Resource tracking by three species of hornbills in Rajaji National Park, Uttarakhand, India

Dissertation submitted to the Saurashtra University, Rajkot in partial fulfilment

of Master's Degree in Wildlife Science

By

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CERTIFICATE

This is to certify that Rekha. A. Warrier of the Wildlife Institute of India has carried out original research titled "Resource tracking by three species of hornbills in Rajaji National Park, Uttarakhand" in partial fulfilment of the Master's Degree in Wildlife Science from Saurashtra University, Rajkot. These investigations were carried out under our supervision at the Wildlife Institute of India from November 2008 to June 2009. We also certify that this work has not been submitted for any other degree of any other university.

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ABSTRACT

Resource tracking is the ability of organisms to adjust to variations in resource availability through numerical or functional responses. Numerical responses may be manifested, by changes in demographic processes or, through changes in movement patterns. Altered space use patterns can result in abundance fluctuations from the local to the landscape levels. An in-depth knowledge, of how resource fluctuations affect patterns of space use and abundance of a species can augment the conservation efforts which are underway for many species. Through this study, responses of three species of hornbills viz, Great Hornbill (*Buceros bicornis*), Oriental Pied Hornbill (*Antharcoceros albirostris*) and Indian Grey Hornbill (*Ocyceros birostris*), to the spatio-temporal variation in fruit abundances were studied in Chilla Range of Rajaji National Park, India.

The study was carried out between December 2008 and April 2009, using a grid based occupancy framework and systematic sampling procedure. A total of 28, 1km grid cells (spatial replicates) were sampled on nine occasions (temporal replicates) for quantifying hornbill responses to fruit abundance patterns. Fluctuations in fruit abundances were assessed by means of phenology transects, which were monitored once every month. Ecological Niche Factor Analysis was done to index the fig fruit availability by modelling fig tree distribution with Eco-geographic variables. Hornbill responses to fruit availability were analysed at two spatial (habitat types and fruit patch level) and temporal scales (winter and summer). Of the three species targeted, data could be consistently obtained only for Oriental pied hornbills. Great hornbills were rarely encountered and Indian grey hornbills were seen commonly only towards the end of the study period. Thus the detailed analysis focussed only on Oriental pied hornbills.

During the study, non fig fruit availability showed severe variations across areas, and over time. The month of March seemed to be the period of absolute non-fig fruit resource shortage. Figs, especially *Ficus rumphii,* were the only species that fruited and helped sustain the frugivore community during this period of scarcity. Thus, *Ficus rumphii* is a potential key stone species for the area. The bias corrected occupancy estimates revealed that Oriental pied hornbills frequented the forest types (Miscellaneous forest) that had high fruit availability in both seasons. At the patch level, intensity of grid use was positively correlated with abundance of non fig fruits in winter ($r = 0.5$, $p<0.01$), and the index of *Ficus rumphii* fruit abundance in summer ($r = 0.31$, $p<0.1$).

The study results show that Oriental pied hornbills tracked resources across the defined spatial and temporal scales. The ability to closely track trends in fruit availability, is probably what helps this species persist in diverse habitats across its distributional range.

1. INTRODUCTION

1.1. The ephemeral nature of resources

Change is the only constant. This oft quoted adage assumes greater relevance when viewed in an ecological context, for, natural ecosystems at any scale of resolution are mosaics of patches which are rarely static. Their elements are in a state of constant spatial and temporal flux. The proximate responses or the ultimate fitness state of individuals are governed by factors which exhibit discontinuities on many scales in time and space. The patterns of these discontinuities produce an environmental patchwork which exerts powerful influences on the distributions of organisms, their interactions, and their adaptations (Wiens 1976). Most organisms therefore, have to contend with transience in suitability of habitat patches. Often in case of vertebrates, the variability in habitat suitability is the result of changes in food availability over space and time. The persistence of a species in a heterogeneous environment would thus depend on its ability to adjust to variations in resource availability. How organisms cope with this heterogeneity depends on their physiology and biology. For example, an organism's ability to cope with spatial heterogeneity may depend on the distance over which it can disperse, while its ability to respond to temporal heterogeneity may depend on its generation time (Fahrig 1992).

1.2. Resource tracking

The functional and/or numerical response of species to spatial and temporal variation in resources is known as *Resource Tracking* (Osawa 2000). Functional responses include behavioural and physiological adaptations to trends in resource availability. Dormancy (Kozakiewiez 1994) and dietary switching (Ray 1995) are some examples of functional responses to resource abundance. Numeric responses may be affected through changes in demography or movement patterns such as nomadic behavior, migrations and altered ranging patterns (Levey & Stiles 1992). In case of highly vagile organisms, like certain bird species, the movement of individuals within and among habitats, in response to variations in food availability, can result in severe fluctuations in population abundance (Kinnaird *et al* 1996). Movement patterns of individuals in this case, would be governed by the logic that, in patchy environments the non-random use of space helps maximize foraging efficiency (Baum 1987) and in such situations, individuals would be expected to select patches with more abundant food resources (Martin 1985).

The space use patterns which govern abundance distribution therefore depends on processes operating at different spatio-temporal scales and varying among both taxa and different geographical regions, yet it seems to be largely influenced by the spatio-temporal distribution of some key environmental resources (Telleri´a & Pe´rez-Tris 2003). This is especially relevant to avifaunal populations and more specifically to avian frugivores who due to their ability to cover large areas during foraging movements can closely track the abundance of fruits. Innumerable studies in the recent past have shown that changes in abundances of frugivorous birds result from altered movement patterns and these closely mirror the fluctuations in fruit abundance (Kinnaird *et al* 1996; Marsden & Pilgrim 2003). Frugivorous birds respond at both spatial (movements among habitats and microhabitats) and temporal (changes in abundance over time) levels to changes in abundance of fruits (Loiselle & Blake 1993). Fruit eating birds thus offer a unique opportunity, to examine the link between resource variation and space use patterns because, unlike other vertebrates their major food resource is conspicuous and can be easily counted.

1.3. Avian frugivores and resource tracking

In tropical forests, fruit abundance fluctuates at various spatial and temporal scales (Whitney& Smith 1998). Fruits occur as a sessile, strongly heterogeneous resource. Their abundance may vary among branches within plant, among individual plants within site, among sites and even among geographical regions, as well as at different scales of the temporal spectrum (Garcia & Pulido 2004). Moreover, the patterns of spatial distribution of fruits within habitats at any given time depends on the horizontal distribution of fruit-producing plants, as well as their relative cover and species richness in the plant community (Herrera 1985). The need to track these resources optimally may even have significantly impacted the life history strategies and demographic patterns of frugivorous birds (Levey 1988). Many tropical frugivores in fact have their breeding seasons in sync with periods of maximum fruit availability (Walker 2006).

Many studies have documented the spatial and temporal responses of frugivorous birds to changes in fruit abundance (Saracco *et al* 2004, Whitney & Smith 1998). From the conclusions of these studies it is apparent that frugivorous birds can cope with spatial heterogeneity of fruit availability at different spatial scales responding positively to fruit abundance (Garcia & Pulido 2004).

Patterns of resource tracking and the scales at which they emerge are closely linked with the foraging behaviour, biology of the species and the cues they employ in locating fruit rich patches. The cues used in locating fruit patches may include visual displays of brightly coloured fruits or plants with conspicuous characteristics (Murray

1987). Birds may also rely on the behaviour of other frugivores to locate fruit patches (Saracco *et al* 2004).

There may be instances where the alterations in space use patterns may not be very strong. This may have to do with the fact that, birds may respond to fruit scarcities by reducing their niche breadth or through dietary switching (Renton 2001).

1.4. Hornbills and resource tracking

Hornbills are large obligate frugivores found in the forests of the old world. Being seed dispersers, they play an important role in the reproductive life histories of many plant species (Howe 1984). Fluctuations in their abundance in an area can therefore have profound effects on the community structure. For this reason there are innumerable studies relating the movement patterns and trends in abundance of various hornbill species with fluctuations in fruit availability. These studies have shown that certain large species of hornbills such as those belonging to the genus *Ceratogymna* which rely on rare fruits are capable of tracking resources through seasonal emigrations (Whitney & Smith 1998). A study on the Sulawesi Red knobbed hornbill revealed that hornbill abundances were significantly correlated with the availability of figs and hence irrespective of habitat characteristics, they chose areas with high fig densities (Kinnaird *et al* 1996). Similar results were obtained in another study in New Britain, Papua New Guinea where, despite the anthropogenic disturbances, Blyth's hornbills (*Rhyticeros plicatus*) used logged forests more, due to the high fruit abundances in those areas (Marsden & Pilgrim 2003).

