

Impact of Habitat Fragmentation on Diurnal Squirrels in Lowland Tropical Forests of Upper Assam, North-East India

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By

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Dedicated to Amma, Appa and Raghu

"There is, however, one natural feature of this country, the interest and grandeur of which may be fully appreciated in a single walk: it is the "virgin forest." Here no one who has any feeling of the magnificent and the sublime can be disappointed; the sombre shade, scarce illumined by a single direct ray even of the tropical sun, the enormous size and height of the trees, most of which rise like huge columns a hundred feet or more without throwing out a single branch, the strange buttresses around the base of some, the spiny or furrowed stems of others, the curious and even extraordinary creepers and climbers which wind around them, hanging in long festoons from branch to branch, sometimes curling and twisting on the ground like great serpents, then mounting to the very tops of the trees, thence throwing down roots and fibres which hang waving in the air, or twisting round each other form ropes and cables of every variety of size and often of the most perfect regularity. These, and many other novel features-the parasitic plants growing on the trunks and branches, the wonderful variety of the foliage, the strange fruits and seeds that lie rotting on the ground-taken altogether surpass description, and produce feelings in the beholder of admiration and awe. It is here, too, that the rarest birds, the most lovely insects, and the most interesting mammals and reptiles are to be found."

- Alfred Wallace on the rainforest of Amazon, from a letter published in the book "*My life*", 1905

DECLARATION

I, **P S Sumashini**, hereby declare that the research work titled “**Impact of habitat fragmentation on diurnal squirrels in lowland tropical forests of upper Assam, north-east India**” carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of work. These investigations were carried out under the supervision of Dr. Manoj V Nair, Prof. Qamar Qureshi and Dr. Amit Kumar at the Wildlife Institute of India from December 2018 to June 2019. I also declare that this work has not been submitted for any other degree of any university.



Date: 30 June 2019

P S Sumashini

Place: Dehradun



भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that **Ms. P S Sumashini** has carried out an original piece of research from the Wildlife Institute of India, titled "**Impact of Habitat Fragmentation on Diurnal Squirrels in Lowland Tropical Forests of Upper Assam, North-East India**", in partial fulfilment of a Master's Degree in Wildlife Science from Saurashtra University, Rajkot, India. The study was carried out under our supervision from December 2018 to June 2019. We hereby certify that this work has not been submitted for any other degree to any University.

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LIST OF ABBREVIATIONS

MGS: Malayan Giant Squirrel

RBS: Red-bellied Squirrel

HSS: Himalayan Striped Squirrel

HBS: Hoary-bellied Squirrel

PLNS: Perny's Long-nosed Squirrel

RCS: Red-cheeked Squirrel

PCQ: Point-centred Quarter

GBH: Girth at Breast Height

PCA: Principal Component Analysis

“Large forest” and “Contiguous forest” have been used interchangeably

EXECUTIVE SUMMARY

Impact of habitat fragmentation on diurnal squirrels in lowland tropical forests of upper Assam, north-east India

The effect of forest fragmentation on a set of ecological parameters, namely, species richness, densities, activity patterns, vertical space use for foraging, diet and nesting characteristics of diurnal tropical tree squirrels was investigated in five forest fragments (three in $<5 \text{ km}^2$ and two in $20\text{-}30 \text{ km}^2$ size classes) and compared against two large forest tracts ($>100 \text{ km}^2$) in upper Assam, north-east India. The study focussed on the four common diurnal squirrels, Malayan Giant Squirrel, Red-bellied Squirrel, Hoary-bellied Squirrel and Himalayan Striped Squirrel.

A set of established trails were used to survey the sites. The diversity of squirrels in the fragments was explained by size of the fragments, intactness of the forest and disturbance levels. The fragments were in a state of continuous degradation, habitat variables being influenced more by disturbance levels than by size. Medium-sized fragments continue to retain the diversity of squirrels by the virtue of small pockets of intact habitat in the fragments, while small fragments have been rendered depauperate by synergistic effects of habitat loss, degradation and hunting.

Density estimation using trails as transects under distance sampling framework revealed that densities of Malayan Giant Squirrel showed a declining trend in medium fragments and the absence of the species in the small fragments. Densities of Himalayan Striped Squirrel were comparable in large forests and medium fragments and the species was not recorded from the small fragments. Densities of RBS were high across all sites, including the small fragments.

Time activity budget, vertical space use for foraging and diet were investigated under the umbrella of changes along basic niche dimensions of time, space and diet. Niche width along time decreased in the fragments for all squirrels suggesting reduced active periods. For the Malayan Giant Squirrel, niche width decreased along the other two dimensions as well in the fragments, suggesting restriction of foraging strata and diet. On the other hand, for the Red-bellied Squirrel, niche width increased along vertical space use and diet axes suggesting expansion of niche in the fragments. These differential responses of species to habitat fragmentation resulted in changes in overlap between species in fragments and a potential alteration of competitive dynamics between species in modified habitat conditions.

Comparing trends in density estimates and responses of squirrels along basic niche dimensions revealed that similar inferences can be drawn from the two assessments about the potential sensitivity of a species to habitat fragmentation. Responses along basic niche dimensions can be possibly used to make prior assessments of responses to habitat alteration before differences in densities, which is a more gradual process, start to show up.

It is clear from the findings of the study that diversity of squirrels depends on quality of habitat. Medium-sized fragments have the potential to retain the diversity of squirrels. They should be prioritized and accorded enough protection to deter further degradation and hunting in these fragments. Malayan Giant Squirrel and Himalayan Striped Squirrel appear to be sensitive to habitat fragmentation, while the Red-bellied Squirrel appears to be tolerant.

Chapter 1

INTRODUCTION

11 Fragmentation of tropical forests

Lowland tropical forests, also referred to as rainforests, are the most species rich ecosystems on earth (Wilson, 1989). Though they occupy less than 6% of the earth's surface, they house more than half of earth's biodiversity. But these forests have shrunk to a great extent over the last century due to agricultural expansion, infrastructure expansion and wood extraction (Geist et al, 2002). As a result, they now exist in small pockets, nestled in a mosaic of non-forested land-uses like agricultural fields, plantations, industries and human settlements.

The lowland tropical forests of Upper Assam have shared the same fate. There are records of felling of these forests right from Ahom times, but deforestation is said to have reached its peak during the British rule when tea estates were established and continued post the British rule (Sharma et al, 2012). Larger chunks of these forests are some of the last remaining lowland tropical forests of Assam, which extend into hilly regions of Arunachal Pradesh. Smaller patches of various sizes, right from 1km² to 25 km², stand isolated amidst tea plantations, paddy fields and expanding human settlements while oil explorations continue to be carried out in these forests.

12 Species loss from fragments

Habitat destruction and degradation are the most important drivers of global biodiversity loss. Some species face immediate risk of extinction, while others imminent. Along with loss of species, there is loss of key ecosystem functions such as reduction in biomass and alteration of nutrient cycles. These effects are most profound

in small, isolated fragments and they magnify over time, raising the question of future of these fragments for the species they harbour and the ecosystem (Haddad et al, 2015).

Species loss from fragments of tropical forests takes place in a multitude of ways, often one factor acting in synergy with another. Reduction in population size, decreased or no immigration into fragments, edge effects, invasion, cascading effects of loss of a particular trophic level, especially top predators, and increased human-induced disturbances such as logging and hunting in the fragments lead to local extinction of species (Turner, 1996). Often, the nature of species loss is predictable with the same set of species being lost from fragments. This results in the communities of the fragments to be nested subsets of those in larger forests (Patterson, 1987).

13 Literature review

1.3.1 Impact of habitat fragmentation on various taxa

Habitat fragmentation has been one of the most well-researched topics across tropical and temperate ecosystems. Long term manipulative experiments were carried out in the Amazon Rainforest. Pioneering work by Thomas Lovejoy and Bill Laurance, called the Biological Dynamics of Forest Fragments Project (BDFFP) was initiated in 1979 and has accumulated over 30 years of data on effects of habitat fragmentation on plant and animal communities of the Amazon. It was found that although certain species may decline or completely disappear in the fragments, certain groups which can tolerate disturbed areas or edges increase. This was found to be true with certain rodents and marsupials, nectarivorous birds, frugivorous bats, some understory insects, pioneer trees and lianas (Laurance et al, 2002). Species that can exploit the adjoining matrix also manage to do well.

In India, research on effect of fragmentation on mammals was spearheaded in the Western Ghats. Demographic and behavioural responses of Lion-Tailed Macaque to fragmentation was studied in the fragments of Valparai (Umaphy et al, 2000). Persistence of other mammals was also examined in the same fragments (Sridhar, TRS Raman & Mudappa, 2008). A study on impact of fragmentation on the Hoolock Gibbon in the forest fragments of Upper Assam revealed declining populations, smaller group sizes and lower adult-juvenile ratios in the fragments (Kakati et al, 2009). Another study on primate communities in the fragments of Upper Assam revealed a declining trend in their populations with the Stump-tailed Macaque being most susceptible to local extinction (Sharma, Madhusudhan & Sinha, 2014).

Arboreal mammals are habitat specialists and especially vulnerable to habitat fragmentation as they depend on trees for food, shelter and movement. Studies suggest that they are sensitive to patch area (Umaphy et al, 2000, Laurance et al, 2004, Sridhar et al, 2008, Sharma et al, 2014). Primates, especially, have disappeared from even large patches (Laurance et al, 2004). Arboreal mammals have also been found to not cross clearings of even 15-100 m, depending on the species, making dispersal through non-forested land-uses a major limiting factor for persistence of these mammals (Laurance et al, 2004). Hence, these mammals may be restricted to these small patches of forest and may eventually become potential candidates for local extinction (Harrison, 1991).

1.3.2 Status of research on tropical squirrels

Arboreal squirrels, both tree and flying squirrels constitute a major component of the animal biomass in the canopy (Eisenberg, 1980; Datta & Nandini, 2015). The larger species perform the functions of seed predation and dispersal, while smaller ones are

pollinators (Hallwachs, 1986; Smythe, 1989; Paschoal & Galetti, 1995; Datta & Nandini, 2015).

