season, the wet season and over the entire year respectively. Niche overlap between Hanuman langurs and bonnet macaques was 0.004, 0.007 and 0.011 during the dry season, the wet season and over the year respectively. Niche overlap between lion-tailed macaques and bonnet macaques was 0.204, 0.705 and 0.315 during the dry season, the wet season and over the year respectively. The Morisita index of niche overlap ranges between 0 and 1. A niche overlap below 0.6 is considered low and above 0.6 is considered high. The data of this study indicate that except for the considerably high niche overlap between lion-tailed macaques and bonnet macaques during the wet season (a time of food abundance), for all other species' pairs, niche overlap was low.

Height Partitioning

The overall foraging height categories used by the primate species are shown in Figure 3. In most of

the scans, all primate species were observed to be present at a height between 6 and 15 m. However, the difference among the species for animal height was significant ($\chi^2 = 1,950.74$, $df = 8$, $P < 0.001$) with Hanuman langurs observed at lower height than lion-tailed macaques and bonnet macaques. Foraging also occurred mostly between a height of 6–16 m (Fig. 3). However, the foraging height among the three primate species differed significantly ($\chi^2 = 936.34$, $df = 8$, $P < 0.001$). Hanuman langurs were present and also foraged mostly at a lower height (1–10 m), bonnet macaques were present and foraged above langurs (at a height 6–15 m) and the lion-tailed macaques were present and foraged in the upper canopy (11 m and above). These differences in foraging height utilization by all three primate species were also significant in dry season ($\chi^2 = 664.74$, $df = 8$, $P < 0.001$) as well as in wet season ($\chi^2 = 301.87$, $df = 8$, $P < 0.001$). However, the difference between bonnet macaques and lion-tailed macaques for foraging height was significant over the

year ($\chi^2 = 71.2$, $df = 4$, $P < 0.001$) and in dry season ($\chi^2 = 66.77$, $df = 4$, $P < 0.001$), but not during the wet season (Fig. 4) ($\chi^2 = 8.15$, $df = 4$, $P = 0.086$). Bonnet macaques were observed in about 4% of scans on ground as they fed on rice paddies in dry season. These data suggest that there was a vertical separation for all activities, especially between langurs and macaques.

Substrate Partitioning

The data on utilization of different substrates for feeding on insects over the year by macaques are presented in Figure 5. Hanuman langurs were never observed to consume fauna. Bark (41.40%) was the most used fauna foraging substrate followed by dry leaf (21.65%), foliage (16.56%) and moss (10.51%) by the macaques (Fig. 5). However, the frequency of the use of different substrates by lion-tailed macaques and bonnet macaques differed significantly. Lion-tailed macaques foraged for insects more

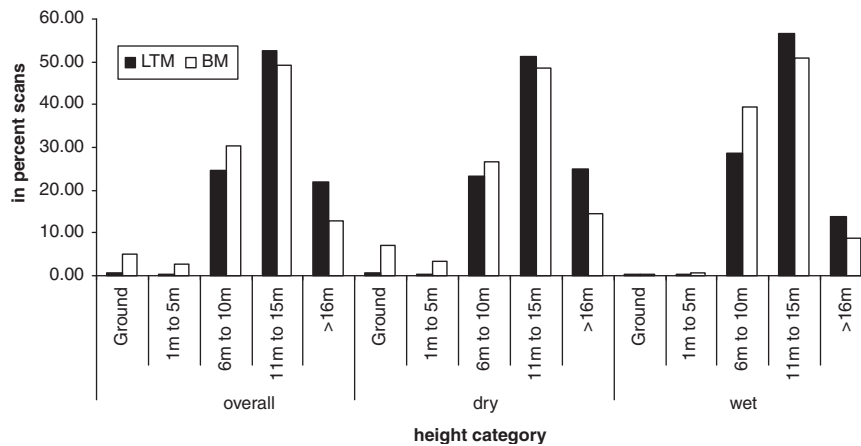


Fig. 4. Use of foraging height categories occurring in percent scans by lion-tailed macaques (LTM) and bonnet macaques (BM) over the year and in dry and wet seasons.

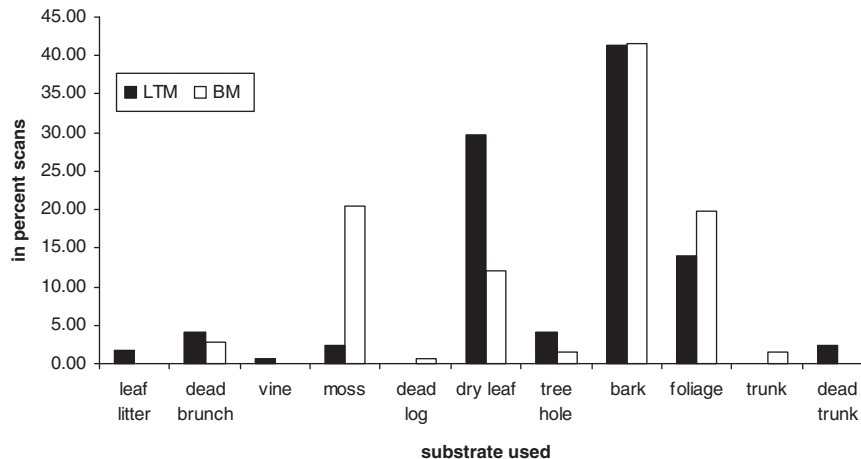


Fig. 5. Use of different substrates for foraging on fauna in percent scans by lion-tailed macaques (LTM) and bonnet macaques (BM).

frequently in dry leaves and tree holes, whereas bonnet macaques foraged more in moss and foliage ($\chi^2 = 39.16$, $df = 5$, $P < 0.01$). A similar pattern of differential use of the substrates by macaques was also observed in the dry season ($\chi^2 = 166.09$, $df = 4$, $P < 0.01$) and the wet season ($\chi^2 = 52.03$, $df = 2$, $P < 0.01$).