India is home to nine species of hornbills (Ali & Ripley). Most studies in the country have focussed on the populations of the Great hornbill residing in the Western Ghats addressing issues concerning breeding biology (Kannan 1994, Mudappa and

Kannan 1997). There is one long term study (Datta 2001) on the ecology of three species of hornbills namely Great hornbill, Oriental pied hornbill and Wreathed hornbill (*Aceros undulatus*) occurring in the forests of Northeast India. A feature common to all these studies is that they have focussed on populations residing in the wet evergreen forests of the country. Oriental Pied and Great hornbill do occur in habitats besides these, such as in the Sal dominated forests at the foothills of the western Himalayas. The Indian Grey hornbill has the widest distributional range, among the three species. There have been no studies on the ecology of this species.

1.5. Present study

The present study deals with patterns of resource tracking among three species of sympatric hornbills in a tract of forest at the foothills of the western Himalayas, viz., Great hornbill (*Buceros bicornis*), Oriental pied Hornbill (*Anthrcoceros albirostris*) and Indian grey Hornbill (*Ocyceros birostris*). This area is very heterogeneous and prone to extreme seasonality. In this context it would be interesting to see how the resident populations of these species respond to changes in fruit availability. Very little is known about these populations with respect to their food habits and breeding biology. The means by which these species partition resources is also not known. Datta & Rawat (2003) found that the Great hornbills and Oriental Pied hornbills in the north east partition resources by differing in diet breadths and fruit preference. They also differed in the size and colour of the fruits they fed on. In this study an attempt has been made to discern the patterns of resource use and partitioning amongst these species.

1.6. Objectives

1) To quantify the space use patterns by the three species of hornbills in response to fruit resource availability.

- a) Testing if the variance in site occupancy by hornbills is a linear function of the fruit tree species richness and variance in fruit abundance.
- b) To determine whether site specific characters such as canopy continuity influences choice of foraging patches.
- c) To understand if these birds select fruiting trees with specific tree height, fruit crop size and fruit size.

2) To elucidate the inter-specific variation in resource use pattern by the three species.

- a) Comparing diet breadths of the three species.
- b) Comparing fruit choice with respect to fruit size and colour.

2. STUDY AREA

2.1. General description

The study was conducted within the Chilla Range of Rajaji National Park (RNP) in the state of Uttarakhand, India (Fig 1.). The park spans over 826 km^2 and falls in the "Upper Gangetic Plain" biogeographic zone (Rodgers & Panwar, 1988). It is divided by the river Ganges into an eastern part comprising Chilla (148 km^2) and Gauhri (70 km^2) Ranges and western part comprising Motichur, Haridwar, Dholkhand East and West, Kansrao and Chillawali Ranges. Both these parts of the RNP are connected by a narrow and heavily disturbed Chilla – Motichur corridor.

The Chilla Range lies ensconced within the folds of the Shivaliks and the outer Himalaya. This range (148 km^2) is characterized by highly dissected and rugged hills ranging from 400m to 1000m drained by numerous streams running north to south, most of which remain dry in late winter and summer. The dry stream beds are locally called '*raus*'. The area is mostly hilly excepting areas near the southern and south eastern boundary. Bounded by the Ganges on the west, the range is drained by Ghasiram and Khara *raus* on the southern boundary, Amgadi, Khara and Mundal through the middle and Mithawali and Luni *raus* near the eastern boundary.

Rainfall ranges from 1,300 to 1,900 mm per year with most of it during the monsoon (July – October) and sporadic rains through the year. With temperatures ranging from 20^0C to 45^0C there are three distinct seasons: winter (November- March), summer (April-June) and monsoon (July – October).

2.2. Vegetation characteristics

The numerous rivers and hills together have resulted in a mosaic of forest types. Broadly, the forests of this region can be categorized as Northern Indian Moist Deciduous Forest and Northern Tropical Dry Deciduous Forest (Champion & Seth 1968), with the major associations being miscellaneous forests on the southern slopes, Sal mixed forests comprising mainly of *Shorea robusta, Mallotus philippensis* and *Ehretia laevis*. Sal is the most dominant species on the northern slope. Besides a mosaic of natural vegetation (forests, woodlands and grasslands), there are a few plantations of teak (*Tectona grandis*) and an extremely aggressive exotic tree *Haplophragma adenophylla*. Both the teak and *Haplophragma* form pure stands and coppice well suppressing natural under-storey vegetation in the study area.

Although the entire Chilla Range is potential hornbill habitat, for the present study approximately a 60 km^2 area was selected as the intensive sampling site after accounting for logistics, ease of sampling and accessibility (Fig 1). The tourist road skirting the intensive study area facilitated access to all the sampling grids. The area also covered a variety of forest types thus providing the necessary gradient in fruit abundances.

The Range is hemmed in from three sides by human habitation. These areas are responsible for the break in habitat contiguity between Chilla Range and the western parts of the Park. Besides the external source of disturbance, the area also has had a history of exploitation at the hands of Gujjar herdsmen who have now been relocated to an area outside the park.

The area has a diversity of floral and faunal speciesThe three hornbill species too occur in good numbers, with Oriental pied being the most common.

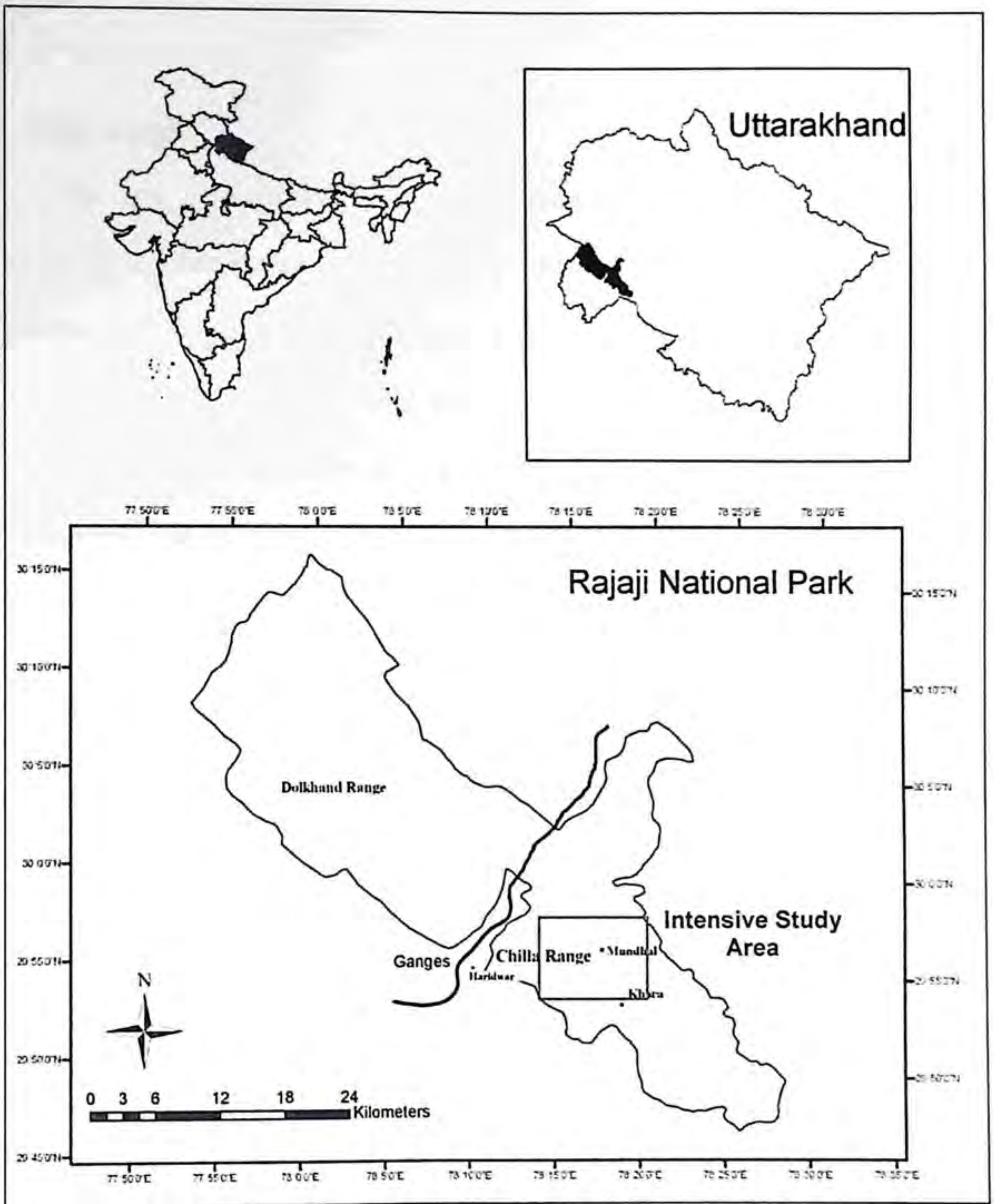

Figure 1. Map of Rajaji National Park, Uttarakhand and the Chilla Range, marked with intensive study area.