Tropical forests of Asia are home to highest diversity of arboreal squirrels, both tree and flying squirrels (Koprowski & Nandini, 2008). Larger squirrel species, the giant squirrels, are also distributed in the Asian tropics. India is home to three species of giant squirrels - Indian Giant Squirrel (*Ratufa indica*), Grizzled Giant Squirrel (*Ratufa macroura*) and Black or Malayan Giant Squirrel (*Ratufa bicolor*). Detailed ecological studies of Indian Giant Squirrel (*Ratufa indica*) have been done in Western Ghats (Borges, 1989) and Central India (Datta & Goyal, 1996). Grizzled Giant Squirrel (*Ratufa macroura*) was studied in southern Western Ghats (Joshua & Johnsingh, 1992).

Studies on impacts of habitat modification on squirrels have been undertaken in the past, pre-dominantly in the North-East - impact of *jhum* cultivation on squirrels and primates (TRS Raman, 1996) in Mizoram, impact of selective logging on squirrels (Datta & Goyal, 2008) in Pakke, Arunachal Pradesh. These studies showed extreme decline in some species or even extirpation from altered land-uses.

Very few studies have looked at the effects of habitat fragmentation on tropical squirrels. Food habits of Indian Giant Flying Squirrel was studied in a forest fragment (Nandini & Parthasarathy, 2008). Persistence of Indian Giant Squirrel in forest fragments was studied as part of a study on arboreal mammals (Umopathy et al, 1995; Sridhar et al, 2008).

While impact of habitat fragmentation on animal communities has been studied widely, and depauperate nature of the communities in the fragments is known. behavioural responses of animals in the fragments have, in general, received scant attention. These responses are crucial for the persistence of species in a modified and limiting habitat

condition. Besides, responses of different species are variable, even if they are closely related. These differential responses in a set of interacting species would alter the relationships between those species in a modified environment (Koprowski, 2005).

14 Niche and changes in niche parameters with environmental uncertainty

Species that are closely related and occur together use similar resources, but in subtly different ways which fosters their coexistence against competitive exclusion. Measuring niche parameters of one population and comparing with those of another helps understand how different species utilize their environment while interacting with other species. While a large number of resources are important for an organism, it might not be possible to measure the niche parameters in all these axes. Pianka (1973) identified three basic niche dimensions - time, space and food.

Two commonly used niche metrics are niche breadth and niche overlap (Futuyma 2002). Niche breadth is a measure of specialization of a species on a set of resources. Also called niche width or niche size, it measures the distribution of individuals of a population within a set of resources. If the individuals are distributed more or less evenly across the set, the species is said to have a broad niche breadth and is less specialized and vice-versa. Niche overlap measures the collective use of resources by two species or the niche space that is shared between two species. When there are multiple species, pairwise measures are calculated for all pairs of species.

Habitat modification because of fragmentation and degradation brings about changes in food densities and species composition, which lead to changes in the interaction between species. When food density is high, specialization on few types of foods is possible. But when food density is low, it is expected that an animal explores a wider range of foods, leading to increase in niche breadth (Schoener 1971). Hence, niche

breadth is expected to increase with environmental uncertainty. With increase in niche breadth of at least one species, niche overlap reduces. This response may, however, be species specific.

15 Objectives

The aim of the project is to study the impact of habitat fragmentation on diurnal squirrels. Comparisons of ecological parameters of squirrels between forest fragments and large forests were done to answer the following specific questions -

1. Is the species composition (richness and density) different between fragments and large forests?
2. What are the responses of squirrels along basic niche dimensions of time, space and diet in altered habitat conditions prevailing in forest fragments?
 - a. Are the activity patterns of squirrels different between large forests and fragments?
 - b. Is horizontal and vertical space use of squirrels different between large forests and fragments?
 - c. Is the diet of squirrels different between large forests and fragments?
 - d. Which species are sensitive to habitat fragmentation?
3. What are the nesting requirements of the squirrels in large forests and fragments?
 - a. What are the tree species used for nesting in large forests and fragments?
 - b. Are the nest heights different between large forests and fragments?

Chapter 2

STUDY AREA

2.1 Location

I conducted the study in the lowland tropical rainforests of Upper Assam. These forests are located in the eastern most end of Assam, in the district of Dibrugarh, sharing borders with Arunachal Pradesh. Considered one of the last remaining lowland tropical forests of the country, these forests now exist in pockets of few large areas and over forty forest fragments of various sizes, most of them isolated from one another, following extensive deforestation in the last two centuries (Sharma, Madhusudhan & Sinha, 2014; Kakati, 2002).

I chose a total of seven sites for the study following a reconnaissance survey in September 2018 (Table 2.1, Fig 2.1). These included two large forest tracts ($>100 \text{ km}^2$), two fragments of medium size class ($20\text{-}25 \text{ km}^2$) and three fragments of small size class ($<5 \text{ km}^2$). The small fragments are the most isolated, separated by an aerial distance of about 50 km from the large forest. The medium fragments are separated from the nearest large forest patch by an average of about 15 km. Of these, five sites were selected as intensive study areas as shown in Table 2.1. The sites are comparable with respect to their vegetation composition though degradation is more severe and is a continuous process in the fragments.

These forest areas are located in Digboi, Doomdooma, Dibrugarh and Tinsukia forest divisions. The large areas fall under the ambit of Dehing Patkai WLS. Two small fragments are a part of Bherjan-Borajan-Podumoni WLS. The rest of the sites are Reserved Forests. The sites were located between $95^\circ 21'28.3$ to $96^\circ 00' 51.1$ E and $27^\circ 05' 35.2$ to $27^\circ 45'11.2$ N.

S.No	Site	Site Type	Size (km ²)	Protection Status	Intensive Study Area
1.	Jeypore	Large	111	RF/ WLS	Y
2.	Soraipong	Large	100	WLS	N
3.	Kakojan	Medium	23.47	RF	Y
4.	Doomdooma	Medium	24	RF	Y
5.	Bherjan	Small	3	WLS	Y
6.	Borajan	Small	5	WLS	Y
7.	Tokoni	Small	3	RF	N

Table 2.1: Study sites. RF: Reserved Forests; WLS Wildlife Sanctuary

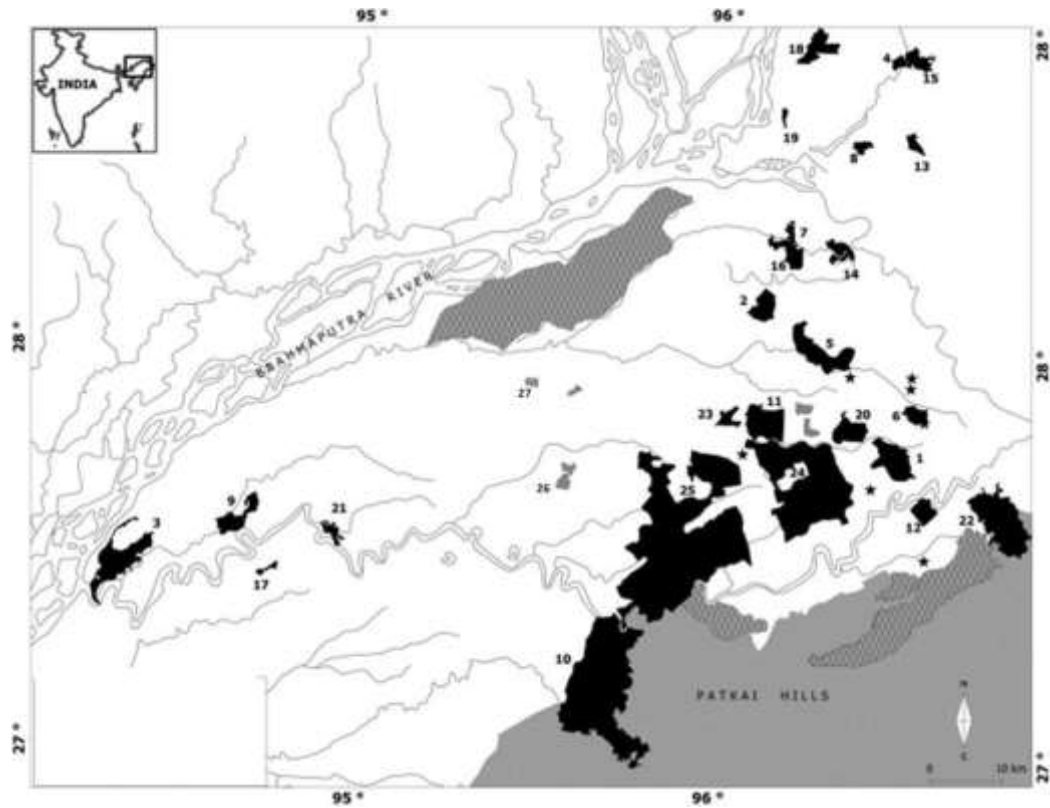


Fig 2.1: Map of the study area. Courtesy: Sharma et al 2012. Sampled sites – 5, 10, 11, 23, 25, 26, 27

2.2 Study period

The study was carried out for a period of seven months in total from December 2018 to June 2019. Field work was covered between mid-December 2018 to April 2019, analysis and writing between May 2019 to June 2019.

2.3 Topography and soil type

Bordered by the foothills of Patkai range in the south and the east, the large forests encompass mostly undulating regions, though flat areas are not uncommon. River Buridehing divides the two large forests. There are also several perennial streams, called nullahs, dissecting these forests. The altitude ranges from 122 to 1600 m above sea level. Soil type is old alluvium. Some of these topographical elements are missing in the fragments which are mostly flat, locally called 'kurkani' (Das, 1965; Chand, 1990; Choudhury, 1995; Kakati, 2002). Streams are also fewer and are not continuously replenished. Soil type of the fragments, which are located slightly more to the north, is again, old alluvium, but of Brahmaputra.

2.4 Climate

The climate is characterized by high humidity and rainfall (2226 to 3644 mm), typical of tropical monsoonal climates. The duration of the monsoon is from June to September with average temperature being 28 °C. December to February is considered dry period, with average temperature being 16°C. March to May is summer.

