Chapter 5 presented time-series data over 16 years from three fragments of the Upper Brahmaputra Valley to show a dramatic decline in the population of six species of primates in them. In one fragment, the Hollongapar-Gibbon Wildlife Sanctuary, however, the populations of all species, except Assamese macaque, have not only persisted over a century but also risen in number. This is an unusual and unique phenomenon given the widespread decline in primate populations in other fragments of the Valley. Hollongapar, therefore, offers an excellent opportunity to understand how primates are able to co-exist in a fragment even after being isolated for over 100 years. An understanding of how primates coexist in this unique site may provide valuable lessons for managing other fragments in the valley. In Chapter 6, I examine how three closely-related macaque species, the rhesus macaque Macaca mulatta, the northern pig-tailed macaque M. leonina, and the stump-tailed macaque M. arctoides co-exist, given that congeners are most likely to compete with each other for the same resources owing to their shared evolutionary and ecological characteristics. This chapter thus aims to identify the mechanisms that enabled the co-existence of sympatric congeners in a fragment.
Chapter 6

Niche partitioning and coexistence of sympatric macaques in a fragmented habitat of the Upper Brahmaputra Valley, northeastern India

Abstract

How closely related species co-exist, especially under conditions of resource limitation remains an intriguing problem in ecology. Having to share space and resources, such species are expected to have evolved a variety of behavioural mechanisms to reduce competition. Understanding such adaptation could also provide clues to design effective conservation strategies for these species. In this chapter, I examine the niche partitioning and co-existence of three congeneric species, the rhesus macaque, pig-tailed macaque and stump-tailed macaque, in a fragment of less than 20 km², the Hollongapar-Gibbon Wildlife Sanctuary, which still harbours a significant proportion of original species pool. An intensive observational study was conducted on two troops each of the three species over a period of 23 months from March 2008 to January 2010. I examined niche partitioning among the macaques along two major axes—space and food. Our results found significant interspecific differences among macaques in their utilisation of both horizontal and vertical space, as well as in their utilisation of food resources. The differential utilisation of space and food has enabled continued co-existence of the three macaque species in this fragment. At the fragment-level and over proximate time-scales, our results explain why primates, particularly the three species of macaques, are able to thrive even after being isolated for over one hundred years. Ecological and behavioural insights gleaned from this fragment will help us understand and promote co-existence of primates in other habitat fragments of the Upper Brahmaputra Valley.
6.1 Introduction

Understanding of how different species coexist in a given area has remained a central issue in community ecology (Elton, 1946; Tokeshi, 1999). Various theories and hypotheses have been advanced to explain the patterns and the underlying mechanisms of species co-existence. The competition exclusion principle (Gause, 1934), one of the early attempts to explain the co-existence of several species, suggests that two species with identical ecological requirements cannot co-exist in the same habitat. The niche concept (Hutchinson, 1957), which represents all resources vital for the survival of a species, remains relevant to our understanding of species co-existence. By segregating along the axes of major resources essential for survival and/or reproduction, two species can co-exist without excluding one another. Niche partitioning is, therefore, perceived as a mechanism that promotes the co-existence of two or more species in a given area. In order to co-exist, the species must partition their niches especially along two major dimensions—habitat and food type (Schoener, 1974). This is particularly true for the closely-related species or congeneres, who, owing to their shared phylogenetic history—similar morphology, physiology, behaviour and ecology—have a greater tendency to compete, and therefore must partition their niches in order to co-exist.

Niche partitioning as a mechanism to promote co-existence has been established in various taxa (MacArthur, 1958; Schoener, 1974; Emmons, 1980; Bagchi et al., 2003) including non-human primates (Terborgh, 1984; Cords, 1986; Ganzhorn, 1989). Sympatric primates are known to use different habitats or microhabitats (Ganzhorn, 1989; Rodman, 1991; Rakotondranary & Ganzhorn, 2011) or vertical space (Ungar, 1996; Singh et al., 2000; Sushma & Singh, 2006; Singh & Roy, 2011; Feeroz, 2012) in order to co-exist. Sympatric primates are also known to partition their food types by either using different food resources or using different parts of the same resource (Terborgh, 1984; Ganzhorn, 1988; Sushma & Singh, 2006). These two axes are the most important niche dimensions (Schoener, 1974) and if sympatric species are able to partition resources along these axes, the likelihood that they can co-exist in a given habitat is high.

A large body of knowledge accumulated on the co-existence mechanisms between closely-related species in communities, inhabiting
relatively intact forest habitats. But as habitats are fragmented, species are increasingly forced to co-occur in smaller patches. Opportunities for spatial separation, earlier available to species, while occurring in continuous habitats, are no longer available in forest remnants. Consequently, species have to share not only the limited space but also compete over similar but limited resources. Yet, our understanding of how closely-related species co-exist in modified landscapes such as habitat fragments is still limited.