3. STUDY DESIGN & METHODS

3.1. Study design

The study was conducted using a systematic, grid based sampling design. A week long reconnaissance survey was undertaken at the start of the study period to get acquainted with the study area and activity patterns of the bird. The intensive study area was divided into 1 km^2 grids. Grid size was decided upon after accounting for the movement pattern of hornbills and the heterogeneity of the study area. Sampling independence was achieved by systematically selecting thirty grids. Two of the grids were inaccessible due to terrain and were subsequently dropped. All further sampling was carried out in the remaining twenty eight grids. The design was broadly aimed, at achieving the characterisation of each of the selected grids on the basis of fruit abundance values, vegetation parameters and also the quantification of the intensity of use of the grids based on hornbill presence.

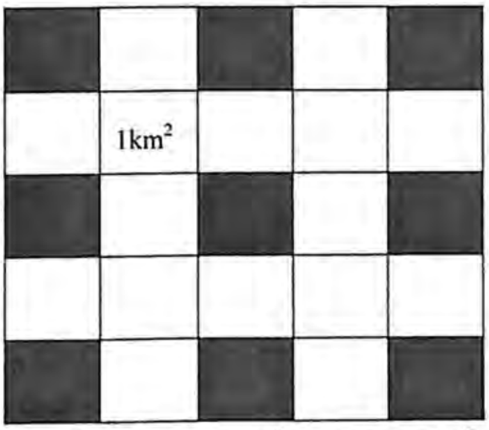

Figure 2. Diagrammatic representation of systematic grid selection

To succinctly answer the questions pertaining to the objectives of this study it is essential to first gain a thorough perspective on the trends in fruit resource availability in the area. Hence, the section on Methods, Results and Discussion have been organised so as to first cover details pertaining to resource availability patterns, followed by details on space use by hornbills and its relation to resources.

3.2. Field methods

The methods employed in the study can be broadly categorised as follows

1) Grid characterisation- Each of the systematically chosen grids were characterised based on winter and summer fruit abundance patterns and broad vegetation characteristics.

2) Space use by hornbills - Occupancy sampling was carried out to quantify intensity of space use patterns.

3.2.1. Grid characterisation

Fruiting phenology of non-fig species

Background- A precise knowledge of the non-breeding season food habits of hornbills in the study area could have immeasurably augmented the outcome of the endeavour. However scientific literature was found wanting in this regard. Most studies on Oriental pied hornbill and Great pied hornbill have been carried out in wet evergreen habitats found in the southern Western Ghats and the Northeast (Datta & Rawat 2003; Kannan & James 1999). Besides harbouring a richer diversity of food species, these areas are also free from the rigours associated with extreme seasonality. As a result there was very little precedent to rely on while drawing a potential food species list for the area. Hence, a flora for the region (Kanjilal & Gupta, rep. 1994) was referred to and a list of all tree species found in the area and which were expected to fruit during the study period (December-April) was drawn. From this list all tree species producing fruits with characters resembling those consumed by hornbills in other areas was teased out. Hornbills are specialized frugivores, i.e., they digest only the pericarp or other soft parts of the fruit and void the seed intact either by defecation or regurgitation (Snow 1981). They typically consume fruits with large seeds covered by nutritious flesh. A study conducted in the Northeast showed that Oriental pied had a preference for small berries while Great pied preferred large drupes and capsular fruits (Datta & Rawat 2003).

The final list comprised of seven non-fig species, and four fig species. The non-fig species comprised of *Limonia acidissima, Murraya koenigii, Diospyros montana, Diospyros melanoxylon, Phyllanthus emblica, Bridelia retusa* and *Ehretia leavis.* The fig species included *Ficus rumphii*, *Ficus bengalensis* and *Ficus glomerata* and *Ficus cunia.* Fruit production in these species was monitored through the study period to quantify fluctuations in hornbill fruit abundances in the study area.

Monitoring protocol- Over the years, varied methods have been employed for the determination of habitat wide fruit abundance values. Most of these methods however lack calibration and universality. Chapman & Wrangham, (1994) discuss the commonly used fruit abundance estimation methods and also detail the pros and cons of each. Some commonly used methods are as follows:

1) Phenology transects – Transects are laid out randomly across the habitat and all individuals encountered along the transects are marked for monitoring.
2) Fruit trails- Existing trails in forests are used and fruit tree species encountered along it are marked for monitoring.

3) Fruit traps- Fruit traps consist of a square frame with a plastic bag suspended from its top, arranged along trails. Fruits falling into this trap are collected and weighed to estimate abundance.

After accounting for the apparent peculiarities in the distribution of certain fruit tree species and difficulties imposed by terrain, phenology transects were deemed suitable. A total of twenty nine phenology transects were laid across the study area in a random fashion so as to achieve maximum representation of the habitat. The transects had a dimension of 200x10m. All individuals of the target species with a girth at breast height (GBH) greater than 10cms, encountered within the plots were marked and tagged with a unique identification code. Tagging was done using red duct-tape and the codes scribed upon them using black marker pens. The GBH of the trees was also recorded. The plots were monitored once at the end of each month for four months. During each monitoring session the presence or absence of ripe fruits on the marked trees was noted. Fruit abundance was then indexed by calculating the proportion of marked trees bearing ripe fruit during each month.

Fruiting phenology of figs

Background- The genus *Ficus*, with 900 odd species forms the most distinctive taxon among the tropical plants (Janzen 1979). Across their distributional range many members of the genus have come to assume the role of keystone species (Lambert 1989; Lambert & Marshall 1991; Terborgh 1986). Characters such as aseasonal fruiting, enormous crop sizes and distinctive intra-crown synchrony in fruit ripening together contribute towards making *Ficus* species indispensable to tropical frugivore communities (Lambert 1989).

Consequently, figs figure prominently in the diets of most hornbill species. About 40 of the 54 extant species of hornbills are known to feed on figs and they feature especially heavily in the diets of Asian hornbills (Shanahan *et al* 2001). A recent study from the Western Ghats on the feeding habits of Malabar pied hornbills showed that nearly sixty percent of the non breeding season diet constituted of fig species (Balasubramanian *et al* 2004). Datta & Rawat (2003) report that in the north-east, during the non-breeding season 74% of all feeding records for Great hornbills and 47% of feeding records for Oriental pied hornbills were on figs. Kannan & James (1999) also report a very high dependence of Great hornbills on fig species. Hence *Ficus* species were considered important resources in this study.

Chilla does not harbour a very high diversity of figs. The list drawn out for phenology monitoring comprised of only four fig species namely *Ficus bengalensis, Ficus rumphii, Ficus cunea, Ficus glomerata*. As per the reference flora (Kanjilal & Gupta 1994) all fig species except *Ficus cunea* were expected to fruit in summer, towards the end of the study period. However during the reconnaissance in December it was observed that *Ficus rumphii* was fruiting. The fruiting continued in a staggered manner all through the study period till the end of March. *Ficus bengalensis* too fruited sporadically during the study period. *Ficus glomerata* was rare in the study area and was never encountered during sampling. Quantifying fig fruit abundance was difficult due to the peculiar distribution and fruiting patterns of the species. *Ficus rumphii* typically occurred as clumps and there seemed to be within clump synchrony in fruiting. For these reasons the species was poorly represented in the phenology plots (3 individuals in 30 plots) and also in the vegetation plots. This hindered the estimation of habitat wide abundance of *Ficus rumphii* trees and fruits. This was done by undertaking Ecological Niche Factor Analysis (ENFA) using GIS and the habitat suitability was estimated for sampled grids.

Vegetation Sampling

The systematically chosen grids were sampled for vegetation composition using random plots. Five plots of dimension 200x10 m were laid within each grid. All trees within the plot with a GBH above 10cms were recorded and their species identity was noted down.