2.5 Vegetation type

The forest type is Assam Valley Tropical Wet Evergreen Forest (category 1B/C1), also called Upper Assam *Dipterocarpus - Mesua* forest (Champion & Seth 1968). These forests are dipterocarp dominated, typical of rainforests of South-East Asia. *Dipterocarpus macrocarpus*, the dominant species, constitutes the emergent trees, standing 40-50 m tall. The canopy is formed by *Mesua ferrea* and *Vatica lanceaefolia*, another dipterocarp. The understorey is generally sparse, with ferns and some woody shrubs. Bamboos, canes and wild banana are common in the valleys and slopes.

The fragments in the Brahmaputra alluvium are characterized by Miscellaneous Forests (category 3/IS2 and 4D/SSI) (Champion and Seth 1968) of mainly deciduous species with patches of evergreen forests owing to prolonged degradation in these fragments (Kakati 2002). Representative species are *Mesua ferrea*, *Dillenia indica*, *Terminalia citrina* and *Lagerstroemia flosreginae*, along with *Bischofia javanica*, *Castanopsis indica* and *Terminalia bellirica*.

2.6 Biodiversity

Tropical forests of North-East India are considered among the world's 34 biodiversity hotspots harbouring Indo-Malayan floral and faunal elements (Myers et al 2000, Mittermeier et al 2011). This region alone sustains around 1,200 bird, 430 mammal, 520 reptile and between 10,000 to 20,000 plant species, many of them endemic and endangered (Chatterjee et al 2006). Jeypore-Dehing forests are home to seven species of cats (Golden Cat, Fishing Cat, Marbled Cat, Tiger, Clouded Leopard, Common Leopard and Leopard Cat) (Kakati 2010).

2.7 Forestry operations

Both the large forests and the fragments had been subjected to extensive forestry operations in the past. Rampant deforestation had taken place for expansion of tea gardens and extraction of natural resources such as natural gas, oil, coal, and forest timber for rail sleepers and boat building (Sharma, Madhusudan & Sinha, 2012).

2.8 Study species

The study focussed on the four common diurnal squirrels, Malayan Giant Squirrel (MGS) (*Ratufa bicolor*), Red-bellied Squirrel (RBS) (*Callosciurus erythraeus*), Himalayan Striped Squirrel (HSS) (*Tamiops mcclllandii*) and Hoary-bellied Squirrel (HBS) (*Callosciurus pygerythrus*). Other squirrels are also present but rarely sighted.

Chapter 3

METHODOLOGY

3.1 Field methods

General protocol was to walk trails and record data of interest. A total of 25 trails were walked across large forests and fragments with replicates (Table 3.1). Number of trails walked per site was in accordance with the size of the site to ensure appropriate coverage of the accessible area. Trail length varied between 1 – 5 km. There were 3 rounds of sampling per site with multiple replicates per round to account for phenological changes with season during the study period. Overall sampling effort was similar between large forest and the fragments put together.

S.No	Site	Size (km ²)	Site Type	Number of Trails	Number of Sampling Days	Total Effort (km)	Total Time (h)
1.	Jeypore	100	L	7	43	143.63	122.30
2.	Soraipong	100	L	2	4	22	19.53
3.	Kakojan	23	M	5	19	54.68	69.00
4.	Doomdooma	24	M	5	12	48.83	39.33
5.	Bherjan	3	S	2	6	30.68	24.00
6.	Borajan	5	S	2	4	11.36	15.25
7.	Tokoni	3	S	2	3	3.5	3.25
			Total	25	91	314.68	292.66

Table 3.1: Sampling effort across sites. L: Large; M: Medium; S: Small Fragment

Trails were walked to assess species richness, densities, vertical space use for feeding, time activity patterns, diet and nesting requirements of the squirrels. Squirrels were observed throughout the day, but mostly in the morning (0600 to 1200 hours) and late afternoon (1400 to 1730 hours). While it was possible to cover all the objectives in the same walk, it was felt that most of the encounters of the squirrels in walks where a

constant pace is maintained were those of squirrels in transit or in search. Observations of feeding and other activities were minimal. Hence, walks for density estimation were separated from those for recording activity which require the observer to wait after the squirrel is spotted in transit or in search. These are referred to as ‘density walks’ and ‘activity walks’, respectively.

Activity bouts were timed during the ‘activity walks’ following focal sampling of the squirrels detected. Activity was timed for however long the squirrel could be kept in sight. Squirrels were also opportunistically followed. However, to maximize effort, activity was also recorded as events using instantaneous scans during ‘density walks’.

3.1.1 Density estimation

Distance sampling approach was used to estimate densities of squirrels. A subset of total trails was used as line transects. Very close trails in the fragments were not considered to avoid over-estimation. Trails were walked at a constant pace (about 1 km/h). Squirrels were detected visually and by their calls. Once spotted, species, number of individuals, age class (if possible), animal bearing, trail bearing, distance from the trail and height were recorded.

3.1.2 ‘Activity walks’

When a squirrel is spotted, species, time of encounter, activity and activity bout were recorded. Activity could be any of the following -

in transit, searching, feeding, resting, vocalising, chasing, grooming, carrying nest material, etc.

If found feeding, the following attributes were recorded for each foraging squirrel:

a. Species

b. Time

c. Foraging height

d. Plant habit (tree/climber/shrub/epiphyte)

e. Plant species

f. Plant part eaten (bark/leaves/ flowers/fruits/seeds). Fruits and seeds were further grouped into size classes and into classes based on type of fruit or seed (berry/fig/seeds).

g. Feeding bout

3.1.3 Nesting characteristics

When a drey was located, height of the drey, position (near the main trunk or peripheral), exposure, status of use and tree species were recorded. Also, about 5 nests were examined opportunistically in the large forest, with due care and caution, when the squirrels were not in the vicinity of the nests.

3.1.4 Vegetation structure and composition

Point-centred Quarter Method (PCQM) was used for evaluating vegetation structure and composition along the trails (Mitchell, 2007). PCQs were carried out roughly at every 100 m - 200 m along the trails unless the point is inaccessible due to terrain or denseness of vegetation at that point. It was ensured that at least 6-7 PCQs are carried out per trail.

Eight trees closest to the observer were enumerated per PCQ, two in each cardinal direction, one of $GBH \geq 30$ cm and another $10 \text{ cm} \leq GBH < 30$ cm. The latter class helps assess the regeneration size class. For each tree, distance from the point, GBH

and height were recorded. Canopy cover was also recorded at every point using a smart-phone app, Canopeo. Additionally, in a radius of 10 m around the point, a quick survey of other tree species, their number and number of lianas was done. This was important from the perspective of capturing species richness as lowland tropical forests are known to be highly diverse and it is likely that many species are missed in the PCQs since only eight closest trees are considered.

3.2 Analytical methods

3.2.1 Density estimation

Densities of squirrels were estimated using the framework of distance sampling (Buckland, 2005). Distance data of perpendicular distances and cluster sizes of different species were analysed using Distance 7.1 software package. Akaike's Information Criterion (AIC) was used to select the best model of the detection function.

The sites were post-stratified into clusters of large forests and fragments. A global detection function was obtained by pooling together sites in each cluster. Overall density estimates and that of each species were obtained at the level of the stratum, i.e. at the level of each site.

3.2.2 Measurement of niche width and niche overlap

Resource states vs Species matrices were constructed to obtain the distribution of each species across the resource states of a niche axis. One matrix each for large forest and fragments were constructed and given as inputs to Species Association Analysis (spaa) functions, an R package, to compute niche width of each species along a niche axis and niche overlap between the species.

For computations of niche width along vertical foraging space, resource states were the heights at which the squirrels were found foraging. 30 states were identified, from the ground up to 30 m, each metre considered a resource state category (Fig 3.1). Number of individuals sighted at each state was used to populate the matrices.

Large					Fragments				
Foraging Height (m)	HBS	HSS	MGS	RBS	Foraging Height (m)	HBS	HSS	MGS	RBS
0	1	0	0	0	0	0	0	0	1
1	0	0	0	1	1	0	0	0	0
2	0	1	0	0	2	0	1	0	1
3	0	0	0	1	3	0	0	0	1
4	0	0	0	0	4	0	1	0	1
5	1	0	0	0	5	0	0	0	2
.					.				
.					.				
.					.				
30	0	0	1	6	30	0	0	0	0

Fig 3.1: A snapshot of foraging heights vs species matrices for large forest and fragments

For computations of niche width along diet axis, resources states were the hierarchical food type variables. Plant parts on which squirrels were found foraging were classified in a hierarchical manner to obtain the resource states as shown in Fig 3.2.

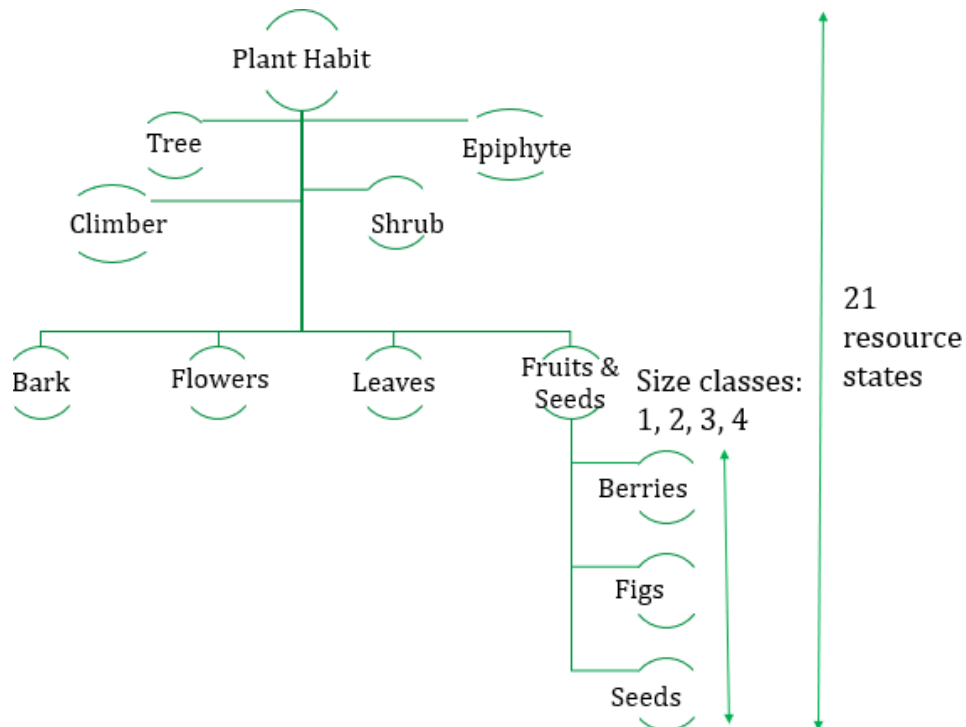


Fig 3.2: Hierarchical food type variables

Data from feeding bouts were converted into proportion of time spent feeding on a particular state for each species and that from feeding events were converted into proportion of individuals of a species found feeding on a particular resource state respectively. Average of these proportions were taken to populate the resource states vs species matrices.