Our time series data of 16 years from three fragments of Upper Brahmaputra Valley (Chapter 5) show a dramatic decline in the population of six species of primates from the smaller fragments. In one fragment—the Hollongapar-Gibbon Wildlife Sanctuary, however, except Assamese macaque, the population of all species, including three macaque species, the rhesus macaque *Macaca mulatta*, the northern pig-tailed macaque the stump-tailed macaque *M. leonina*, and *M. arctoides* have not only stabilized but also increased. The large fragment, therefore, is anomalous in that it has still a very high diversity and abundance of primates, so an understanding of how primates co-exist there may have valuable lessons for managing other fragments. In this study, I specifically ask how three congeneric macaque species partition resources along two primary niche axes—of space and food in a fragmented habitat.

We focused on congeneric macaques as they were more likely, given their shared phylogenetic history, to compete over resources than they were with the other three sympatric primates—western hoolock gibbon *Hoolock hoolock*, capped langur *Trachypithecus pileatus* and Bengal slow loris *Nycticebus bengalensis*, which were less closely related to the macaques.

From a conservation point of view, an understanding how species manage to co-exist despite the effect and consequences of habitat compression is crucially important to formulate conservation strategies for them. By identifying the niche dimensions in which species could potentially segregate or converge, we could design better conservation measures, particularly when species use similar resources that are likely to beget interspecific competition. For example, if species use similar resources in short supply, management practices could be designed to either reduce their convergence of resource use by offering supplementary resources or by increasing the availability of the limited resources through other means. Although Hollongapar is not necessarily the most representative of the average fragment in the Upper
Brahmaputra Valley, it can further our understanding of how primates can co-exist in these fragments.

6.2 Methods

6.2.1 Study area and species

The Hollongapar-Gibbon Wildlife Sanctuary is located in the Jorhat district of Assam state, northeastern India. It was declared as reserved forest in 1881 and a wildlife sanctuary in 1997. The sanctuary was once an integral part of the foothill forests of the Patkai range of Nagaland. The Hollongapar forest became fragmented and lost its connectivity with the adjacent foothill forests after the establishment of extensive tea gardens during 1880–1920. The original area of the sanctuary was 20.98 km², approximately 3 km² has, however, since been cleared to establish an army camp. As a result, the effective size of the sanctuary is currently c.17.98 km², a quarter of which is highly degraded and devoid of any canopy. It is also intersected by a railway line that has fragmented its core area (Figure 6.1).

The sanctuary falls under the North East India Biogeographic Zone (9) and NE Brahmaputra Valley Biogeographic Province (9A) (Khatri, 2009). The original vegetation type of the sanctuary was Assam Plains Alluvial Semi-Evergreen Forests with wet evergreen forest patches present sporadically (Champion & Seth, 1968). The sanctuary had a long management history and almost two third area of the sanctuary is covered by artificially regenerated forests (Duarah & Saikia, 2003; Khatri, 2009). The elevation ranges from 110 to 120 m ASL. In addition to tea gardens, the sanctuary is also surrounded by human settlements. Most of the marginal people of these settlements harvest non-timber forest produce and occasionally also fell trees in the fragment. Based on the rainfall, the study period was divided into two seasons. The study period between October to March was considered as dry period when the average monthly rainfall was < 100 mm and the period between April to September was treated as the wet season because the average monthly rainfall was > 100 mm (Figure 6.2). The average maximum and minimum temperatures were 28°C and 19°C respectively.

Originally seven species of primates were present in the sanctuary (Srivastava et al., 2001), of which the Assamese macaque has become locally extinct since 2005 (Chapter 5; Sharma et al., 2012). Of the remaining six species, the Bengal slow loris Nycticebus bengalensis is a nocturnal prosimian while the
remaining five species, the rhesus macaque *Macaca mulatta*, northern pig-tailed macaque *M. leonina*, stump-tailed macaque *M. arctoides*, capped langur *Trachypithecus pileatus* and the western hoolock gibbon *Hoolock hoolock* are diurnal. The detailed biology of each species has been provided in Chapter 1.

**Figure 6.1** Map of the study area

**Figure 6.2** Monthly rainfall data from the Tocklai Tea Research Station, Jorhat, which is approximately 10 km from the Hollongapar-Gibbon Wildlife Sanctuary. The dotted line denotes an arbitrary cut-off used to separate the study period into two broad seasons.
The populations of the five diurnal species in this fragment have not only stabilised but also increased in abundance during the last 16 years. Our survey in 2008 (Chapter 5) reported very high densities of these species in the sanctuary (Table 6.1). Hoolock gibbons were observed to have the highest troop density (1.4 troops/km²) whereas stump-tailed macaques occurred at the highest individual density (12.96 individuals/km²).

6.2.2 Selection and habituation of the study troops

Two troops of each macaque species were selected for the study, which was carried out from March 2008 to January 2010. However, the actual behavioural observations were initiated only in November 2008 and continued till January 2010. The intervening period between March 2008 and November 2008 was utilised for troop selection and habituation as well as to carry out a detailed census of the primates of the sanctuary. The group size and age-sex classification of the study troops are presented in Table 6.2.