Interspecific Interactions

In total, only 15 interactions were observed among species-pairs during this study. Lion-tailed macaques had one tolerant and two intolerant interactions in the dry season with Hanuman langurs and no interactions in the wet season. Lion-tailed macaques had one and two tolerant interactions in the dry and the wet seasons respectively with bonnet macaques. There was no intolerant interaction observed between two macaque species. Hanuman langurs and bonnet macaques interacted nine times. There were five tolerant and one intolerant interaction in the dry season and three tolerant interactions in the wet season. The congeneric lion-tailed macaques and bonnet macaques, despite considerable niche overlap especially during wet season, had only tolerant interactions. Further, correlations between niche overlap and tolerant interactions (Spearman $r = -0.32$, $N = 3$, $P = 0.79$), and niche overlap and intolerant interactions ($r = -0.82$, $N = 3$, $P = 0.39$) were nonsignificant. These data suggest that most of the interactions among the primate species were tolerant.

DISCUSSION

Closely related sympatric species are expected to employ processes that lead to resource partitioning that make the coexistence of species possible. In this study, although several tree species were shared by each of the three primates, the majority of the diet of *M. radiata*, *M. silenus* and *S. entellus* included plant parts or their phenophases that were exclusively used by only that species. Overall, the major dietary item of Hanuman langurs was leaves whereas in the bonnet and lion-tailed macaques fruits and insects were most common. In a polyspecific association, omnivorous species like macaques with a wide dietary flexibility can avoid interspecific competition with other taxa by altering their dietary preferences [Dammhahn & Kappeler, 2008; Schreier et al., 2009].

The primarily folivorous langurs largely foraged in the middle canopy and the primarily frugivorous-faunivorous macaques largely foraged in the upper canopy. Such vertical separation in feeding heights has also been observed in sympatric long-tailed macaques, white handed gibbons, orangutans and Thomas' langurs [Ungar, 1996], as well as in many other primates inhabiting the same forest communities. In this study, the two macaque species used different heights for foraging, especially in the

dry season. In the wet season they foraged and fed at a similar height in the canopy as they shared more common resources.

During this study, the overall food niche overlap in primate species' pairs was small. This overlap became even smaller during dry season when the fruit availability was low. Pyke et al. [1977] proposed that food niche separation, especially for fruits, should occur more during the period of resource scarcity. Such niche separation was observed between *Ateles belzebuth* and *Lagothrix lagothricha* in Colombia [Stevenson et al., 2000]. In the Tai forest, *Cercopithecus petaurista*, *Cercopithecus campbelli* and *Cercopithecus diana* foraged at different heights in the forest, and the diet overlap between *C. campbelli* and *C. diana* decreased when the fruit availability was low. In the Anaimalai Hills of the Western Ghats, niche separation between Nilgiri langurs and lion-tailed macaques became more marked during the dry season characterized by low fruit availability [Singh et al., 2001].

The invertebrate faunal component in the diet of both species of macaques was considerable. However, except for bark, lion-tailed macaques and bonnet macaques used different substrates for foraging on insects across the entire year. We could not identify the faunal species consumed by the macaques but it is possible that these species were different in different substrates.

During the wet season, there was evidence of high niche overlap between lion-tailed macaques and bonnet macaques, as both consumed mostly fruits of *A. roxburghii*, *G. gummigutta*, *S. gardneri* and *K. attenuata* among other tree species (Table III). These resources were abundant during the wet season (Fig. 2). In most tropical forests, the productivity of flowers and fruits increases with an increase in the moisture level during the wet season [Lahann, 2008; Zimmerman et al., 2007]. High overlap for common food items during period of high food abundance has been reported in many sympatric primates [Baltrunaite, 2001; Guillotin et al., 1994; Yamagiwa & Basabose, 2005]. Interspecific feeding competition may become unimportant, even under conditions of high niche overlap when sympatric species exploit the same resources during periods of high food abundance [Goulson & Darvill, 2004]. In this study interspecific aggressive intergroup encounters were rare ($N = 3$) and occurred only between bonnet macaques and lion-tailed macaques during the wet season, a period of high food availability. On the contrary, most intergroup encounters were tolerant ($N = 12$), even those occurring in the dry season.

Evidence of interspecific aggression over food has been reported among sympatric bonnet macaques, lion-tailed macaques and Nilgiri langurs. In the Anaimalai Hills of the Western Ghats bonnet macaques were occasional visitors to the rainforest from the adjoining deciduous forest, and they had a

high niche overlap with lion-tailed macaques due to the shared use of flowers of *Cullenia exarillata* and fruits of *Ficus microcarpa* [Sushma & Singh, 2006]. At this site, interspecific encounters were frequent and bonnet macaques dominated both lion-tailed macaques and Nilgiri langurs during these encounters. No such hierarchy was observed among this study species as the resource competition was little.

We therefore conclude that in this study region, unlike in other areas of the Western Ghats, bonnet macaques, lion-tailed macaques and Hanuman langurs coexist year-round in sympatry due to partitioning of their food resources resulting in limited niche overlap. Similarly, high food abundance despite high seasonal niche overlap during wet season also prevented feeding competition.

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