Levin’s measure of niche width:

Measures the uniformity of distribution of individuals among the resource states.

$$B = 1/\sum(p_i^2)$$

where, B = Levin’s measure of niche width,

p_i = proportion of individuals found using resource state i

Morisita's measure of niche overlap:

Measures joint use of a resource by two species.

$$O = 2\sum p_{ij} p_{ik} / (\sum p_{ij}^2 + \sum p_{ik}^2)$$

where, O = Morisita's measure of niche overlap between species j and k

p_{ij} = Proportion resource i is of the total resources used by species j

p_{ik} = Proportion resource i is of the total resources used by species k

3.2.3 Composition of diet in large forest and fragments

Principal Component Analysis (PCA) was used to check if the composition of the diet differed between the sites by visualizing the positions of the sites in a simplified multi-dimensional space of hierarchical food type variables. PCA transforms the space containing these large number of variables into another space with fewer variables that are linear combinations of these variables. Function 'prcomp' in the stats package in R was used to perform PCA. Functions from 'factoextra' package were used to obtain biplot of variables and sites in the new PCA dimensions. Loadings and rotations of original variables on the transformed PCA dimensions were used to understand contributions of different food types in different sites.

3.2.4 Difference between nest heights in large forest and fragments

ANOVA was used to test for difference in nest heights between large forests and fragments. Multiple pairwise comparisons using *post-hoc* Tukey's HSD were also performed to identify pairs of site types with significant difference in nest heights. This analysis was done keeping in mind possible implications on nesting success and predation as nest height and position of the nest might influence these processes.

Chapter 4

RESULTS

4.1 Vegetation structure in large forests and fragments

Nature of the trails varied within and among sites with some trails being dense and others relatively open. Table 4.1 lists site-wise structural parameters summarised from trail-wise estimates.

Site	Type	Stem density (stems/Ha)	Basal area (m ² /Ha)
Jeypore	Large	803.31±318.41	35.04±14.02
Soraipong*	Large	672.46	18.17
Kakojan	Medium	952.13±418.04	51.49±24.22
Doomdooma	Medium	326.83±31.83	15.094±1.45
Bherjan*	Small	728.30	21.76
Borajan*	Small	602.82	35.05
Tokowoni*	Small	818.71±553.11	23.04±0.95

Table 4.1: Structural vegetation parameters of sites. *sites where only one trail was sampled for vegetation parameters owing to small size of the site or logistical issues.

Fragments generally had lower stem density compared to large forests indicating that they were degraded and relatively open. Even if their stem densities were higher as in some cases, basal area was lower indicating scarcity of mature trees or that these sites were composed of regenerating forests.

4.2 Species richness of squirrels in large forests and fragments

Species richness of large forests and medium fragments were found to be similar with about three to five species, while species richness fell in the small fragments with a maximum of two species recorded (Table 4.2). The MGS has been lost from most of the fragments sampled, recorded only from one medium fragment. The RBS is the most common squirrel across all the sites. The HSS was not recorded from the small fragments. This could be an artefact of detection owing to the small size of the squirrel.

Besides these common squirrels, RCS was recorded from a medium fragment, Kakojan, and PLNS from Soraipong. Fig 4.1 lists the number of detections of the common diurnal squirrels recorded from the sampled sites, both systematic and anecdotal.

Site	Type	Number of Species Recorded	Species Recorded
Jeypore	Large	4	MGS, RBS, HSS, HBS
Soraipong	Large	5	MGS, RBS, HSS, HBS, PLNS
Kakojan	Medium	5	MGS, RBS, HSS, HBS, RCS
Doomdooma	Medium	3	RBS, HSS, HBS
Bherjan	Small	1	RBS
Borajan	Small	2	RBS, HBS
Tokoni	Small	1	RBS

Table 4.2: Species recorded from various sites. MGS: Malayan Giant Squirrel; RBS: Red-bellied Squirrel; HSS: Himalayan Striped Squirrel; HBS: Hoary-bellied Squirrel; PLNS: Perny's Long-nosed Squirrel; RCS: Red-cheeked Squirrel

4.3 Density estimates of squirrels

Density estimates of the species are listed site-wise from Table 4.3 to Table 4.7.

Detections of HBS in most of the sites were outside the transects because of which density could not be estimated for this species.

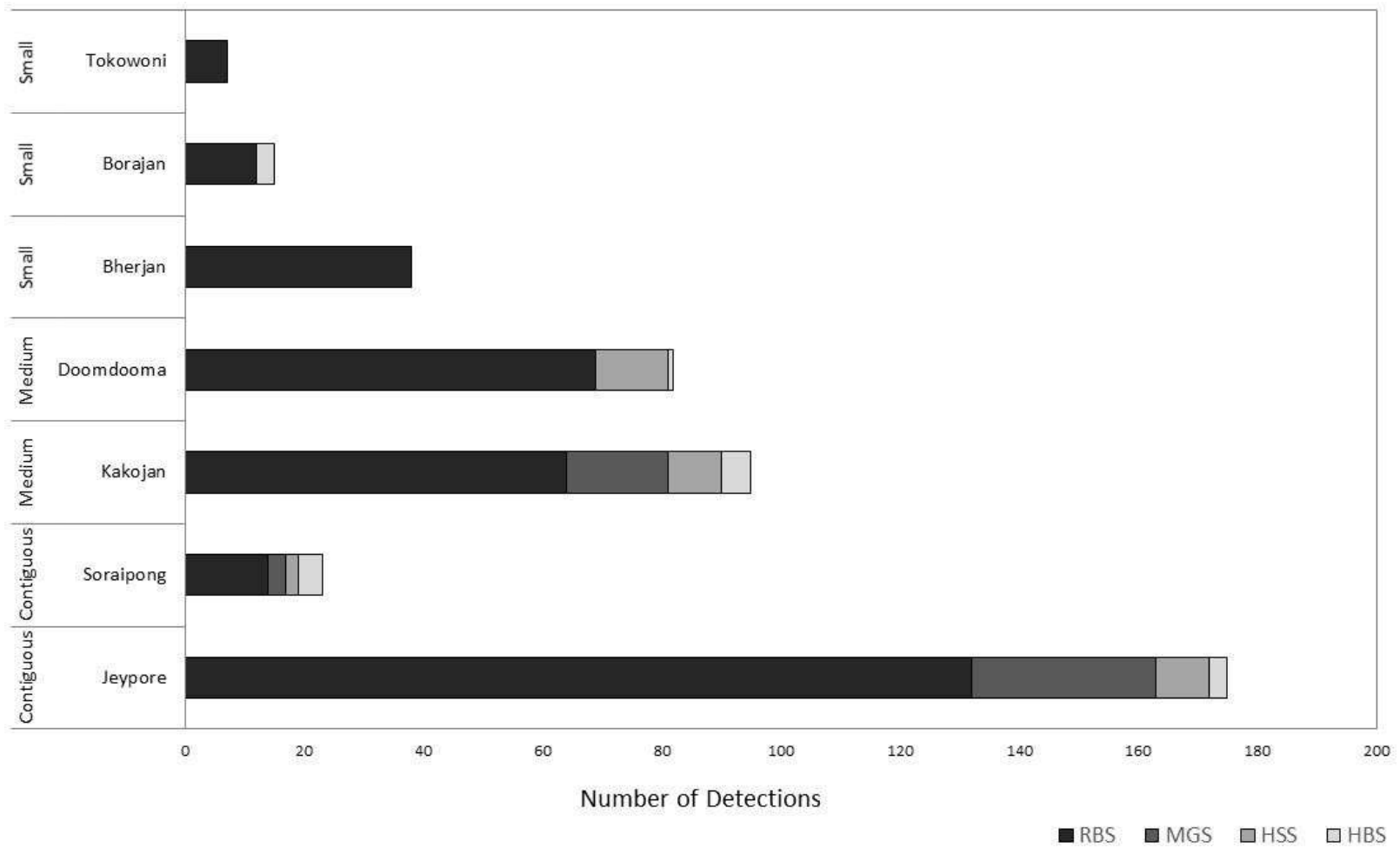


Fig 4.1: Number of detections of common diurnal squirrels in large forests and fragments

Species	Effort (km)	Model Fit	AIC	ER	%CV	ESW	p	Density of groups	E(S)	Individual Densities
overall	68.127	hazard rate	843.65	1.644	15.9	17.23	0.34454± 0.036	47.715± 9.0808	1.2345± 0.046	58.906 ±11.425
MGS	68.127	uniform	130.7886	0.205	33.25	32.995± 6.2970	0.70231± 0.13404	3.1141± 1.1940	1.108± 0.079	3.4504± 1.3459
RBS	68.127	hazard rate	555.443	1.111	18.95	16.944+ 2.00	0.338± 0.0401	32.919± 7.3576	1.3254± 0.066	43.630± 9.9954
HSS	68.127	uniform	114.5778	0.24	31.43	16.049± 3.0964	0.65883± 0.12711	7.7741± 2.8668	1.00	7.7741± 2.8668
HBS	68.127									

Table 4.3: Encounter rates and density estimates of squirrel species in Jeypore RF (large forest).