Table 6.1 Number of troops, total number of individuals, and troop and individual density of the five primate species in the study area

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of troops</th>
<th>Number of individuals</th>
<th>Solitary individuals</th>
<th>Troop density (Troops/km²)*</th>
<th>Individual density (Individuals/km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhesus macaque</td>
<td>4</td>
<td>&gt;174</td>
<td>-</td>
<td>0.22</td>
<td>9.68</td>
</tr>
<tr>
<td>Pig-tailed macaque</td>
<td>4</td>
<td>75</td>
<td>-</td>
<td>0.22</td>
<td>4.17</td>
</tr>
<tr>
<td>Stump-tailed</td>
<td>2</td>
<td>233</td>
<td>-</td>
<td>0.11</td>
<td>12.96</td>
</tr>
<tr>
<td>macaque</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hoolock gibbon</td>
<td>25</td>
<td>101</td>
<td>5</td>
<td>1.40</td>
<td>5.89</td>
</tr>
<tr>
<td>Capped langur</td>
<td>12**</td>
<td>146</td>
<td>-</td>
<td>0.67</td>
<td>8.12</td>
</tr>
</tbody>
</table>

* Although the total area of the sanctuary is 2,098 ha, the effective area on which the survey was carried out was only 1,798 ha. It was not carried out on 300 ha, which has been given in lease to the Military Engineering Services (MES). The chances of encountering troops in this area were low owing to the degraded nature of the habitat although stump-tailed macaques and rhesus macaques were occasionally observed to move across the area.

** A troop (consisting of 8 individuals) has been reported from outside the sanctuary, near a forest patch adjacent to the northern fringe of the sanctuary, by the local people. This troop was not included in the density analysis.
Table 6.2 Age-sex structure of the study troops of the stump-tailed, pig-tailed and rhesus macaques

<table>
<thead>
<tr>
<th>Troop code</th>
<th>Group size</th>
<th>Home range in ha (MCP)</th>
<th>AM</th>
<th>AF</th>
<th>A?</th>
<th>SAM</th>
<th>SAF</th>
<th>SA</th>
<th>JUV</th>
<th>INF</th>
<th>UI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stump-tailed macaque</strong></td>
<td>ChenjianSTM</td>
<td>102</td>
<td>913</td>
<td>20</td>
<td>25</td>
<td>0</td>
<td>0</td>
<td>17</td>
<td>22</td>
<td>18</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>BaidhiaSTM</td>
<td>131</td>
<td>288</td>
<td>18</td>
<td>30</td>
<td>0</td>
<td>14</td>
<td>3</td>
<td>6</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td><strong>Pig-tailed macaque</strong></td>
<td>SassiPTM</td>
<td>29</td>
<td>159</td>
<td>4</td>
<td>8</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>CharialiPTM</td>
<td>20</td>
<td>153</td>
<td>4</td>
<td>4</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>5</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td><strong>Rhesus macaque</strong></td>
<td>MelengRM</td>
<td>54</td>
<td>590</td>
<td>8</td>
<td>10</td>
<td>4</td>
<td>4</td>
<td>1</td>
<td>6</td>
<td>12</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>LipcutRM</td>
<td>20</td>
<td>193</td>
<td>5</td>
<td>6</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>4</td>
</tr>
</tbody>
</table>

MCP: Minimum convex polygon method; AM: Adult males; AF: Adult females; SAM: Subadult males; SAF: Subadult females; SA: Subadult individuals of unidentifiable sex; JUV: Juveniles; INF: Infants, A?: Unidentified adults; UI: Unidentified.

![Diagram of troop home ranges](image)

Figure 6.3 Home range of the study troops in the study area

The home ranges of the study troops, calculated using the minimum convex polygon method, have also been presented. The home-range of the pig-tailed and stump-tailed macaque troops completely overlapped with one another whereas those of the stump-tailed and rhesus macaques were separate. The rhesus macaques were mostly found on the forest edges and in the
surrounding matrix habitat of human settlements and tea plantations (Figure 6.3). Two other troops of rhesus macaques were also located at the edges of the forest. A third troop of pig-tailed macaques occurred within the home range of stump-tailed macaques whereas a fourth group was found in the southern part of the sanctuary and was partially located within the home ranges of the study troops of pig-tailed and stump-tailed macaques (Figure 6.3).

6.2.3 Behavioural observations

Instantaneous scan sampling (Altmann, 1974) was conducted on all the visible adult males and females of each troop from dawn to dusk on each observation day, when the individuals were most active. Only the visible members of the troop were scanned as the troops were large and the individuals often widely spread out, sometimes even up to a radius of 500 m in the case of pig-tailed macaques. It was, therefore, virtually impossible to detect all the troop individuals given the short time available for each scan, which was set to a maximum of 20 min in order to maximise the number of individuals observed in each scan. Each species was followed for about four to five days every month and the following data were collected: Date and time of each scan, age and sex of the scanned individual (adult male, adult female or adult individual of unidentified sex), behaviour displayed (including feeding, foraging, resting, moving, social interactions and other behaviour), animal height (on a tree, shrub, bamboo or the ground), tree and shrub height, animal prey item (invertebrates or vertebrates), food plant species and the part fed on, and the habit and phenophase of the food plant. We broadly apportioned the various behavioural activities into the following categories:

