Foraging Patterns of Birds in Resource Partitioning in Tropical Mixed Dry Deciduous Forest, India

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Abstract: A study was undertaken in the tropical mixed dry deciduous forest of India. Direct observation on foraging of birds was made on twelve days in a month within four hours after sunrise with direct observation. For each foraging attempt microhabitat details such as the foraging height, substrate, method, canopy and the plant species were recorded. Vegetation profile consisted of tree species from 2 to 6m and shrubs from 0 to 1m height. In total, 3982 foraging observations were made on 36 bird species. A higher percentage of foraging manoeuvre was recorded at 3-6m height. 29 bird species were gleaner. Majority of the canopy layers used for foraging of bird species were edge edge (23%) followed by ground (18%) and middle lower (17%). Grey Jungle Fowl, Vernal Hanging Parrot and Red-rumped Swallow are specialists. The highest mean niche overlap among the species was found in method followed by canopy and height. The two major guilds are gleaner and sallier.

Keywords: Foraging Method, Foraging Substrate, Foraging Canopy, Foraging Height, Guild, Niche Overlap, Resource Partitioning, Tropical Mixed Dry Deciduous Forest

1. Introduction

Birds prefer some specific habitats and coexist as guilds with the available pattern of food resources [1]. Guild segregates themselves into specific ecological niches by adopting foraging behaviour and differs in microhabitat use and foraging tactics [2]. The foraging tactics include various methods to exploit the resources. Insectivore birds exhibit different methods of exploiting resources such as gleaning, sallying, probing, pouncing and hawking [3], [4], [5].

Although resource partitioning has been well documented for bird species from temperate forests [3], [6], [7], no such studies are available in India except the study of Gokula and Vijayan [5] in the dry deciduous forest of Mudumalai Wildlife Sanctuary. Moreover, knowledge of the ways in which birds exploit resources within a forest will increase the understanding of their habitat use and the essential requirements for their survival. The following objectives were set to analyse the patterns of feeding behavior, method of feeding and microhabitat use by birds in the mixed dry deciduous forest.

2. Study Area

The study was undertaken in the tropical mixed dry deciduous forest of Anaikatty hills [8], the foothills of the Nilgiri in the Nilgiri Biosphere Reserve, Western Ghats, India situated at an elevation of about 610-1200m above MSL between 76° 39' and 76° 47'E and from 11° 5' to 11° 31'N in Coimbatore, TamilNadu, Southern India. The climate is moderate and pleasant for most part of the year except summer which is relatively hot and dry.

Based on the climate, four different seasons were observed as follows. *Southwest monsoon (June, July and August):* The study area received 5% of the total annual rainfall during this season. The mean rainfall received was around 40 mm. *Northeast monsoon (September, October and November):* The study area received more than half (69%) of the total annual rainfall during this season. The mean rainfall received was around 500 mm.

Winter (December, January and February): It was the least rainy period of the year with the annual rainfall of 34 mm. This season was the colder period with the minimum

temperature falling to 18°C. *Summer (March, April and May)*: This area received 21% of the annual rainfall in this season from the pre-monsoon showers. This was the period of maximum temperature, which leaped up to 37°C with low relative humidity.

Temperature varied between 18°C and 37°C and Relative humidity showed fluctuation in different seasons between 31% - 75% at 08:30 hrs. and 72% - 89% at 17:30 hrs. Monthly windspeed varied between 3 and 14 km/h. The tropical mixed dry deciduous forest, India has the major tree community of *Acacia leucophloea*, *Ziziphus mauritiana*, *Chloroxylon swietenia*, *Albizia amara*, *Tamarindus indicus*, *Albizia lebbeck*, *Acacia polyacantha*, *Diospyros ferrea*, *Cassia fistula* and *Commiphora caudata*. Major shrubs are *Chromolaena odorata*, *Elaeodendron glaucum*, *Pavetta indica*, *Lantana camara*, *Randia dumetorum*, *Premna tomentosa*, *Flacourtia indica* and *Mundulea sericea*.

3. Materials and Methods

Foraging records of birds were made during May 1999 to May 2001 on twelve days in a month from the tropical mixed dry deciduous forest, India. Most of the observations were done within four hours after sunrise. This is the most active foraging time for birds [9]. Only initial record was taken from any individual encountered as done by MacNally [7] to provide precise estimate of foraging location rather than that of the subsequent ones [10].

Table 1. Definition of foraging activities used to assess guild structure of avifauna.