Species	Effort (km)	Model Fit	AIC	ER	%CV	ESW	p	Density of Groups	E(S)	Individual Densities
overall	8.99	hazard rate	843.65	1.22	9.15	17.23± 1.8013	0.34454± 0.036	35.513± 4.9337	1.2345± 0.046	43.843± 6.3077
MGS	8.99	uniform	130.7886	0.333	57.74	32.995± 6.2970	0.70231± 0.13404	5.0569± 3.0750	1.108± 0.079	5.6029± 3.4307
RBS	8.99	hazard rate	555.443	0.667	49.94	16.944+ 2.00	0.338± 0.0401	19.694± 10.110	1.3254± 0.066	26.103± 13.463
HSS	8.99	uniform	114.5778	0.11	100.11	16.049± 3.0964	0.65883± 0.12711	3.4654± 3.5331	1.00	3.4654± 3.5331
HBS	8.99							NRT		NRT

Table 4.4: Encounter rates and density estimates of squirrel species in Soraipong RF (large forest).

Species	Effort (km)	Model Fit	AIC	ER	%CV	ESW	p	Density of Groups	E(S)	Individual Densities
overall	27.09	hazard rate	671.987	1.51	29.09	18.789± 1.8405	0.46972± 0.046	40.276± 12.363	1.2645± 0.045	50.929 ± 15.740
MGS	27.09	uniform	34.011	1.845	51.12	30.00	1	3.076± 1.572	1.2± 0.2	3.691± 1.9848
RBS	27.09	hazard rate	547.2654	0.996	22.42	19.155+ 2.0855	0.478± 0.0521	26.017 ± 6.4850	1.2659± 0.052	32.934 ± 8.3213
HSS	27.09	uniform	53.923	0.147	62.88	20.000	1	3.6914± 2.3212	1.2222± 0.146	4.5117± 2.8884
HBS	27.09							NRT		NRT

Table 4.5: Encounter rates and density estimates of squirrel species in Kakojan RF (medium fragment). ER: Encounter Rate; ESW: Effective Strip Width; E(S): Estimate of cluster size; p: detection probability; NRT: Not Recorded on Transect

Species	Effort (km)	Model Fit	AIC	ER	%CV	ESW	p	Density of Groups	E(S)	Individual Densities
overall	18.38	hazard rate	671.987	1.904	36.56	18.789± 1.8405	0.46972± 0.046	50.675± 19.181	1.2645± 0.045	64.079± 24.363
RBS	18.38	hazard rate	547.2654	1.632	32.78	19.155+ 2.0855	0.478± 0.0521	42.606± 14.718	1.2659± 0.052	53.935± 18.764
HSS	18.38	uniform	53.923	0.272	59.23	20.000	1	6.800± 4.0284	1.2222	8.3122± 5.0241
HBS	18.38							NRT		NRT

Table 4.6: Encounter rates and density estimates of squirrel species in Doomdooma RF (medium fragment).

Place	Species	Effort (km)	Model Fit	AIC	ER	%CV	ESW	p	Density of Groups	E(S)	Individual Densities
Bherjan	RBS	8.24	hazard rate	547.2654	1.577	0	19.155+ 2.0855	0.478± 0.0521	41.182 ± 4.4839	1.2659± 0.052	52.133± 6.0710
Borajan	RBS	4.11	hazard rate	547.2654	1.459	0	19.155+ 2.0855	0.478± 0.0521	38.107± 4.1491	1.2659 ± 0.052	48.240± 5.6176
Tokoni	RBS	3.00	hazard rate	547.2654	1.667	0	19.155+ 2.0855	0.478± 0.0521	43.506 ± 4.7369	1.2659± 0.052	55.074 ± 6.4134

Table 4.7: Encounter rates and density estimates of squirrel species in Small Fragments. ER: Encounter Rate; ESW: Effective Strip Width; E(S): Estimate of cluster size; p: detection probability; NRT: Not Recorded on Transect

MGS showed a declining trend in the medium fragments, being absent from one of them. It was absent from the small fragments. Densities of RBS were comparable across all sites though densities were slightly lower in sites with MGS and visibly high numbers of other primates. Densities of HSS were comparable across medium fragments and large forests. It was not recorded from the small fragments.

4.4 Changes along basic niche dimensions of time, space and diet with habitat fragmentation

4.4.1 Horizontal segregation

The four common diurnal squirrels in the large forests can be grouped as dwellers of forest-interior and that of forest edges and plantations. Very few detections of HBS (16) from all sites put together suggests that HBS are low in number in the interior of the forests. They have been found to inhabit forest edges, degraded areas and plantations in previous studies (Datta & Goyal, 2008). There is no other form of horizontal spatial segregation between MGS, HSS and RBS which dwell in the forest interior.

4.4.2 Vertical segregation

There was vertical stratification amongst different species in the form of difference in extent of vertical column used for foraging. The RBS utilized the entire vertical column for feeding, followed by HSS, while MGS was restricted to the canopy (Fig 4.2). There was about 40% overlap in the heights used in large forests, pairwise measures of overlap given in Table 4.7.

The overlap of foraging heights of RBS and MGS with HSS increased in the fragments, while that of RBS and MGS did not change much.

Species	HSS		MGS		RBS	
	Large	Fragment	Large	Fragment	Large	Fragment
HSS	1	1	0.403	0.509	0.407	0.551
MGS	0.403	0.509	1	1	0.425	0.393
RBS	0.407	0.551	0.425	0.393	1	1

Table 4.7: Pairwise niche overlap between foraging heights used in large forest and fragments (overlap values range from 0 to 1, 0 indicating no overlap and 1 complete overlap)

Niche width value of vertical space use for feeding increased for the RBS in fragments, suggesting greater use of available lower foraging heights in the fragments compared to large forests (Fig 4.3). RBS used heights in the range 8-18 m more often in the fragments (Fig 4.4), as against greater use of >25m in large forest.

Test of proportion found relative use of these strata different between large forest and fragments ($p=0.0118$, $p=0.0264$). On the other hand, niche width decreased for MGS, suggesting greater restriction of foraging strata in the fragments. MGS can be seen to be restricted to 18-22 m (Fig 4.4).