1. Feeding: Handling and ingestion
2. Foraging for animal prey: Active search for any invertebrate or vertebrate prey species underneath leaves in the canopy or at any other level of a tree, split bamboo stems and ground leaf litter
3. Resting: Period of inactivity, including sleeping
4. Moving: Any locomotor behaviour, resulting in a change in the spatial position of an individual
5. Social interactions: Allogrooming and other affiliative behaviour, agonistic behaviour, mating, and play
6. Other behaviour: Vigilance, defecating, urinating, shaking of one’s own body, sneezing, startling, yawning, autogrooming and vocalising

The number of scan records on the three study species were 11,062, 16,723 and 6,471 for the rhesus macaque, stump-tailed macaque and pig-tailed macaque respectively (Table 6.3) while the total contact hours for the three species were 387, 336 and 352 hours respectively. It should be noted that comparable time was spent on sampling each species (Table 6.3).

<table>
<thead>
<tr>
<th>Species</th>
<th>Troop Code</th>
<th>Group Size</th>
<th>Individual Scan</th>
<th>Total contact hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhesus macaque</td>
<td>LipcutRM</td>
<td>20</td>
<td>6,395</td>
<td>226</td>
</tr>
<tr>
<td></td>
<td>MelengRM</td>
<td>54</td>
<td>4,667</td>
<td>161</td>
</tr>
<tr>
<td>Stump-tailed macaque</td>
<td>ChenijanSTM</td>
<td>110</td>
<td>11,931</td>
<td>259</td>
</tr>
<tr>
<td></td>
<td>BoidhiaSTM</td>
<td>130</td>
<td>4,792</td>
<td>77</td>
</tr>
<tr>
<td>Pig-tailed macaque</td>
<td>SassiPTM</td>
<td>20</td>
<td>4,394</td>
<td>254</td>
</tr>
<tr>
<td></td>
<td>CharialiPTM</td>
<td>29</td>
<td>2,077</td>
<td>98</td>
</tr>
</tbody>
</table>

6.2.4 Location of the troop

The location of each study troop was monitored at five-min intervals during the observation period by recording the physical coordinates of the approximate centre of the troop with the help of a handheld GPS (Garmin Map 60Cx). At the end of each observation day, all the location data were downloaded using the software GPS Trackmaker.

6.3 Analysis

6.3.1 Time-activity budget

Chi-square test for proportions (Gibbons, 1971) was used to test for differences in different behavioural activities of the three macaque species during the dry and wet seasons.
6.3.2 Co-occurrence of three macaque species

Location data on the six troops of the three macaque species were used for a co-occurrence analyse, in which the data on the two troops of each species were combined to obtain species-wise locations. Given that aggregation/separation were also a function of the spatial scale at which the analysis is carried out, eighteen grids of different size (smallest = 50 × 50 m and largest = 5000 × 5000 m) were created and all the location data were overlaid in it. Using the grid and location overlap 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 co-occurrence analysis, each grid was treated as ‘site’ and each species (n = 3) was represented as rows.

We used C-score of Stone and Roberts (1990) to evaluate species co-occurrence patterns, the detailed method for which is outlined in Chapter 5 Section 4.3.4. However, we used the fixed-equiprobable model (SIM2) to evaluate the co-occurrence model. In this model, the row sum, that is, number of grids a species can occupy, is held constant whereas the grids were treated as equally suitable for occupation by any species.

We calculated the Standardised Effect Size (SES) to examine whether the segregation of species was non-random or not. SES was calculated as

\[
\frac{I_{\text{obs}} - I_{\text{sim}}}{SD_{\text{sim}}}
\]

where, \(I_{\text{obs}}\) = The observed index, 
\(I_{\text{sim}}\) = The simulated index, and 
\(SD_{\text{sim}}\) = The standard deviation of the simulated index, calculated as square root of the variance 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 would indicate a non-random species segregation and values lower than -1.96, a non-random species aggregation (Wittman et al., 2010). The analysis was performed using software EcoSim, version 7.71 (Gotelli & Entsminger, 2004).
6.3.3 Height use by the three macaque species

The height use—animal height, feeding height and foraging height—of the three macaque species have been presented as box-whisker plots. As these data for the species were not normally distributed, the non-parametric Wilcoxon rank-sum test of difference was used to test for significant differences in median tree height used by the species.