Foraging method	Sub categories
Sally	Above canopy-sally
	Below canopy-sally
	Herb-sally
	Shrub-sally
	Sally (sally to the ground)
	Flower-glean
Glean	Fruit-gleaning
	Ground-gleaning
	Litter-gleaning
	Main trunk-gleaning
	Secondary branch-gleaning
	Twig-glean
Pounce	Leaf-glean
	Ground-pounce
	Ground-probing
Probing	Litter-probing
	Main trunk-probing
	Secondary branch-probing
Tear	Leaf-tear
Hover	Hovering/aerial capture

For each foraging attempt microhabitat details such as the foraging height, substrate, method, canopy and the plant species at which the prey was found were recorded. *Foraging attempts* were assigned to 12 height categories. A *substrate* is the place from where food is taken by birds in 7 different areas. *Foraging methods* of birds were categorized as, *Glean*, *Probe*, *Sally* or *fly catching* and *Pounce*, To cluster the species

on a micro level, these methods were classified further into finer levels based on the substrate, which is given in Table 1 and described by Crome [3] and expanded by Holmes *et al.*, [4], Ramsen and Robinson [11] and MacNally [12].

The *canopy layers* used by the bird species were classified into ten layers and were possibly distinguished from three layers namely lower canopy, middle canopy and upper/edge canopy (Figure 1). Lower canopy was further distinguished as lower center, lower middle and lower edge. Middle canopy was classified further into middle center, middle middle and middle edge. c). Upper/edge canopy was classified as edge center, edge middle and edge edge. d). Birds, which do not use plant at all for its prey was grouped under ground/air/under canopy.

Figure 1. Diagrammatic Representation of the Canopy Layers of a Plant.

As thirty independent observations are recommended to represent the behavior of a bird accurately [13], species with more than 30 observations were taken for analysis.

4. Statistical Analysis

4.1. Specialist-Index J'

The foraging specialization of each foraging parameter (method, substrate, height and canopy) was analyzed using the Shannon-Weaver [14] index. These values were then converted to a standardized range using the formula $J' = H'/H_{\max}$ (Where J' = specialization and $H_{\max}$ = the maximum H' value) following Crome [3] and Recher *et al.* [6]. J' value ranges between one and zero, with foraging specialization increases as J' decreases.

4.2. Niche Overlap

The extent to which resource use overlaps between species pairs is niche overlap. The degree of species overlap in niche utilization for the different categories recorded (foraging method, substrate, canopy and foraging height) has been quantitatively expressed using Horn's index [15].

4.3. Cluster Analysis

To compare foraging behavior (substrate, height, canopy use and method adopted) by various species, cluster analyses were performed on a data matrix (species * characteristics), following Holmes *et al.* [4]. This analysis used the

unweighted pair group clustering method with arithmetic averages (UPGMA) and Squared Euclidean Distance [16], [17]. The SPSS statistical software [18] was used for the data analyses.

5. Results

In total, 3982 foraging observations were made on 36 species in the tropical mixed dry deciduous forest, India (Table 2).

Table 2. Number of foraging records on each bird species observed in the tropical mixed dry deciduous forest during 1999-2001.

S. No	Common name of the species	Scientific name	Family	Number of foraging observations
1	GREY JUNGLEFOWL	Gallus sonneratii	Phasianidae	94
2	INDIAN PEAFOWL	Pavo cristatus	Phasianidae	36
3	BLOSSOM-HEADED PARAKEET	Psittacula roseate	Psittacidae	45
4	MALABAR PARAKEET	Psittacula columboides	Psittacidae	225
5	VERNAL HANGING PARROT	Loriculus vernalis	Psittacidae	53
6	BLUE-FACED MALKOHA	Phaenicophaeus viridirostris	Cuculidae	74
7	GREEN BEE-EATER	Merops orientalis	Meropidae	42
8	CHESTNUT-HEADED BEE-EATER	Merops leschenaultia	Meropidae	56
9	COMMON HOOPOE	Upupa epops	Upupidae	35
10	BROWN-HEADED BARBET	Megalaima zylanica	Capitonidae	31
11	STREAK-THROATED WOODPECKER	Picus xanthopygaeus	Picidae	28
12	PALE-BILLED FLOWERPECKER	Dicaeum erythrorhynchus	Picidae	124
13	RED-RUMPED SWALLOW	Hirundo daurica	Hirundinidae	49
14	RED-WHISKERED BULBUL	Pycnonotus jocosus	Pycnonotidae	84
15	RED-VENTED BULBUL	Pycnonotus cafer	Pycnonotidae	102
16	WHITE-BROWED BULBUL	Pycnonotus luteolus	Pycnonotidae	333
17	BLACK BULBUL	Hypsipetes leucocephalus	Pycnonotidae	74
18	COMMON IORA	Aegithina typhia	Irenidae	368
19	BLUE-WINGED LAFBIRD	Chloropsis cochinchinensis	Irenidae	115
20	TAWNY-BELLIED BABBLER	Dumetia hyperythra	Muscicapidae	125
21	JUNGLE BABBLER	Turdoides striatus	Muscicapidae	240
22	YELLOW-BILLED BABBLER	Turdoides affinis	Muscicapidae	189
23	BLYTH'S REED WARBLER	Phylloscopus reguloides	Muscicapidae	128
24	COMMON TAILORBIRD	Orthotomus sutorius	Muscicapidae	40
25	GREENISH WARBLER	Phylloscopus trochiloides	Muscicapidae	159
26	LARGE-BILLED LEAF WARBLER	Phylloscopus magnirostris	Muscicapidae	147
27	ASIAN PARADISE FLYCATCHER	Terpsiphone paradise	Muscicapidae	82
28	PLAIN FLOWERPECKER	Dicaeum concolor	Dicaeidae	74
29	PURPLE-RUMPED SUNBIRD	Nectarinia zeylonica	Nectariniidae	361
30	LOTEN'S SUNBIRD	Nectarinia lotenia	Nectariniidae	90
31	PURPLE SUNBIRD	Nectarinia asiatica	Nectariniidae	57
32	JUNGLE MYNA	Acridotheres fuscus	Sturnidae	72
33	BLACK-HODED ORIOLE	Oriolus xanthornus	Oriolidae	41
34	BLACK DRONGO	Dicrurus macrocercus	Dicruridae	73
35	ASHY DRONGO	Dicrurus leucophaeus	Dicruridae	33
36	WHITE-BELLIED DRONGO	Dicrurus caerulescens	Dicruridae	103
	Total			3982