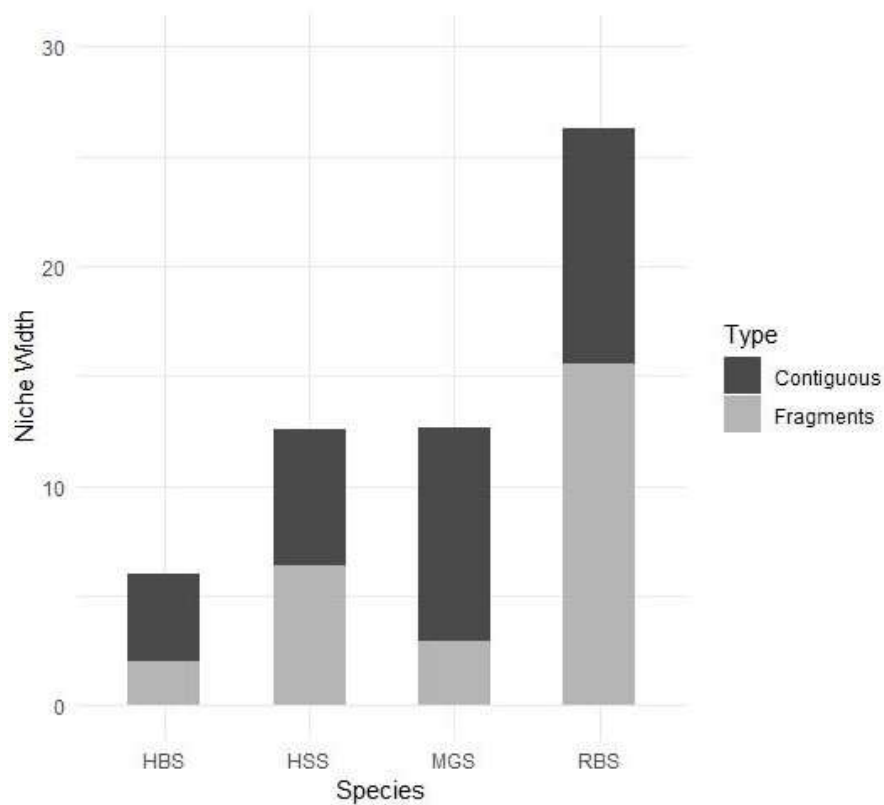


Fig 4.3: Niche width of vertical space use for foraging

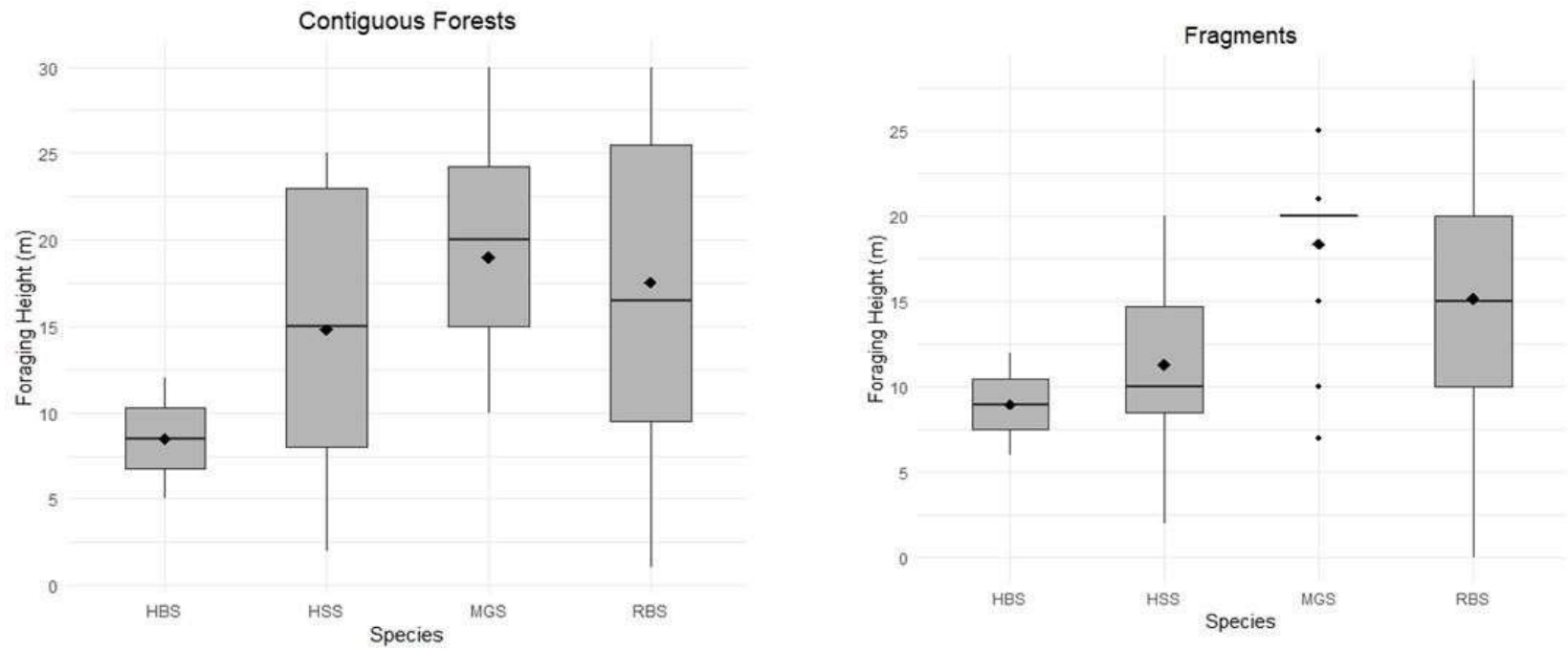


Fig 4.2: Extent of use of vertical column by MGS, RBS, HSS and HBS in the large forest and fragments with means.

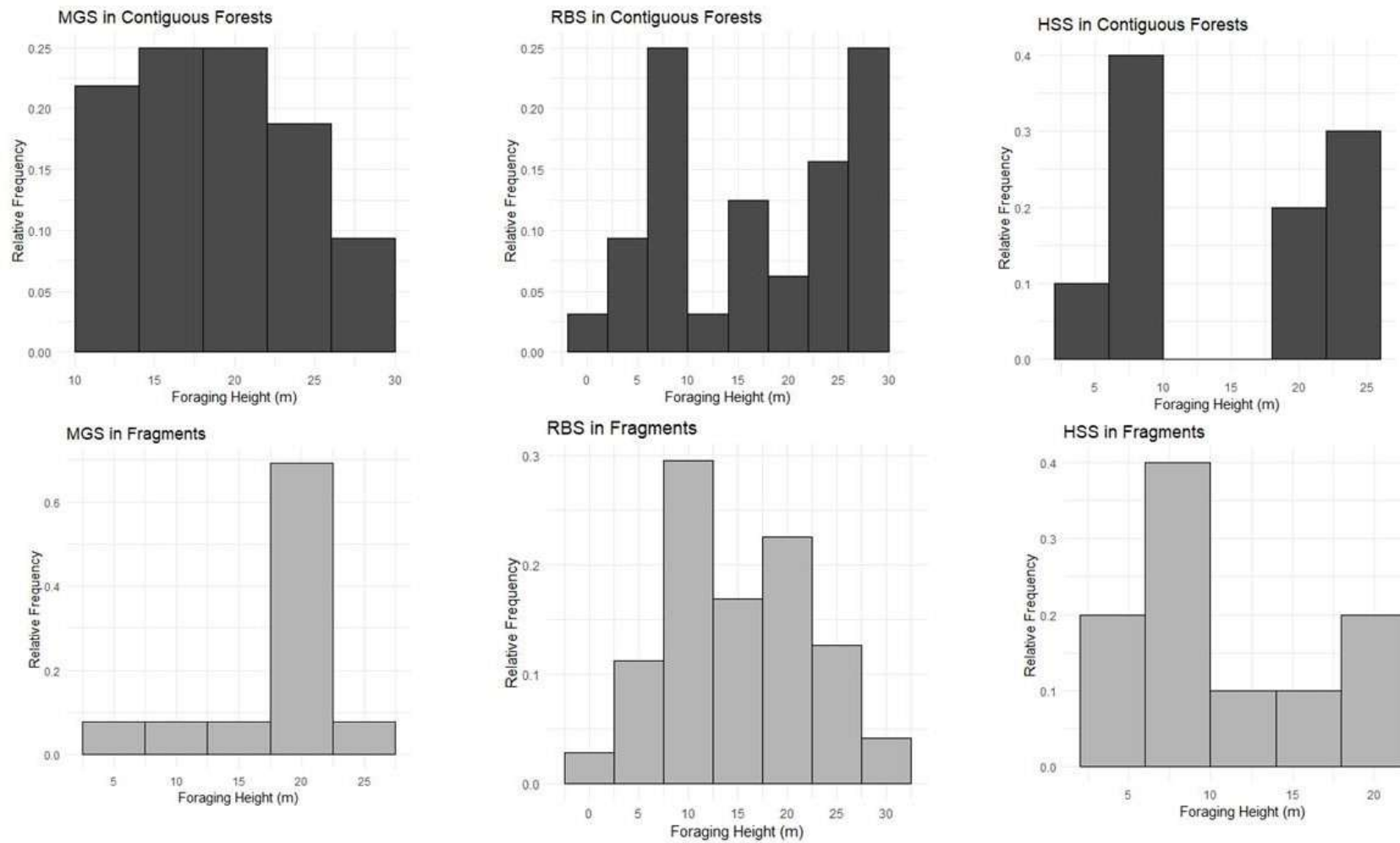


Fig 4.4: Relative frequency of foraging at different strata by MGS, RBS and HSS in large forest and fragments

4.4.3 Diet

Two Proportions Z Test revealed no significant difference between proportions of different broad plant parts (bark, flowers, fruits, leaves and seeds) in the diet of squirrels in large forest and fragments, except leaves. There was no significant difference species wise either. Hence, there was a need to look at finer differences.

Principal Component Analysis (PCA) resulted in three different clusters of sites namely, large forest, medium fragments and small fragments respectively, based on the finer, hierarchical food type variables. PC1 explained 72% of the variance in the data, while PC2 explained 16% (Fig 4.5).

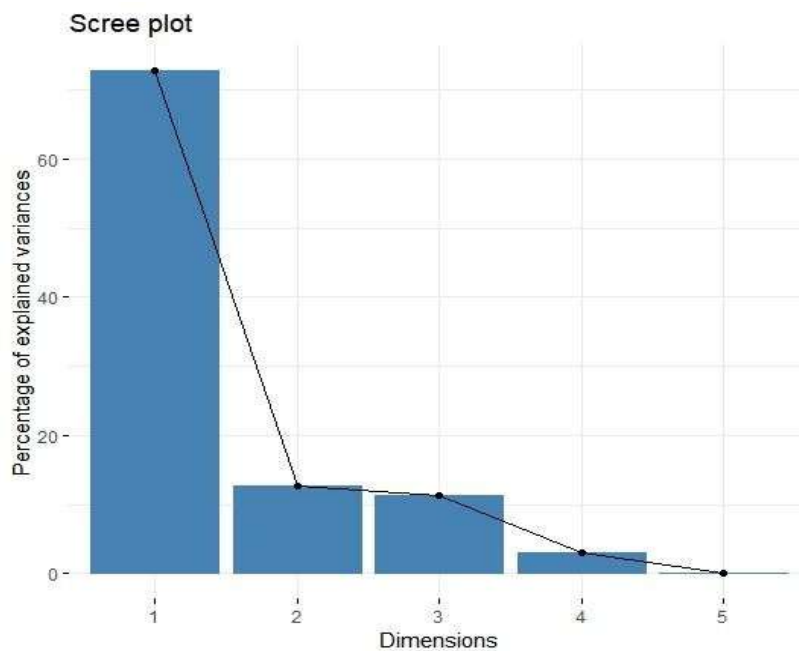


Fig 4.5: Percentage of variance explained by the Principal Components PC1 to PC5

PCA revealed that though proportions of fruits and seeds may not be very different in large forests and fragments, the composition is completely different. Seeds of large arillate fruits like *Chisocheton* spp, *Dysoxylum* spp contributed significantly to PC1 in the direction of the large forest, while berries, figs and seeds of climbers contributed

the most in the direction of medium fragments. Small fragments were characterized by contributions from seeds of climbers, especially those that produced pods, and epiphytic figs (Fig 4.6).