6.3.4 Niche breadth

The niche breadth of all the three macaques was measured using Levin’s Index (Hurlbert, 1978; Krebs, 1989):

\[ B = \frac{1}{\sum p_j^2} \]

where, \( B = \) Levin’s measure of niche breadth, and

\( p_j = \) Fractions of items in the diet that are of food category \( j \)

This index of niche breadth was standardised to express it on a scale of 0 to 1. Hulbert (1978) suggested the following measure for standardised niche breadth:

\[ B_A = \frac{B - 1}{n - 1} \]

where, \( B = \) Levin’s niche breadth

\( B_A = \) Levin’s standardised niche breadth

\( n = \) Number of possible resource states

The food resources considered in this analysis included food plant species, plant parts and invertebrates or any other animal prey. All invertebrates and other animal prey species were treated as a single category. If the macaques were observed to feed on more than one part of the same plant species, they were considered distinct food resources.
6.3.5 Niche overlap

In order to examine the extent of resource overlap between pairs of macaque species, we used Pianka’s Overlap Index (Krebs, 1989):

\[
O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} (p_{2i}^2)(p_{1i}^2)}}
\]

where,

- \( O_{12} \) = Pianka’s measure of niche overlap between Species 1 and 2
- \( p_{ii} \) = Proportion of Resource \( i \) in the total resources used by Species 1
- \( p_{2i} \) = Proportion of Resource \( i \) in the total resources used by Species 2
- \( n \) = Total number of resources

Pianka’s (1973) measure ranges from 0 (no overlap in resource use) to 1 (a complete overlap in the resources used).

6.4 Results

6.4.1 Time-activity budgets

Figure 6.4 and Table 6.4 depict the time-activity budgets of the three study macaque species and compare them across the dry and wet seasons during the study period. The three macaque species spent considerable time in feeding, foraging and moving in both seasons, an indication that food resources were clearly responsible for shaping much of the time-activity budget of the study troops.
**Figure 6.4** Time-activity budgets of the three macaque species during the dry and wet seasons
Table 6.4  Proportion of different activities in scan between two seasons and the result of the chi-square χ² test of three macaque species during dry and wet seasons

<table>
<thead>
<tr>
<th>Pig-tailed macaque</th>
<th>FEEDING</th>
<th>FORAGING</th>
<th>MOVING</th>
<th>RESTING</th>
<th>SOCIAL INTERACTIONS</th>
<th>OTHER BEHAVIOUR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Season (%)</td>
<td>45</td>
<td>6</td>
<td>30</td>
<td>12</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Number of scan</td>
<td>1246</td>
<td>163</td>
<td>822</td>
<td>345</td>
<td>129</td>
<td>78</td>
</tr>
<tr>
<td>Wet Season (%)</td>
<td>32</td>
<td>6</td>
<td>37</td>
<td>16</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Number of scan</td>
<td>1166</td>
<td>234</td>
<td>1374</td>
<td>593</td>
<td>223</td>
<td>98</td>
</tr>
<tr>
<td>Chi-square χ²</td>
<td>116.85</td>
<td>0.57</td>
<td>41.81</td>
<td>17.06</td>
<td>5.87</td>
<td>0.08</td>
</tr>
<tr>
<td>Degree of freedom</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt; 0.001</td>
<td>0.440</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>0.015</td>
<td>0.783</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Rhesus macaque</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Season (%)</td>
<td>32</td>
<td>1</td>
<td>27</td>
<td>26</td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>Number of scan</td>
<td>1489</td>
<td>64</td>
<td>1235</td>
<td>1184</td>
<td>465</td>
<td>168</td>
</tr>
<tr>
<td>Wet Season (%)</td>
<td>25</td>
<td>1</td>
<td>35</td>
<td>31</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Number of scan</td>
<td>1590</td>
<td>33</td>
<td>2263</td>
<td>2023</td>
<td>427</td>
<td>120</td>
</tr>
<tr>
<td>Chi-square χ²</td>
<td>79.08</td>
<td>22.87</td>
<td>83.89</td>
<td>41.02</td>
<td>43.53</td>
<td>33.24</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>p-value</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
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</tbody>
</table>

<table>
<thead>
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<th>Stump-tailed macaque</th>
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<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
<tr>
<td>Dry Season (%)</td>
<td>33</td>
<td>3</td>
<td>47</td>
<td>7</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Number of scan</td>
<td>2164</td>
<td>188</td>
<td>3080</td>
<td>464</td>
<td>437</td>
<td>161</td>
</tr>
<tr>
<td>Wet Season (%)</td>
<td>28</td>
<td>3</td>
<td>50</td>
<td>12</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Number of scan</td>
<td>2887</td>
<td>297</td>
<td>5099</td>
<td>1261</td>
<td>514</td>
<td>165</td>
</tr>
<tr>
<td>Chi-square χ²</td>
<td>48.42</td>
<td>0</td>
<td>9.44</td>
<td>115.03</td>
<td>21.11</td>
<td>15.1</td>
</tr>
<tr>
<td>Degree of freedom</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>p-value</td>
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<td>1</td>
<td>0.002</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
6.4.2 Co-occurrence of three macaque species

We first examined the use of physical space by the three congeneric macaques in the study area. The co-occurrence analysis indicated a non-random segregation of the three species in the sanctuary (Appendix S6.1). The segregation was, however, scale-dependent (Figure 6.5). The pair-wise co-occurrence of the species, as reflected in their SES values (see Methods, Section 6.3.2 for details) suggested, for example, that at a finer scale, stump-tailed macaques were strongly spatially segregated from rhesus macaques although, as could be expected, both species began to aggregate at larger spatial scales (Figure 6.5). In contrast, pig-tailed macaques exhibited relatively weaker segregation from both stump-tailed and rhesus macaques across different grid size (Figure 6.5).