Nomenclature following Grimmette *et al.* (1998)

5.1. Foraging Height

All the 12 height categories were utilized by 36 bird species in the tropical mixed dry deciduous forest, India (Table 3). Although most species fed over a broad range of heights, they were grouped according to the layer of vegetation in which the majority of their foraging was recorded. Foliage was partitioned as three layers of strata; ground (0m), shrub/short trees (0.1-3), and tree layers (>3).

In the community as a whole, a higher percentage of foraging manoeuvre were recorded in the layers of 3-6m height.

Six species foraged mainly at ground level. Among them, Grey Junglefowl absolutely used the ground layer while Jungle Myna, Yellow-billed Babbler, Indian Peafowl, Common Hoopoe, and Jungle Babbler showed variety in their height preference.

The 0.1-3m height category of shrub and short tree layers

were utilized by Blossom-headed Parakeet, Tawny-bellied Babbler, Loten's Sunbird, Common Tailorbird, Red-vented Bulbul, White-browed Bulbul, Blyth's Reed Warbler, Purple-rumped Sunbird and Asian Paradise Flycatcher.

The tree layer (>3m) was used by 21 bird species. Within the tree layers, higher percentage of foraging manoeuvre was recorded in the 3-6m height category. All the foraging attacks of the Ashy Drongo, Large-billed Leaf Warbler, Black Drongo, Vernal Hanging Parrot and Red-rumped Swallow were at >6m height. For the foraging community as a whole in the tropical mixed dry deciduous forest, a higher number of foraging manoeuvres was recorded in the tree layers (>3m height).

5.2. Foraging Substrate

Majority of the bird species used foliage (24 bird species) followed by twigs (22 bird species) as their substrate (Table 4). Only 11 species used ground and flower to find their food.

The ground-foraging guild was with five species viz. Jungle Babbler, Grey Jungle fowl, Indian Peafowl, Common Hoopoe and Yellow-billed Babbler.

Streak-throated Woodpecker and Black-Hooded Oriole largely obtained their prey from the trunk. In addition to this substrate, these birds also used twigs and fruits. Five bird species such as Blyth's Reed Warbler, Bluewinged Leafbird, Plain Flowerpecker, Black Bulbul and Large-billed Leaf Warbler used this substrate. Blue-faced Malkoha, Greenish Warbler, Tawny-bellied Babbler, Common Tailorbird and Common Iora used exclusively twigs as substrate (Table 4). Only Vernal Hanging Parrot alone used flower as its substrate while Parakeets used fruit predominantly with a little overlap of flower. Other species such as Bulbuls and Large Green Barbet used this substrate and also other substrates for their prey. Red-rumped Swallow obtained its prey exclusively from air. Drongos predominantly used air for their prey and in addition, they also used foliage to a lesser extent.

Table 3. Percentage of prey attacks by different species of birds at various height categories in the tropical mixed dry deciduous forest, India.