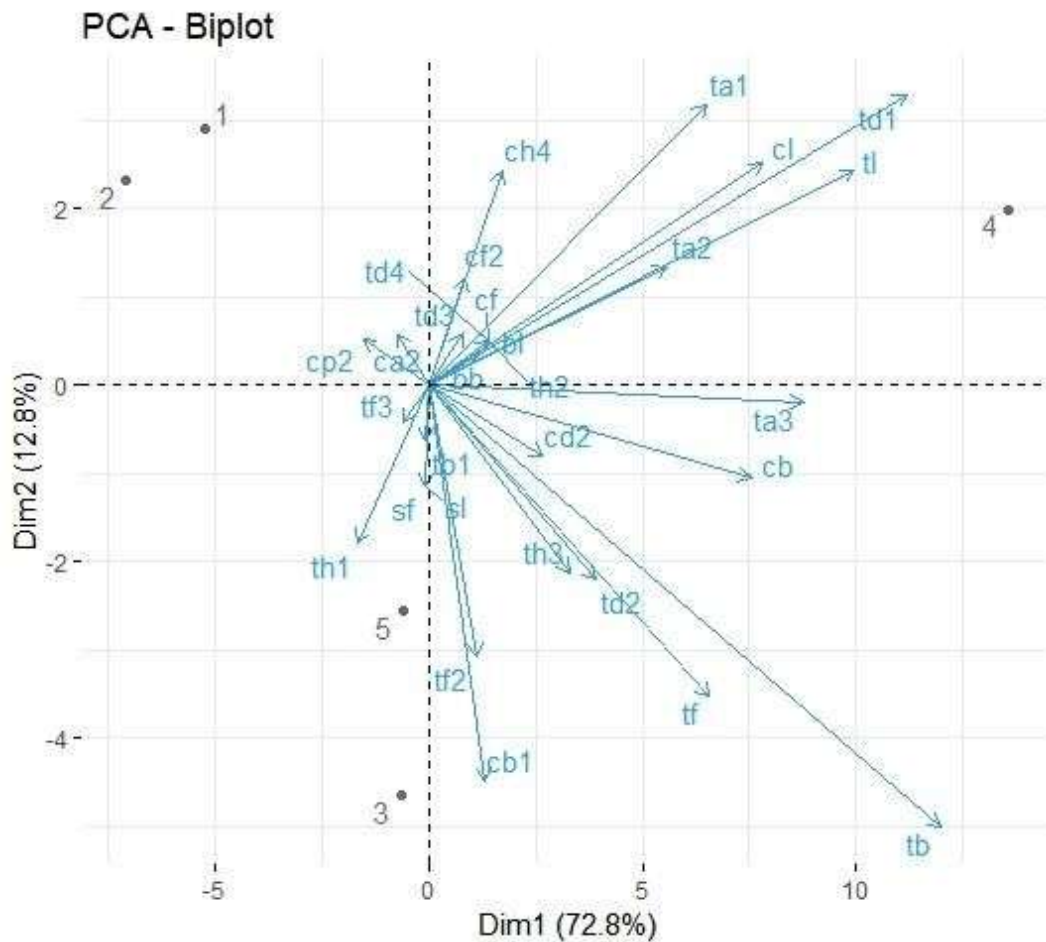


Fig 4.6: Principal Component Analysis Biplot of hierarchical food type variables (represented by arrows, length of the arrow is proportional to its contribution to Principal Components) and individual sites along PC1 and PC2. Sites 1 and 2: Small Fragment, Sites 3 and 5: Medium Fragments and Site 4: Large forest

Overlap in the diet between MGS and RBS decreased, while that of RBS and HSS increased in the fragments (Table 4.8).

Species	HSS		MGS		RBS	
	Large	Fragment	Large	Fragment	Large	Fragment
HSS	1	1	0.129	0.246	0.217	0.400
MGS	0.129	0.246	1	1	0.702	0.337
RBS	0.217	0.400	0.702	0.337	1	1

Table 4.8: Pairwise overlap in diet between the squirrel species in large forest and fragments
Niche width value along diet axis decreased for MGS in the fragments, suggesting greater restriction of diet of MGS in the fragments, while it increased for RBS suggesting expansion of diet (Fig 4.8).

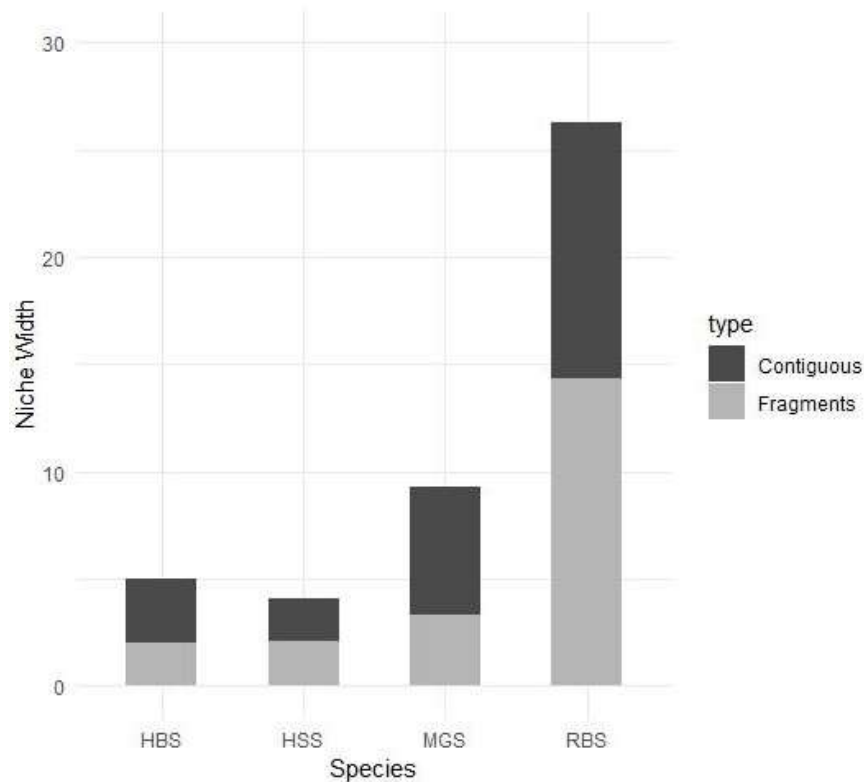


Fig 4.7: Niche width of HBS, HSS, MGS and RBS along diet axis in large forest and fragments

4.4.4 Time

Activity of squirrels in the fragments was very restricted with respect to time. I observed a bimodal peak in the activity of RBS with complete lull in activity between early morning and late afternoon hours. Though a bimodal activity pattern also exists in the large forest, the dip in activity around noon and post noon is not pronounced.

Proportion of time spent on major activities like feeding, searching, resting and vocalising were compared between large forest and fragments using the test of proportion for MGS and RBS (species with sufficient data) respectively (Fig 4.8).

Time spent on resting increased for both MGS (resting: $\chi^2 = 24.426$, $df=1$, $p= 7.721e-07$) and RBS ($\chi^2 = 22.018$, $df=1$, $p \text{ value} = 2.7e-06$) suggesting reduced active periods in the fragments.

Interestingly, time spent on feeding also increased for RBS in the fragments, while time spent on vocalizing decreased. This is indicative of reduced time spent on social activities in the fragments as this species uses vocalization for guarding their territory and for attracting mates (Tamura et al 1988).

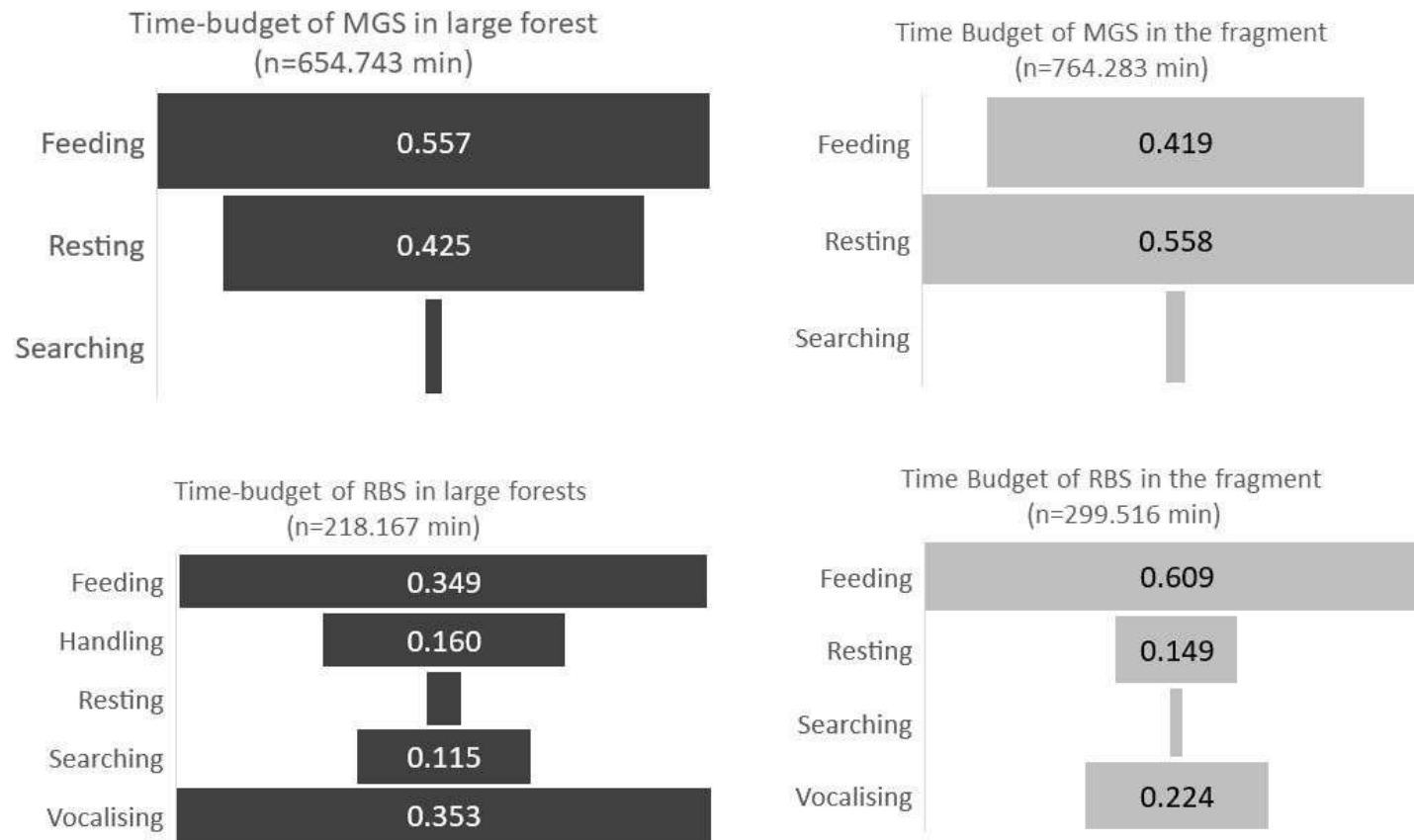


Fig 4.8 Time budget of MGS and RBS in large forest and fragments for major activities – feeding, resting, searching, vocalising.

4.5 Nesting characteristics

4.5.1 Nest heights in large forests and fragments

A total of 99 nests, both in use and disintegrated, were recorded across the large forests and fragments. About 58 nests were recorded in the large forests, 32 nests from medium fragments and 9 nests from small fragments. 28 of the 32 nests recorded from medium fragments were in Kakojan RF, where the MGS is found. The average nest height was found to decrease with decreasing fragment size (Fig 4.10). Nest heights in large forests and fragments were found to be significantly different ($F=6.022$, $p=0.00344$).