3.2.2 Quantifying space use by hornbills

Most studies use species density responses to resource abundance when demonstrating resource tracking (Levey, 1988; Kinnaird *et al.* 1996; Whitney & Smith, 1998). Densities in these cases are typically quantified using line transects or mist netting procedures. These methods are useful in situations where there exists a high resident bird population. Rajaji forms the nothwestern range limit for Great pied and Oriental pied hornbills and they exist here in low densities. Transect based density estimations would have lead to very high variance on the estimate due to low density and patchy distribution because of the tendency of the species to flock. Therefore it was decided to use an occupancy based estimate of space use to study the species response to fruit availability.

Each of the twenty eight systematically chosen grids were sampled over a sampling session of 4 consecutive days. The sampling was done thrice each month for 3 months. The effort was kept constant across grids by searching for hornbills along an approximately six hundred meter long random trail. A grid was considered occupied if hornbills were sighted or heard within it. Each time a hornbill flock was sighted, observations on species identity, flock size, perch tree species and position on tree were noted down. The sampling was carried out between seven and eleven in the morning, a period which coincides with the maximum feeding time for hornbills.

3.3. Analyses

3.3.1. Estimate of fruit abundance

Monthly fruit abundances were indexed based on the proportion of marked individuals of a species fruiting in each transect. The grid-wise fruit abundances were calculated by assigning each grid to three of the nearest phenology transects. The abundance value was arrived at by multiplying the density of the species in the grid with the average proportion of individuals of the same species fruiting in the respective phenology transects.

All individuals of *Ficus rumphii* encountered during occupancy sampling, vegetation sampling and other random walks were recorded and their GPS locations were noted. These presence points were then used in the Environmental Niche Factor Analysis (ENFA) to define the grids with appropriate habitat suitability values. The ENFA (Hirzel *et al* 2002) modelling in the study was performed using the software Biomapper 4.0 (Hirzel *et al* 2002). Hutchinson's (1957) ecological niche theory forms the basis for ENFA. The analysis uses the information in ecological and habitat variables associated with species presence points and builds a predictive distribution model. The habitat suitability map that is created is a geographical representation of the habitat suitability indices.

Five topographic, one physiognomic and two compositional variables were used as the Eco-geographic variables (EGV) in the model. The topographic variables were;

slope, aspect, elevation, distance from large seasonal rivers and distance from small seasonal drainage lines. The Normalised Difference Vegetation Index (NDVI) an index of vegetation cover was the physiognomic variable used. The compositional variables used were the interpolated values for tree species richness and hornbill fruit-tree species richness. The variables were selected based on field observations on the distribution pattern of the species. *Ficus rumphii* tended to occur in clumps along seasonal river beds. Most trees were found in the lower elevations and on relatively flat areas. There also appeared to be a distinct community affinity. The species was commonly encountered in the species rich mixed miscellaneous forest patches which also harboured a higher diversity of hornbill fruit tree species. The maps for the explanatory variables were prepared using ARC-GIS and Idrisi software.

3.3.2 Habitat characterisation

Hierarchical clustering was adopted to stratify the grids based on the vegetation community they harboured. The tree species encountered while sampling, were ranked based on their overall abundance within the study area. The species found within each grid were then assigned a score based on their representation in the sampling plots. If a species was encountered in all five sampling plots within the grids then it was assigned a score of 5 and if it was encountered only in one it was assigned a score of 1 and so on. These species scores for the top 14 most abundant species in the study area were used to cluster the grids. Only the top fourteen species were used because they were sufficient to differentiate between the broad vegetation classes found in the study area.

The individual grids were further characterised based on the following parameters

1) Average tree density

2) Tree species richness

3) Richness of hornbill fruit species (includes all potential hornbill fruit species)

4) Density of species that fruited during the study period.

3.3.3. Occupancy estimates

The presence-absence matrix generated over nine sampling sessions divided into winter (six sessions) and summer (three sessions) were analysed to obtain naïve (No of grids with presence/Total no of grids) and bias corrected occupancy estimates (MacKenzie et al. 2002). The analysis was done using software, Presence 2.0 applying a single season occupancy model (Hines 2006). The assumptions for a closed population which is central to the occupancy estimation is met by the fact that, the study is being conducted in the non breeding season and these birds are not known to range very widely. Oriental pied hornbills in Thailand had daily ranges of about 5-6 km^2 while Great hornbills daily ranges are about 7 km^2. The intensive study site is spread over nearly 60 km^2 with human habitations along two of its boundaries. An ingression of species from other areas is therefore unlikely, thus ensuring geographic closure. Even in the rare event of violation of the closure assumption, by ingression of individuals from adjoining populations, the results are unlikely to be confounded, since, the response variable is space use linked to fruit availability and not species abundance.

3.3.4. Hornbill responses to variation in fruit abundance

Hornbill responses to spatio-temporal variation in fruit abundances were tested at two spatial scales and temporal scales. The smaller of the two spatial scales in this study is defined by the individual grids which span entire fruiting patches. The larger of the two spatial scales refers to the different habitat types defined by the vegetation community they harbour. Based on the patterns in fruit availability the study period was divided into two temporal scales i.e. winter (December- February) and summer (February- April).

Response of hornbills to fruit abundance patterns at the smaller scale were discerned by testing for correlations (Zar 1999) between intensity of gird use by hornbills and fruit abundances in grids. Intensity of grid use implies, the total number of occasions on which hornbills were sighted over the entire sampling session. Occupancy estimates obtained for each forest type cluster were linked to fruit abundances by testing for statistical significance of differences in fruit abundance between the strata.

All analyses were performed using MS Excel 2003, SPSS 8 (SPSS Inc.) and ArcGIS 9.1. The variables used in the analysis were tested for normality and homoscedasticty. In situations where these conditions weren't met, necessary transformations were carried out.

4. RESULTS

4.1. Patterns in fruit availability

A total of 424 individual trees belonging to 5 species were marked for monitoring along 29 transects. Individuals of all of the target species except *Diospyros montana, Terminalia bellerica, Bridelia retusa* and figs were well represented along the transects. *Diospyros montana* and *Bridelia retusa* were rare and were never encountered in the phenology and vegetation plots. Only four individuals of *Terminalia bellerica* were recorded in all of the twenty nine transects while the three fig species together accounted for only five individuals.

Among the non-fig species, *Limonia acidissima* and *Phyllanthus emblica* fruited consistently for two months, with fruiting terminating towards the end of February. The few individuals of *Terminalia bellerica* too fruited for the same length of time. Opportunistic encounters of individuals of *Diospyros montana* revealed that this species too fruited during the initial part of the study period. Ripe non-fig fruit abundance was at its lowest in the month of March (Figure 3.), following which species such as *Ehrertia laevis* and *Diospyros melanoxylon* started fruiting. However these fruits did not ripen until the end of the study period and therefore have not been considered. Thus lean period in non-fig fruit availability essentially lasted from the end of February till the end of March.

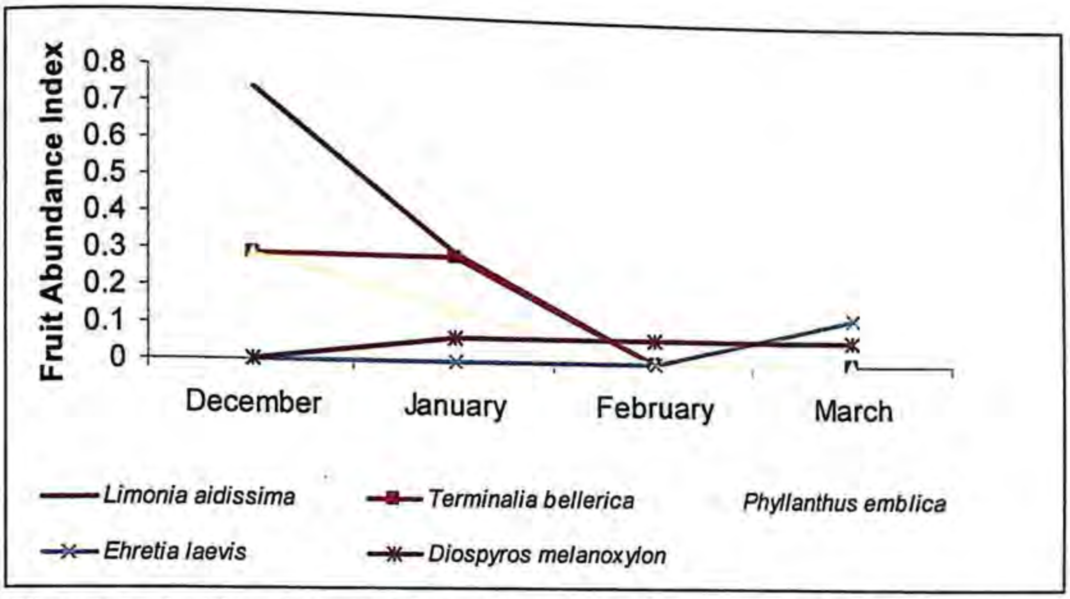

Figure 3. Fruiting patterns of non-fig species during the study period

The seasons were delineated on the basis of the trends in fruit availability as discerned from the phenology plots. Habitat wide non-fig fruit abundance was at its lowest at the end of February. Thus winter lasted from December to the end of February and summer from March onwards.