![Figure 6.5 Spatial segregation among all macaques and between species-pairs at different spatial scales. The SES values (see text for details) indicate the level of segregation between species across different grid sizes. The upper and lower dashed lines represent the variance at 1.96 and -1.96 respectively. Values larger than 1.96 indicate non-random species segregation while values lower than – 1.96 indicate non-random species aggregation](image-url)

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6.4.3 Height use by the three macaque species

Having determined the levels of segregation exhibited by the three study species in horizontal space, we examined whether they also segregated themselves in vertical space. Pig-tailed macaques were observed to occur at relatively greater heights than did rhesus and stump-tailed macaques (Figure 6.6) while the stump-tailed macaque was the most terrestrial of the three species. In general, there was significant differences in the tree heights at which the three species were observed (Table 6.5).

The pig-tailed macaque also used relatively higher tree strata than did the rhesus and stump-tailed macaque while foraging (Figure 6.7) and feeding (Figure 6.8). The foraging and feeding heights, too, were significantly different for the three macaques (Table 6.5).

![Box plot of animal heights](image)

**Figure 6.6** The heights at which the three macaque species were observed across the study period. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The bold horizontal bar represents the median value while the outliers are shown as whiskers. The total number of individual scan records (n) is shown for each species.
Table 6.5 Differences in median tree height used by the different macaque species across the study period, and for foraging and feeding. The Wilcoxon rank-sum test was used to compare the median values.

<table>
<thead>
<tr>
<th>Height</th>
<th>Species-pair</th>
<th>Test statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>W</td>
</tr>
<tr>
<td><strong>Animal height</strong></td>
<td>Pig-tailed macaque</td>
<td>59573655.0</td>
</tr>
<tr>
<td></td>
<td>Rhesus macaque</td>
<td>98163327.0</td>
</tr>
<tr>
<td></td>
<td>Rhesus macaque</td>
<td>127902095.0</td>
</tr>
<tr>
<td><strong>Feeding height</strong></td>
<td>Pig-tailed macaque</td>
<td>5734892.0</td>
</tr>
<tr>
<td></td>
<td>Rhesus macaque</td>
<td>10177967.0</td>
</tr>
<tr>
<td></td>
<td>Rhesus macaque</td>
<td>9932212.0</td>
</tr>
<tr>
<td><strong>Foraging height</strong></td>
<td>Pig-tailed macaque</td>
<td>28877.5</td>
</tr>
<tr>
<td></td>
<td>Rhesus macaque</td>
<td>186794.0</td>
</tr>
<tr>
<td></td>
<td>Stump-tailed macaque</td>
<td>36402.5</td>
</tr>
</tbody>
</table>

Figure 6.7 The foraging heights of the three macaque species. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The bold horizontal bar represents the median value while the outliers are shown as whiskers. The total number of individual scan records (n) is shown for each species.
Figure 6.8  The feeding heights of the three macaque species. The upper box represents 75 percentile and the lower box, 25 percentile of the data. The bold horizontal bar represents the median value while the outliers are shown as whiskers. The total number of individual scan records (n) is shown for each species

6.4.4  Niche breadth and overlap

Finally, we compared the niche breadth and overlap in the diet used by the three study species in the dry and wet seasons across the study period. In the dry season, pig-tailed and rhesus macaques had a relatively greater proportion of fruits in their diets (Figure 6.9) whereas the stump-tailed macaque spent a higher proportion of time feeding on root cortices. During the wet season, however, fruits constituted the major part of the diet for all the species. Stump-tailed and rhesus macaques fed significantly on leaves in both the seasons but leaves constituted only a minor part in the diet of pig-tailed macaques in both seasons.
Figure 6.9 Proportion of different items in the diet of the three macaques across the dry and wet seasons. PTM = Pig-tailed macaque; RM = Rhesus macaque; STM = Stump-tailed macaque.

The standardised niche breadth index was highest for the rhesus macaque (0.25) while it was small for both the pig-tailed (0.10) and stump-tailed macaques (0.09; Figure 6.10). Moreover, the niche breadth of pig-tailed and rhesus macaques were comparable across the wet and dry seasons but, surprisingly and contrary to what could be expected, that of the stump-tailed macaque was larger in the wet season than in the dry season.