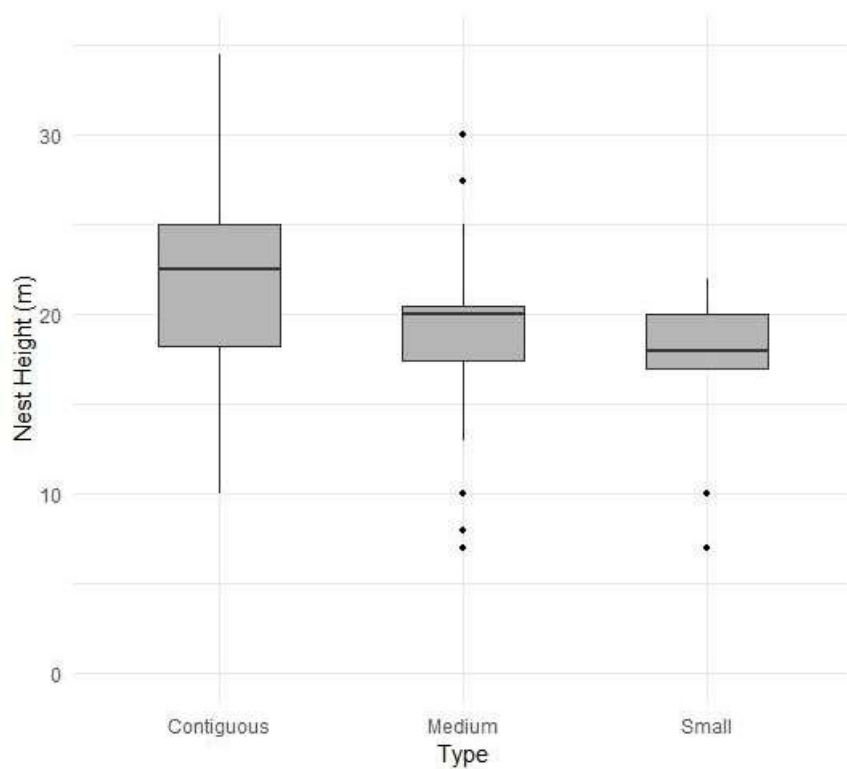


Fig 4.9: Nest heights across sites.

4.5.2 Nesting tree species in large forests and fragments

Nahor (*Mesua ferrea*) emerged as the tree species on which maximum number of nests were found, both in large forests and fragments, followed by Hollong (*Dipterocarpus macrocarpus*), Hingori (*Castanopsis indica*) and Seleng (*Sapium baccatum*) in the large forests and Ajar (*Lagerstroemia speciosa*) in the fragments, respectively.

Chapter 5

DISCUSSION

5.1 Habitat fragmentation and squirrel species diversity

Forest structure is a crucial factor which determines the habitat preferences of arboreal mammals (Lemos et al, 1992; Datta & Goyal, 1996). Within each size class of sites sampled, there was a gradient of degradation. Borajan was more degraded than Bherjan or Tokowoni (Table 4.1) and Doomdooma more degraded than Kakojan amongst the medium fragments. Basal area of Bherjan was low despite high values of stem density, suggesting that average GBH of trees present is low and that mature trees were scarce.

The observed species richness of the site was explained by size of the site, lower variation in stem density and higher basal cover. Hence, species composition is closely linked to the quality of the habitat. Medium fragments which have managed to preserve the intactness of the habitat, even if it is in some pockets of the fragment, continue to retain the diversity of squirrels and have the potential to do so in the longer run, if accorded appropriate protection. However, small fragments harboured a maximum of two species, RBS and HBS. It is clearly seen that small fragments are depauperate. Synergistic effects of habitat loss, degradation and hunting can be seen in the small fragments.

High stem density, basal cover and canopy cover are primary habitat requirements for MGS. Large trees of appropriate girth and height which are important for its nesting (TRS Raman, 1996; Datta & Goyal, 2008; *pers obs*) are scarce in small fragments. Besides, large body size makes it susceptible to hunting, even more so in a small area. These factors shed some light on its absence from most of the fragments.

With smaller body size than MGS, RBS is a perfect generalist with respect to its habitat requirements. It occupies both dense and degraded patches of the fragments. It uses the vertical column to a greater extent and has a wider dietary spectrum. While MGS seems to be an obligate tree-nesting species, requiring trees of appropriate height and canopy structure for nest-making, RBS does not seem to have such a strict requirement. It nests in trees of smaller girths and heights. It also uses dense climbers and tree holes if not trees.

HSS was not recorded from the small fragments. While it is possible that its detection is affected by its size, most of the detections of HSS in large forests and medium fragments were on large trees of GBH around 200 cm, where it was found chipping out bark (Park et al, 2012). Hence, presence of large trees, belonging to certain families, may be important for sustaining HSS. It does appear to be a habitat specialist (Datta & Goyal, 2008).

5.2 Habitat fragmentation and squirrel densities

While species richness differed across fragments, overall squirrel densities were comparable across sites mostly due to the preponderance of one species, RBS. But, when looked at the species level, differences in densities emerge. Density of MGS showed a declining trend in the medium fragment and the species was absent in the small fragments. The densities of HSS in the medium fragments were comparable with the large forests. RBS on the other hand, is found in high densities across all the sites, even in the small fragments. Also, since the fragments sampled during the study are not the result of recent fragmentation events (more than 100 years since fragmentation happened), densities are not in a transitory or non-equilibrium state.

Highest estimates of densities of tropical squirrels (including all the study species) were recorded from tropical semi-evergreen forests of Arunachal Pradesh (Datta & Goyal, 2008). Estimates obtained from this study in the lowland dipterocarp forests of Upper Assam are much lower than these estimates, nearly half as low.

The densities of MGS were comparable with that of another giant squirrel, *Ratufa affinis* reported from similar dipterocarp hill forests in Malaysia (1.3 ± 0.61) (Saiful & Nordin, 2004). But, densities of RBS were 10 times as high as other *Callosciurus* species in those forests ($5.35 \pm 1.73/\text{km}^2$, $3.29 \pm 1.54/\text{km}^2$). Competition with avian frugivores and especially primates that occurred in high densities were speculated as possible reasons for low densities of squirrels in those forests. Converse of this scenario arises in this study where densities of RBS were found to be slightly high, especially in sites where MGS was absent and other primates like Hoolock Gibbon and Capped Langur are in low densities (Sharma et al, 2012), higher than densities in large forests. With absence of MGS and low densities of primates that are direct competitors for fruits and leaves, it is possible that RBS, being an extremely generalist species, respond with higher densities in those fragments.

Fragments may also subsidise high densities of squirrels by increased productivity. Since fragments are relatively open, there was proliferation of non-woody climbers in all the fragments sampled. The results of PCA based on hierarchical food type variables also suggested greater dependence of RBS on climbers in the fragments (Fig 4.6).

The squirrels in fragments could also be benefited from less predation pressure in the fragments. Mammalian predators are negatively impacted by forest fragmentation (Virgos et al, 2002). Densities of mammalian predators in isolated fragments are known

to be very low. And raptor presence was also visibly low in the fragments. Reduced predation pressure may have facilitated increase in the density of the squirrels.

5.3 Habitat fragmentation and changing realized niches of squirrels

Responses of even closely related species to habitat fragmentation vary greatly (Koprowski, 2005). Measuring the responses of an individual species and looking at collective responses of interacting species helps understand how habitat modification and other anthropogenic activities are altering relationships between species.

Niche width of MGS decreased along all the three basic niche dimensions - time, vertical space and diet in the fragments. This implies reduced active periods, restricted foraging strata and restricted diet for MGS in the fragments. Niche width of RBS decreased along time but increased along vertical space and diet axes in the fragments. This suggests reduced active periods, but greater use of some strata and expansion of its dietary spectrum, the latter two being related.

Overlap between RBS and MGS along time, space and diet reduced in the fragments, with a sharp decrease in overlap along diet and time. Overlap between RBS and HSS increased with overlap in diet almost doubling in fragments. There was also increase in overlap along vertical space. Hence, habitat modification alters the overlap between species with or without alteration of species composition. This may potentially have an effect on competitive dynamics between species in the fragments.

Reduced active periods in fragments for all species suggests that change along time axis is the fundamental response to habitat fragmentation. This manifested in the form of an activity pattern with distinct bimodal activity pattern of squirrels with peaks during

early morning hours and late afternoon hours with complete lull in activity in between these peaks.

5.4 Density assessments and comparisons along basic niche dimensions

It can be seen that similar inferences can be drawn from traditional density assessments and responses along basic niche dimensions (Table 5.1). For example, densities of MGS declined in the fragments, it was restricted in vertical space, time and diet. While densities of RBS showed an increasing trend in the fragments, it also seemed to be more flexible with respect to diet and use of vertical space.

Niche width is expected to increase under conditions of environmental uncertainty (Macarthur & Levins, 1967). Reduced niche width in unfavourable conditions can be considered an indication of sensitivity as is the case of MGS and HSS.

Species	Medium	Small	Space	Time	Diet	Sensitivity
MGS	↓	X	↓	↓	↓	Sensitive
HSS	↓	Not recorded	↓	↓	No change	Appears to be sensitive
RBS	↑	↑	↑	↓	↑	Tolerant

Table 5.1: Summary of findings. ↓ indicates declining trend, ↑ indicates increasing trend, X indicates absence.

CONCLUSION AND WAY FORWARD

The findings from this study clearly show that medium-sized fragments have the potential to retain the diversity of squirrels. Protection of these fragments against logging and hunting should be prioritized for safeguarding squirrel diversity in the fragments.

Malayan Giant Squirrel and Himalayan Striped Squirrel, the largest and the smallest squirrels in the body-size continuum seem to be sensitive to habitat fragmentation, while the Red-bellied and Hoary-bellied Squirrel are tolerant. Altered habitat conditions may have changed the nature of interactions between sympatric squirrels by changing the amount of overlap between species.

Niche width can be used as an important predictor of response of a species to habitat alteration. Responses along basic niche dimensions can be possibly used to make prior assessments of a species to habitat alteration as changes in densities may take time to play out.

CAVEATS

1. Interactions with primates which depend on similar resources could not be quantified.
2. Sampling effort at all sites was not enough to resolve the differences in responses in medium and small fragments. Also, combining widely different site sizes in terms of effort was challenging.
3. Analysis of diet can be refined further after identification of climbers and shrubs.

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