Due to difficulties in estimating fig fruit abundances for the area, an index for the same was derived based on Habitat Suitability Index model (ENFA). First five principal components which together explained 95.8% of the variation in the distribution of the species (Table 1.). The results indicate that *Ficus rumphii* occurring in the area have a moderate marginality and moderate tolerance (Table 2.), indicating certain habitat choice and low niche breadth. Generally, the species with high marginality and high specialisation would be expected to be habitat specialists. In the case of *Ficus rumphii*, it is not a staunch habitat specialist (Figure. 4).

Table 1. ENFA eigenvalues.

Factors	Value	Explained Specialisation	Cumulative Explained Specialisation
1	9.21	0.37	0.37
2	7.54	0.30	0.67
3	2.61	0.10	0.77
4	1.96	0.07	0.85
5	1.44	0.05	0.91
6	0.98	0.04	0.95
7	0.62	0.02	0.98
8	0.49	0.02	1

Table 2. Marginality, Specialisation and Tolerance values for *Ficus rumphii*

Marginality	Specialisation	Tolerance (1/S)
0.42	1.76	0.57

All of the selected EGV's contributed consistently in the prediction of *Ficus* occurrence. The first column in the score matrix (Table.3) is the marginality factor. Each component of the marginality factor expresses the marginality of the focal species on that eco-geographic variable. Distance from seasonal rivers, slope and elevation are important contributors to the prediction of the species presence. Marginality of the species was negatively affected by distance from seasonal rivers, seasonal streams, slope and elevation. Tree species richness had a mild positive effect on marginality. This essentially implies that, the model predicts low elevation, flat areas close to water sources as potential *Ficus rumphii* habitat. This is consistent with field observations too, for the species was invariably found along the banks of rivers on relatively flat ground. The remaining factors in the score matrix explain species specialisations on each eco-geographic variable. Higher the value of each component greater is the specialisation of the focal species with respect to that variable. Accounting for the five factors used in the analysis, it can be seen that elevation, distance form seasonal rivers and streams and tree species richness have a moderate impact on species specialisation values. These factors were used in the computation of the habitat suitability map which is a geographic representation of the probabilities of occurrence of *Ficus rumphii* in the area. Following this, mean probability values were extracted for each of the sampling grids and these were tested for correlations with the intensity of grid use by hornbills.

Table 3. ENFA score matrix.

	Factor1	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**
Aspect	0.11	0.15	0.38	0.15	-0.61
Elevation	-0.23	-0.93	0.45	-0.33	0.10
Distance from stream	-0.33	-0.00	-0.48	-0.26	-0.26
Fruit species richness	0.03	-0.14	0.11	0.39	0.17
NDVI	-0.25	-0.00	-0.03	-0.30	-0.36
Distance from seasonal rivers	-0.73	0.20	0.07	0.00	0.40
Slope	-0.34	0.12	-0.31	0.73	-0.42
Tree species richness	0.30	-0.12	-0.53	-0.05	0.17

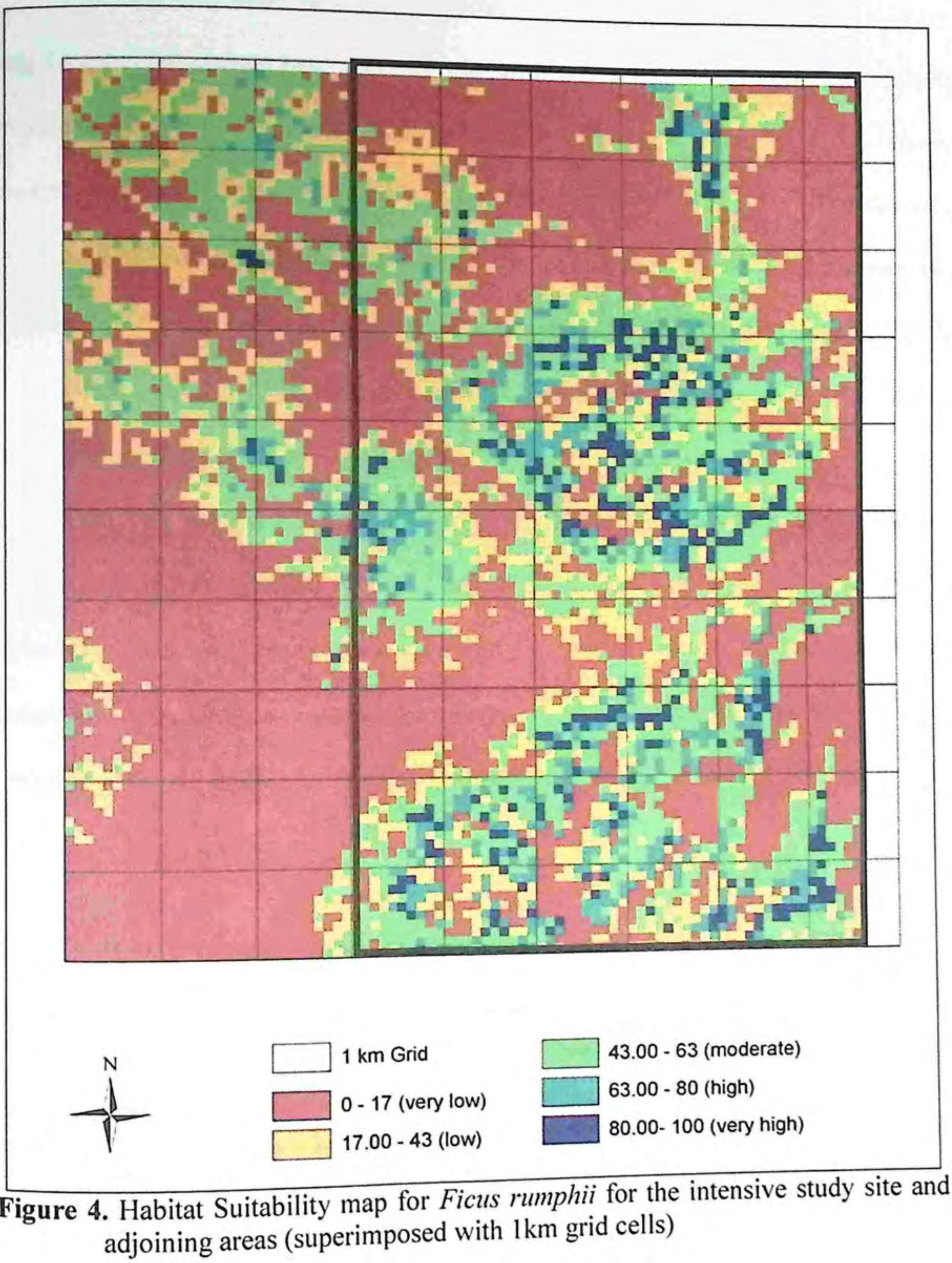

Figure 4. Habitat Suitability map for *Ficus rumphii* for the intensive study site and adjoining areas (superimposed with 1km grid cells)

4.2. Habitat types in the study area

The intensive study area was composed of a mosaic of forest types. However, using hierarchical cluster analysis on the 14 most dominant species (Table 4), broadly two vegetation communities were identified (Table 5, Figure 5). These are 1) Sal (*Shorea robusta*) dominated forest (SF) and 2) Miscellaneous forest (SF). The SF areas were composed predominantly of Sal and associated species such as *Terminalia tomentosa*, *Anogeissus latifolia*, *Casia fistula*, *Cordia dicotoma* and *Lagerstromia parviflora*. The MF areas, on the other hand were composed of a multitude of species with no particular species dominating.

Two small clusters comprising one grid each were also formed. These represent the *Tectona grandis* plantation patch and the *Trewia nudiflora- Jatropha quercus* community found along the Ganges respectively. Due to the inconsequential size of these clusters they were dropped from further analysis. The vegetation communities occurring in the four clusters together fairly represent the heterogeneity in forest types found within the intensive study area.

Table 4. Species used in Cluster analysis.