The pig-tailed macaque and the rhesus macaque had the highest overlap in the niche breadth of their diet (0.60), followed by that between the rhesus and stump-tailed macaques (0.17); the diet overlap was least between the pig-tailed and stump-tailed macaques (0.10). There was also a marked seasonal difference in niche breadth overlap. Rhesus macaques had the highest overlap with stump-tailed macaques during the wet season (0.42) but with pig-tailed macaques during the dry season (0.62). Pig-tailed macaques, on the other hand, had very low overlap with stump-tailed macaques, both in the dry and wet seasons.
**Figure 6.10** Seasonal and annual niche breadth of the three macaque species. RM = rhesus macaque; PTM = pig-tailed macaque; STM = stump-tailed macaque

**Figure 6.11** Seasonal and annual niche overlap among the three macaque species. RM = rhesus macaque; PTM = pig-tailed macaque; STM = stump-tailed macaque
6.5 Discussion

Our results indicate that niche partitioning may actually promote the coexistence of the three congeneric macaque species in the study area. The partitioning was observed along both axes examined in this study—space and food. Horizontal space partitioning was strongest between stump-tailed and rhesus macaques while there was a high degree of overlap between stump-tailed and pig-tailed macaques. These two species, however, significantly partitioned their vertical space and also exhibited very low overlap in their diet niche. The pig-tailed and rhesus macaques, in contrast, had a high overlap in their diet. It is thus entirely possible that the three species have partitioned their space and diet to the extent that it has been possible for them to co-exist in the Hollongapar forest patch that has undergone extensive degradation over the years. The results of our study are also in congruence with those obtained with other sympatric congeneric primates elsewhere (Cords, 1986; Sushma & Singh, 2006; Rakotondranary & Ganzhorn, 2011; Feeroz, 2012).

A close examination of the time-activity budget of the three species suggested that all three macaques spent considerable time in feeding, foraging and movement. Such activity, driven by a search for food resources, perhaps reflects the patchy distribution of resources in the sanctuary. There was, therefore, a higher possibility of the study troops confronting one another during these behavioural activities and hence, a potentially higher probability of competition for food resources.

The co-occurrence analysis suggested that the spatial segregation of the three species was non-random. The most significant separation in this regard was between the stump-tailed and rhesus macaques. Stump-tailed macaques were found mostly in the forest interiors whereas the rhesus macaque, being a weed species (Richard et al., 1989), almost exclusively utilised the forest edges and the surrounding matrix habitats. Such differential habitat choice, therefore, might be an important mechanism to reduce interspecific competition (Ganzhorn, 1989) and promote species co-existence (Schoener, 1974). We believe that this particular segregation in horizontal space use may be driven by the availability of important food plants and roosting trees of these two species.
The most important food resources of the stump-tailed macaque in the study site during the dry season were a shrub, *Forrestia mollissima* and *Schizostachyum polymorphum*, a bamboo, both distributed in the forest interiors. Insects and the plants *Acacia auriculiformis* and *Lantana camara*, the most important food resources of the rhesus macaque in the dry season were, however, amply distributed in the surrounding vegetation matrix and tea plantations. In the wet season, this species used common resources such as the fruits of *Sapium baccatum* and *Litsae monopetela* but in different peripheral localities of the study site. Moreover, the two macaques differed in their choice of roosting trees and sites. Stump-tailed macaques mostly used various *Ficus* species, *Artocarpus chama* and *Dipterocarous retusus* as their roosting trees, which were again mostly located in the interior forest patches. The rhesus macaque, on the other hand, preferred bamboo species and trees such as *Lagerstroemia flos-reginae*, which were located either at the edge of the forest or near human habitations.

The pig-tailed macaque also segregated from the rhesus macaque, particularly at smaller spatial scales. Like the stump-tailed macaque, pig-tailed macaques too almost always used the forest interiors for their daily activities. During winter, rhesus macaques spent considerable time inside the forest feeding on the fruits of *Castonopsis indica*, a food species shared commonly with pig-tailed macaques. During this time, therefore, the two species did come in direct contact but tended to avoid one another on such occasions. The pig-tailed and stump-tailed macaques in our study area also exhibited high spatial overlap but similarly avoided confrontation when they encountered one another. Similar patterns of space use and non-aggressive interactions have also been observed between sympatric bonnet and lion-tailed macaques in the Western Ghats mountains (Singh & Roy, 2011) and between pig-tailed and rhesus macaques in Bangladesh (Feeroz, 2012).

Species that co-occur in the same habitat and extensively overlap in their use of horizontal space could, however, partition themselves in vertical space. An overlap in one niche axis but differentiation in another potentially critical resource axis could, therefore, also promote the co-existence of species competing for resources. In our study, we found a distinct vertical partitioning among the three species of macaques although all of them could potentially use and were indeed occasionally observed to utilise all the vertical strata. Pig-
tailed macaques appeared to use the highest canopy layer more than did the other two species. As this macaque extensively fed on the fruits of large trees such as *Ficus* spp., *Castonopsis indica* and *Garcinia sopsopia*, they also used the middle canopy layer. They also foraged on insects under the foliage of *Vatica lanaeefolia*, a dominant middle-canopy tree in the sanctuary. In Bangladesh, Feeroz (2012) found similar tree-height use by pig-tailed macaques. The stump-tailed macaque, on the other hand, was predominantly terrestrial as its most preferred food plants – shrubs and young bamboo shoots – were also of relatively shorter height. The height use by rhesus macaque was intermediate between these two macaques. The rhesus macaque was almost exclusively arboreal inside the forest, probably to avoid predators such as the leopard and python but they were largely terrestrial when they foraged and travelled outside the forest. Although insects constituted major components of the diet of both pig-tailed and rhesus macaques, the height at which they foraged was different. As mentioned above, the pig-tailed macaques foraged mainly in the middle canopy whereas rhesus macaques used the lower canopy. Such differential height use has, therefore, also possibly served to promote the coexistence of the three study species just as it has in other primate and vertebrate communities (Emmons, 1980; Estrada & Coates-Estrada, 1985; Ungar, 1996; Singh *et al.*, 2000; Sushma & Singh, 2006; Singh & Roy, 2011; Feeroz, 2012).