Species	Density/Ha	Rank
Malotus philippensis	46.68	1
Holorrhaena antidysentrica	22.25	2
Shorea robusta	19.07	3
Ehretia laevis	17.07	4
Cassia fistula	14.43	5
Limonia acidissima	9.21	6
Murraya koenigii	5.82	7
Anogeissus latifolia	4.75	8
Aegel marmelos	3.64	9
Trewia nudiflora	2.54	10
Syzigium cumini	2.25	11
Terminalia tomentosa	2.18	12
Jatropha quercus	1.79	13
Milusa velutina	0.71	14

Table 5. Habitat types in the study area

Cluster Id	No of Grids	Dominant vegetation community
SF (Sal & associated species forest)	16	*Shorea robusta-Malotus philippensis-Terminalia tomentosa*
MF (Mixed miscellaneous forest)	10	*Malotus philippinensis-Casia fistula-Ehretia laevis*
Tectona patch	1	*Tectona grandis* pure stand
Trewia patch	1	*Trewia nudiflora- Jatropha quercus*

Rescaled Distance Cluster Combine

```
 C A S E     0         5        10        15        20        25
 Label  Num  +---------+---------+---------+---------+---------+

          3   -+
          9   -+-+
         25   -+ +---+
          6   ---+   I
          4   -+---+ +---+
          7   -+   I I   I
          8   -----+-+   +---+
          5   -----+     I   I
         20   -+---------+   I
         24   -+             I
         10   -+-------+     I
         26   -+       +-----+-----+
         17   -----+---+     I     I
         23   -----+         I     +-+
         13   -------+-------+     I I
         15   -------+             I I
          2   ---------------------+ +-------------------------+
         18   -------------+---+     I                         I
         21   -------------+   I     I                         I
         16   -----+---+       +-----+                         I
         22   -----+   +-----+ I                               I
         19   ---------+     I I                               I
         11   ---+-+         +-+                               I
         12   ---+ +-+       I                                 I
         27   -----+ +---+   I                                 I
         14   -------+   +---+                                 I
         28   -----------+                                     I
          1   -------------------------------------------------+
```

Figure 5. Dendrogram of grid clusters using Average Linkage (Between Groups).

4.3. Habitat types w.r.t. fruit availability

The overall density of non fig species that fruited during the study period was significantly higher in the MF area ($t_{0.05(2),24} = -5.946$, $p<0.05$) (Figure 6).

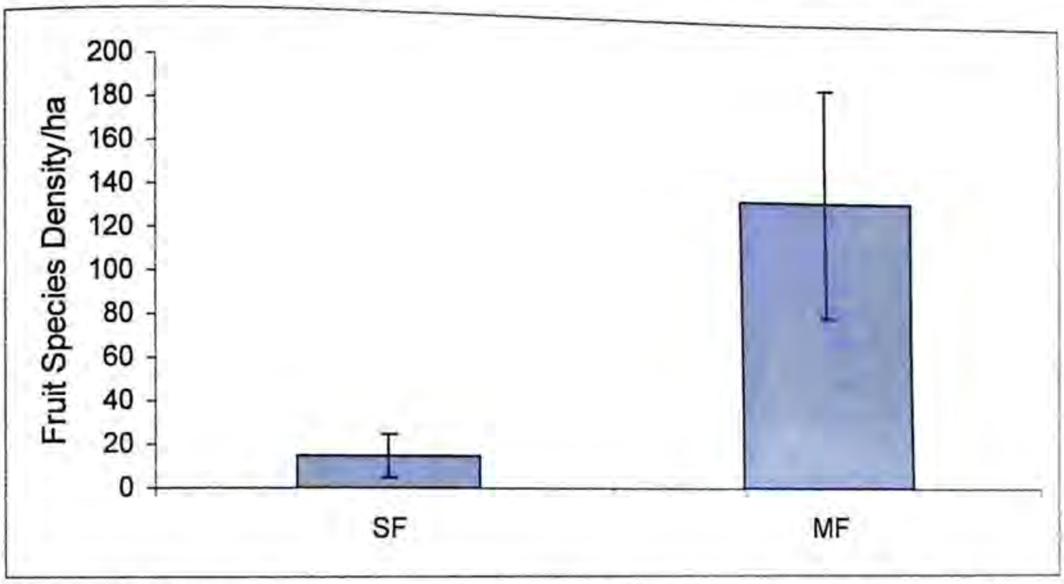

Figure 6. Differences in mean densities (± CI) of species that produced fleshy fruits during the study period.

A Man-Whitney U test revealed that the winter non-fig fruit abundance in the MF area was significantly higher than in SF ($U_{0.05\ (2),\ 24} = 41$,$p<0.05$). A non-parametric test was resorted to because the winter data set for SF was skewed with many zeros. There was no significant difference in non-fig fruit abundance in both areas during summer ($t_{0.05\ (2),\ 24} = -1.146$, $p= 0.263$) (Fig. 7). While within site fruit abundances in the SF areas remained consistently low across seasons, there was a variation in the MF areas and showed a significant drop in ripe non-fig fruit abundance in summer ($U_{0.05(2),\ 24}$=20, $p=$ 0.021).

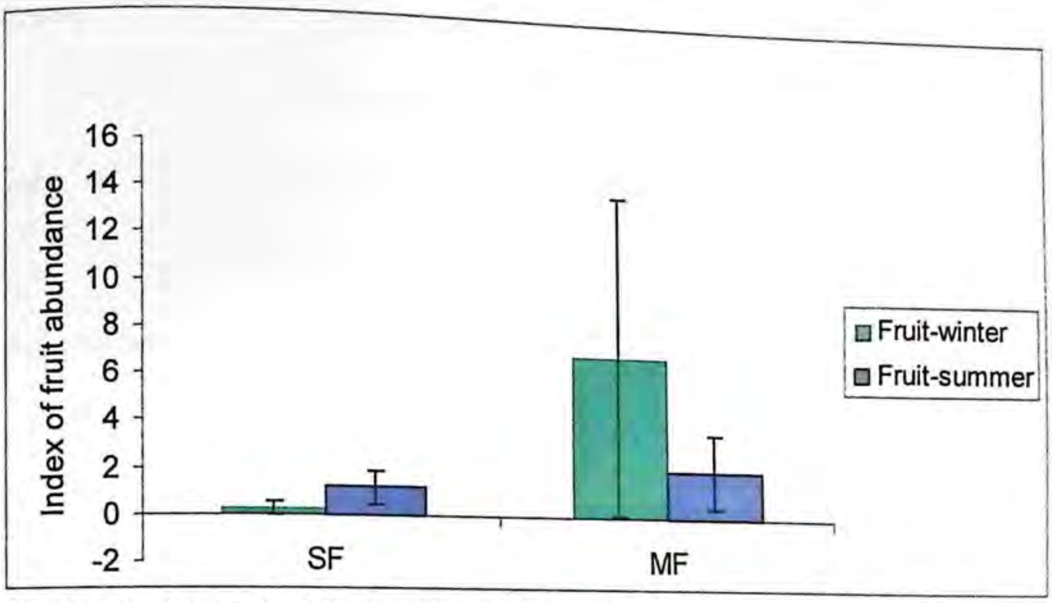

Figure 7. Mean (± CI) abundance of non-fig fruits in the two habitats types for winter and summer. Y axis represent fruit abundance indices.

The general trend in *Ficus rumphii* density was higher in the MF areas, although the mean probability of occurrence was not statistically different for the two areas ($t_{0.05\,(2).\,24}$ = -1.590, p= 0.125).

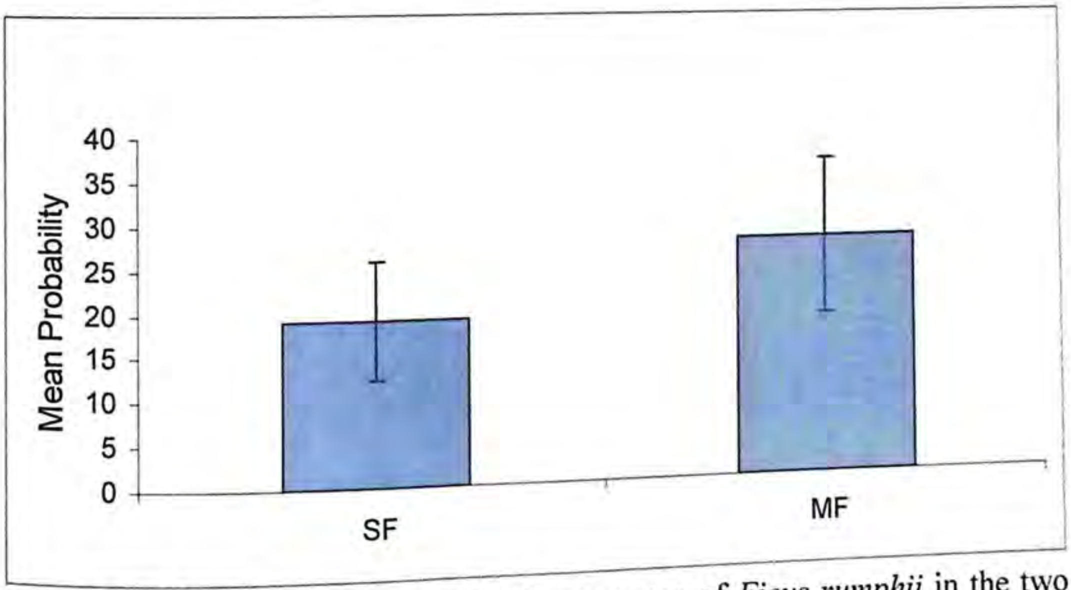

Figure 8. Mean probability (±CI) of occurrence of *Ficus rumphii* in the two habitat types. The probabilities for the individual grids were extracted from the

4.4 Patterns of space use by hornbills.

Naïve estimate for Oriental pied hornbills for both habitats in winter was 0.6 (60% of the grids) and in summer, 50% of the grids in MF and 30% grids in SF were occupied. Although the naive estimates were similar for these two different habitats, bias corrected estimate indicate that in both seasons the MF areas were used at a substantially higher proportion by the species (Table 6, Figure 9). Given the detection probability being same for these two habitats, the occupancy value clearly relate to variation in the intensity of space use by the hornbill in these habitats.

Table 6. Occupancy patterns for Oriental pied hornbill

Cluster	Occupancy(winter)	Detection probability	Occupancy(summer)	Detection probability
MF	0.64 (0.17)	0.36 (0.08)	0.72 (0.31)	0.31 (0.16)
SF	*	0.12 (0.03)	0.32 (0.16)	0.38 (0.18)

*- The occupancy was too low to be computed. Error values are mentioned in the parenthesis.

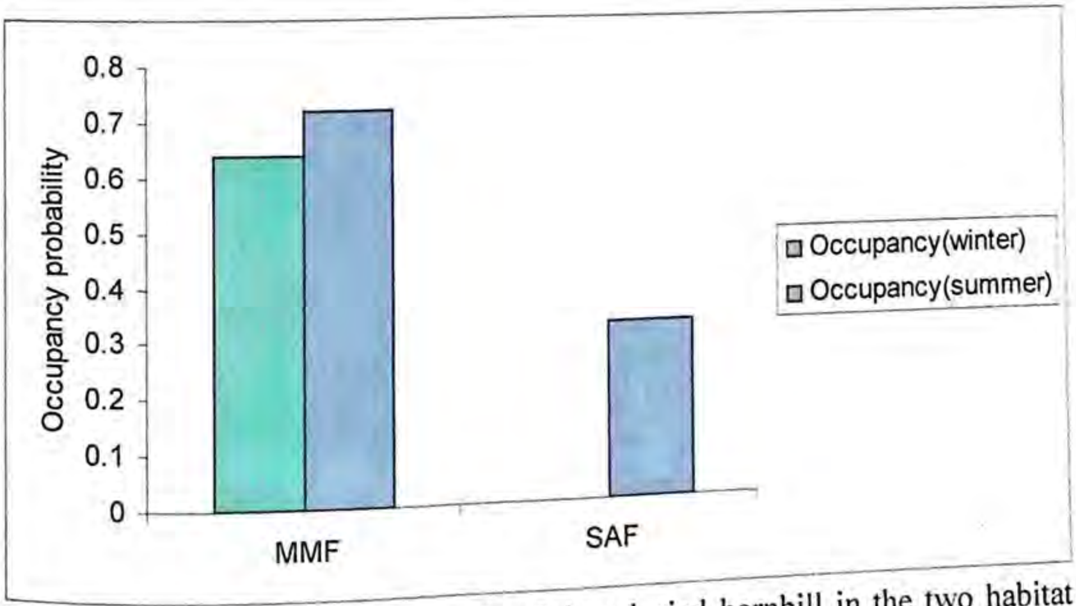

Figure 9. Occupancy estimates for Oriental pied hornbill in the two habitat types for winter and summer.

Occupancy estimates for Indian grey hornbill yielded spurious results due to very low positive values. Naïve (0.4) and bias corrected occupancy estimate (0.6) for Great hornbill could be computed only for winter (Table 7). It was rarely seen in SF in both seasons and in summer it was absent from the MF areas too.

Table 7. Occupancy patterns for Great hornbill

Cluster	Occupancy(winter)	Detection probability	Occupancy(summer)	Detection probability
MF	0.60 (0.31)	0.16	*	0.06
SF	*		*	*

*- The occupancy was too low to be computed. Error values mentioned in the parenthesis

4.5. Intensity of space use by hornbills and fruit abundance patterns

The intensity of space use by Oriental pied hornbills at patch level in winter was found to be significantly correlated to abundance of non-fig fruits (r=0.5, p= 0.01). In summer the intensity of grid use was significantly correlated to the mean probability of occurrence of *Ficus rumphii* after controlling for density of fruit tree species (r= 0.31, p= 0.08) (Table 8). However, the significance is relevant only at the 90 % confidence level. The significance level for this step was relaxed under the premise that the Habitat Suitability model has potentially overestimated probabilities in certain grids of the SF cluster. No significant correlations were obtained between intensity of grid use with structural and compositional attributes such as tree density and tree species richness, indicating the choice is linked to factors other than these. Interestingly, fruit tree species richness and density of species that fruited did not correlate with hornbill space use pattern, suggesting that hornbills visited only those areas where fruits where actually present in good abundance.

For the available data in winter, none of the variables were significantly related to space use patterns by Great hornbills.

Table 8. Factors correlated with intensity of grid use by Oriental pied hornbills

	Non-fig fruit abundance	Mean probability of *Ficus rumphii* presence	Tree density	Tree species richness
Intensity of grid use by Oriental pieds hornbill (winter)	R= 0.482 (p<0.05)	Not significant (p>0.1)	Not significant (p>0.1)	Not significant (p>0.1)
Intensity of grid use by Oriental pieds hornbill (summer)	Not significan (p>0.1)	R= 0.307 (p< 0.1)	Not significant (p>0.1)	Not significant (p>0.1)

4.6. Resource partitioning among the three hornbill species

Instances of feeding were recorded for the three species during occupancy sampling and also opportunistically. All three species of hornbills in the area were extremely shy and observations on feeding were few. Hence no conclusive results were obtained on interspecific variation in resource use. However, presented below is a list of fruits the three hornbill species were seen feeding on;

Table 9. Fruit species consumed by the three hornbill species

	Great Hornbill	Oriental Pied Hornbill	Indian Grey Hornbill
Limonia acidissima	-	+(n=7)	+(n=3)
Terminalia bellerica	+(n=5)	+(n=3)	-
Diospyros montana	-	+(n=2)	-
Phyllanthus emblica	-	-	-
Bridelia retusa	-	+(n=2)	-
Ficus rumphii	+(n=7)	+(n=13)	+(n=16)

\+ Birds seen feeding on the species

\- Birds never seen feeding on the species.

n Number of observations.

5. DISCUSSION

5.1 Spatio-temporal variation in fruit abundance

Non-fig fruit availability fluctuated dramatically through the course of the study. Ripe, non-fig fruit availability lasted from early December to late February. The winter fruit abundance was highest in the MF areas. However, even within this forest type there was considerable patchiness in fruit availability (Figure 7). The summer fruit abundance is both areas comprised predominantly of the raw fruits of *Diospyros melanoxylon* and *Ehretia laevis.* Six non-fig species fruited during this period, however, only three of them namely, *Limonia acidissima*, *Phyllanthus emblica* and *Terminalia bellerica* were common enough to significantly contribute to the overall fruit abundance. *Limonoia acidissima* is a small statured tree producing small berries. As a result, fruits of this species were potentially available only to Oriental pied and Indian grey hornbills. The other two species; *Bridelia retusa* and *Diospyros montana* were very rare in the study area. Oriental pied hornbills were seen harvesting fruits of all of the five species while Great hornbills were observed feeding only on *Terminalia bellerica.* Feeding observations on Indian grey hornbills were few in the initial months of the study period. However, they were seen harvesting the fruits of only L*imonia acidissima* (Table 9). Tropical dry forests are known to be more seasonal than wet evergreen forests and tend to experience greater fluctuations in resource abundance. However, these results bring a whole new perspective to the idea of resource scarcities in hornbill habitats. Datta & Rawat (2003) reported 41 non fig food species in the diet of hornbills during the non-breeding season, which also coincides with the period of resource scarcity in those areas.