Rhesus macaques displayed the broadest niche breadth among the three species in both seasons, dry and wet. Being generalists, they were clearly able to utilise a great variety of resources both from the forest as well as from the surrounding habitat matrix. The niche breadth of rhesus macaques was consistent across seasons, an indication that they were not particularly selective in their choice of food resources. The niche breadth of pig-tailed macaques, a more specialist species, was virtually identical across seasons but the overall niche breadth was narrow. This species thus used similar, but a few selective, resources in both seasons. The stump-tailed macaque had a very narrow niche breadth during the dry season, contrary to expectations, as they used two readily available resources, *Forrestia mollissima* and *Schizostachyum polymorphum*, almost exclusively during this season. It, however, had a wider niche breadth during the wet season when it used a greater diversity of food plant species. Our results are thus in variance with earlier studies, which suggested that the diet niche breadth is larger during the dry season when fruit availability is low.
and smaller during the season of higher fruit availability (Schoener, 1971). The root cortices, bamboo shoots and leaves that constituted a major part of the diet of the stump-tailed macaque was abundant during dry season in our study area. Overall, however, the niche breadth of this macaque was narrow, once again indicating that this species, like the pig-tailed macaque, is a diet specialist.

The rhesus macaque had a high food niche overlap with the pig-tailed macaque in both seasons but it was especially high during the dry season when both species fed on insects and the fruits of Castanopsis indica, a species abundant in the sanctuary. Moreover, the species produced a significantly large crop of fruits and they lasted almost two months of the dry season. The niche overlap between the rhesus and stump-tailed macaques was high during the wet season as both species fed on the fruits of Sapium baccatum and Litsaea monopetela. The two species, however, used trees in different localities within their home range. The stump-tailed macaques visited Sapium baccatum trees in the forest interiors and Litsaea monopetela in the degraded part of the sanctuary whereas rhesus macaques exclusively used Sapium baccatum at the edge of the sanctuary and a few scattered trees of Litsaea monopetela in the surrounding matrix habitats. Several studies have shown that despite a high overlap in the use of abundant resources by different species in an area, the patterns of resource utilisation could significantly influence the structure of communities (Terborgh, 1984; Sushma & Singh, 2006). In our study too, there are species such as the pig-tailed and stump-tailed macaques that exhibit a high overlap in their use of horizontal space. And yet, they have been able to achieve a strong partitioning of the available, possibly limited, resources by evolving rather different use of vertical space and a low niche overlap in their diet across seasons.

6.6 Caveats and limitations

It must be pointed out that, in this study, we have not examined intra-specific interactions, which is an important mechanism that shapes species co-existence in a particular habitat (Chesson, 2000). In fact, stable co-existence is possible when levels of intra-specific interactions tend to be greater than those of inter-specific interactions (Chesson, 2000). A detailed study is essential to examine the extent and nature of intra-specific interactions among the different
macaque species in the sanctuary. Although the three macaque species showed differential space and food use, the results must be viewed in the context of the disappearance of the Assamese macaque and the possible competitive exclusion of this species from the sanctuary. It is difficult to determine whether the disappearance of the Assamese macaque from this fragment is due to stochastic events or more deterministic processes such as competition. Our census had revealed the species to occur at a very low density in the recent past, as compared to the other species that had increased in abundance during the same period. It is most likely that the other primate species, particularly the three macaques with their large group sizes, might have kept the population of Assamese macaque low, a level from which the species was perhaps never able to recover. Stable co-existence, however, demands that species recover from occasional low densities (Chesson, 2000), a requirement that at least the Assamese macaque was not able to meet in Hollongapar.

6.6 Conservation implications

Our results provide clear evidence of niche partitioning being able to promote the co-existence of congeneric macaques in a small, potentially resource-limited, fragment of the Upper Brahmaputra Valley. Such partitioning of resources may have allowed primates to persist in this fragment even after being isolated for a century. The study also provides evidence that only a few key food resources may be used extensively by certain species, such as the pig-tailed and stump-tailed macaques, and are, therefore, critical for the continued survival of some of these rare species in this and other similar fragments. It is crucial that such food species be maintained and, if necessary, increased in these areas. We have also demonstrated the presence of other, more generalist, species like the rhesus macaque, which extensively uses the vegetation matrix surrounding the forest. The management of such a matrix of habitats could thus not only improve the survival of such species but could also reduce their interactions with other, more specialist, species as well as with humans in the surrounding villages, thus effectively lessening human-wildlife conflict prevalent around certain fragments of the Upper Brahmaputra Valley.
6.7 Literature cited


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