This is in stark contrast to what was observed in the present study site where individuals of only 5 non-fig species and one fig species were observed producing ripe fruits.

Figs are known to fruit in an aseasonal and asynchronous manner. Of the four fig species found in the area, *Ficus rumphii* was the only fig species that bore fruit consistently during the course of the study. The species was widespread but typically occurred in clumps along stream courses. While the species itself fruited in a staggered manner, there seemed to be some sort of within clump synchrony in fruiting. Following the drop in the non-fig fruit production in late February, only *Ficus rumphii* was observed fruiting. The species potentially played a vital role during the period of non-fig resource scarcity. Through February and March, a majority of the opportunistic feeding records for all three hornbill species were on *Ficus rumphii. Ficus bengalensis* too fruited sporadically; however, the individuals of this species were not as abundant.

Figs, despite their poor nutritional quality are indispensable to the sustenance of frugivores communities (Lambert 1989). Myriad studies have shown the contribution of figs to the diet of hornbills. Figs contribute significantly to the diet of Great hornbill (Datta & Rawat 2003; Kannan & James 1999). In the present study too, majority of the opportunistic feeding observations for great hornbills were on figs. Hornbills in the north east are known to consume fruits of at least seven fig species (Datta & Rawat 2003). In Sulawesi Red knobbed hornbill abundances in an area were found to be controlled by fig fruit abundances (Renton 2001). In Chilla Range, during the course of this study, *Ficus rumphii* potentially played the role of a keystone. Whether this is a one off event, or, the species consistently assumes this role across years can be known only through continued phenology monitoring in the area.

5.2. Space use by Oriental pied hornbills

Whether intensity of space use by hornbills is a linear function of fruit abundances and fruit tree densities was tested across two spatial scales over two seasons. The occupancy estimates for oriental pied hornbills reveal that they used Miscellaneous forest (MF) area almost exclusively during winter. The use of the MF and SF areas went up significantly in summer. Comparisons of the two sites revealed, that they differed significantly only in their mean winter non-fig fruit abundances and mean densities of fruit species. It may therefore be speculated that, across the two forest types, hornbill use of space in winter was governed by abundances of non-fig fruits. The increased occupancy estimates for both sites, in summer, is possibly due to the fact that birds were tracking *Ficus rumphii* fruit production. The fig species occurs in a patchy manner across both forest types with the MF area potentially harbouring them in higher densities. Due to its patchy distribution, harvesting this resource would require increased ranging on the part of hornbills. Besides this, summer also marked the beginning of the Oriental pied breeding season, as courtship displays were seen between pairs. During the breeding, season flocks are known to break up and pairs of birds forage independently (Kemp 1995). Space use in this season may also be partly governed by the need to find suitable nesting sites.

The responses to fruit availability at the scale of the fruit patch (grid) were corroborated by the correlation values. Grid use in winter was strongly correlated with the non-fig fruit abundance and in summer with the mean probability of occurrence of *Ficus rumphi.* A higher probability of occurrence of *Ficus rumphii* trees also implies a higher probability of availability of fig fruits since, the species does not show synchronous fruiting. The results also suggest that space use in both seasons were not governed by non-transient variables such as tree species density, fruit tree species richness, overall tree species richness and density of species that fruited during the study period.

Oriental pied hornbills seem to have tracked fruit resources consistently across two spatial scales. In winter the birds foraged in the MF areas which had higher overall fruit abundance and within this area they seem to have selected more productive patches. In summer too space use patterns were consistent with distribution of *Ficus rumphii* at both spatial scales.

Oriental pied hornbills are also known to practice dietary switching. In the north-east, the diet of this species in the non-breeding season also comprises of a small percentage of invertebrates (Datta 2001). The contribution of invertebrates to the diet of hornbills is likely to be higher in Chilla owing to the low diversity and density of fruit species. Thus in both seasons space use may also have been partially influenced by the abundance distribution of arthropods in the area.

These results are in concordance with other studies where birds responded positively to fluctuations in resource abundance across spatial scales (Cotton 2007; Levey 1988; Marsden & Pilgrim 2003; Renton 2001; Rey 1995; Saracco et al 2004). Jordano (1994) demonstrated, frugivore assemblages successfully tracking changes in the productivity of an understorey shrub species across and within habitat patches. In another study, birds successfully tracked the abundance of fruits in olive orchards across multiple spatial scales (Rey 1995). In both these studies, the bird species in question had the ability to range over large areas and also the tendency to flock. These birds could track resources at large spatial scales possibly because, flocks of wide ranging birds are better able to detect and respond to landscape level cues (Garcia & Oritz –Pulido 2004). Studies on *Ceratogymna* hornbills have shown that the species is capable of showing large scale migrations between habitats in response to fluctuations in fruit abundances (Whitney & Smith 1998). Oriental pied hornbills are not known to range very far (Datta 2001). However these conclusions are again based on the populations residing in comparatively less seasonal forests. The population in the study area responded to spatial fluctuations in fruit abundances through increased local movements. Whether this trend holds at landscape and regional levels can only be known from further investigations.

The occupancy patterns for Great hornbills were queer, in that, the species was rarely sighted post winter. The winter sightings were mostly confined to particular areas where they were invariably seen foraging on the fruits of *Ficus rumphii*. Their disappearance from the area can potentially be explained by the fact that they are known to be early breeders and require trees with big girth classes for nesting (Datta 2001). In the study area, trees of such dimensions are commonly available on the slopes of the outer Himalayan range. The birds potentially were using these areas in summer. Intensity of grid use by Great hornbills in winter did not correlate significantly with non-fig fruit abundances. This was expected because, species such as *Limmonia acidissima* which contributed most prominently to fruit abundance is a small sized berry occurring on medium sized trees which cannot be easily harvested by Great hornbills. These birds rely heavily on figs (Kannan & James 1999). However, fig fruit abundance also did not correlate significantly with the space use patterns of the species in both seasons. This may have been because of the low densities in which the species occurs in this area.

Grey hornbills were infrequently sighted during the early part of the study period. Sightings, however, improved considerably towards the end of the study. In both seasons the detections were too low to enable investigations into factors controlling the space use for this species.

Resource scarcities rarely become severe enough to result in large scale mortalities of vertebrates (van Schaik *et al.*1993). However, seasonal resource scarcities are a reality that most species have to contend with. Organisms, over an evolutionary time scale have acquired the ability to circumvent this predicament. In this study, Oriental pied hornbills responded to changes in fruit abundance by altering ranging patterns. Across their distributional range, Oriental pied hornbills occupy and flourish in a variety of habitats, which vary in their proclivity for resource fluctuation. The ability of these birds to closely track resources through alterations in ranging patterns and diet are probably what enables them to persist in these diverse habitat types.

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APPENDIX

List of Tree species that were expected to fruit between the months of December and April (Kanjilal & Gupta, rep. 1994).

S.No.	Species	Family
1	*Acacia catechu*	Mimosaseae
2	*Anogeissus latifolia*	Combretaceae
3	*Bauhunia vahlii*	Caesalpinnieceae
4	*Bischofia javanica*	Euphorbiaceae
4	*Cassia fistula*	Caesalpinnieceae
5	*Dalbergia sissoo*	Papilionaceae
6	*Ehretia laevis* *	Boraginaceae
7	*Embelica officinalis* *	Euphorbiaceae
8	*Ficus bengalensis* *	Moraceae
9	*Ficus cunia* *	Moraceae
10	*Ficus glomerata* *	Moraceae
11	*Ficus rumphii* *	Moraceae
12	*Haldina cordifolia*	Rubiaceae
13	*Helicteres isora*	Sterculiaceae
14	*Holarrhena antidysenterica*	Apocynacae
15	*Jatropha curcas*	Euphorbiaceae
16	*Kydia calycina*	Malvaceae
17	*Limonia acidissima* *	Rutaceae
18	*Millettia auriculata*	Papilionaceae
19	*Murraya koenigii* *	Rutaceae
20	*Murraya panniculata* *	Rutaceae
21	*Sapium sebiferum* *	Urticaceae
22	*Stereospermum suaveolens*	Bignoniaceae
23	*Tectona grandis*	Verbenaceae
24	*Terminalia alata*	Combretaceae
25	*Terminalia belerica* *	Combretaceae
26	*Trewia nudiflora*	Euphorbiaceae
27	*Zizyphus mauritiana*	Rhamnaceae
28	*Zizyphus xylopyra*	Rhamnaceae

* Potential hornbill food plants in the dry season.