Name of the bird species	Foraging heights (m)												H'
	0	0.1-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	>10	
Grey junglefowl	100	0	0	0	0	0	0	0	0	0	0	0	0.0
Common hoopoe	91	0	0	3	0	0	3	3	0	0	0	0	1.9
Yellow-billed babbler	97	2	0	0	0	0	1	0	0	0	0	0	0.4
Jungle babbler	81	6	4	4	1	1	2	0	0	0	0	0	0.7
Indian peafowl	77	23	0	0	0	0	0	0	0	0	0	0	1.5
Jungle myna	39	19	0	0	0	0	21	3	18	0	0	0	1.5
Blossom-headed parakeet	0	88	0	0	0	0	0	0	0	0	2	9	0.3
Tawny-bellied babbler	0	72	24	4	0	0	0	0	0	0	0	0	0.7
Loten's sunbird	0	44	11	2	8	19	8	6	2	0	0	0	1.7
Common tailorbird	0	48	30	10	8	5	0	0	0	0	0	0	0.9
Red-vented bulbul	0	40	15	6	14	1	4	5	1	3	0	12	1.8
White-browed bulbul	2	16	30	22	17	12	1	1	1	0	0	0	0.9
Blyth's reed warbler	0	27	30	18	15	8	2	0	0	0	1	0	1.5
Purple-rumped sunbird	0	22	18	9	14	16	11	6	3	1	1	1	0.9
Asian paradise flycatcher	0	18	26	45	5	5	1	0	0	0	0	0	1.4
Brown-headed barbet	0	0	6	29	10	6	19	16	10	0	0	3	2.3
Black bulbul	0	0	0	26	0	3	38	24	0	0	9	0	1.5
Red-whiskered bulbul	0	14	19	24	8	12	12	7	1	1	1	0	2.2
Streak-throated woodpecker	0	0	7	21	57	0	11	0	4	0	0	0	0.3
Green bee-eater	0	19	0	0	52	7	0	0	0	0	0	21	0.7
Malabar parakeet	0	3	2	3	32	28	12	4	7	3	4	3	1.2
Blue-winged leafbird	0	0	0	5	30	39	17	5	2	1	1	0	1.4
Purple sunbird	0	5	23	2	19	7	28	0	11	0	5	0	2.2
Pale-billed flowerpecker	0	4	9	10	27	16	21	4	3	3	3	1	1.9
Common iora	0	3	13	17	22	17	15	7	2	0	2	2	0.9
Blue-faced malkoha	19	14	3	5	20	23	8	4	0	3	0	1	2.3
Greenish warbler	0	0	1	8	16	25	18	6	16	3	2	7	1.5
Plain flowerpecker	0	0	8	14	15	42	13	0	8	0	0	0	1.8
Black-hooded oriole	0	0	0	0	10	51	17	7	2	2	0	10	1.4
White-bellied drongo	4	1	0	1	13	22	14	17	12	10	4	4	2.1
Chestnut-headed bee-eater	2	5	7	2	2	16	16	13	13	0	2	23	2.7
Ashy drongo	0	0	0	0	3	15	30	15	3	0	18	15	1.9
Large-billed leaf warbler	0	1	6	12	19	28	22	7	3	2	1	0	1.5
Black drongo	8	3	1	3	4	0	21	10	22	3	7	19	2.4
Vernal hanging parrot	0	0	0	0	2	0	2	2	34	8	53	0	0.9
Red-rumped swallow	0	0	0	2	0	29	0	0	0	0	59	10	0.6

Table 4. Percentage use of various foraging substrates by different species of birds in the tropical mixed dry deciduous forest, India.

Name of the bird species	Ground	Trunk	Foliage	Twigs	Flower	Fruit	Air
ASHY DRONGO	0	0	0	0	24	0	76
BLACK BULBUL	0	1	45	49	0	5	0
BLACK DRONGO	0	0	1	0	0	0	97
BLACK-HOODED ORIOLE	0	66	0	32	0	2	0
BLOSSOM-HEADED PARAKEET	0	0	0	0	7	93	0
BLYTH'S REED WARBLER	0	0	56	44	0	0	0
MALABAR PARAKEET	0	0	0	0	2	98	0
BLUE-FACED MALKOHA	24	8	9	35	0	23	0
GREY JUNGLEFOWL	97	0	3	0	0	0	0
BLUE-WINGED LEAFBIRD	0	0	56	17	20	8	0
COMMON HOOPOE	91	6	0	3	0	0	0
COMMON IORA	0	0	27	72	0	0	0
JUNGLE BABBLER	81	2	0	17	0	0	0
JUNGLE MYNA	39	3	0	0	53	6	0
LARGE-BILLED LEAF WARBLER	0	0	90	10	0	0	0
BROWN-HEADED BARBET	0	6	6	0	0	87	0
VERNAL HANGING PARROT	0	0	0	0	100	0	0
LOTEN'S SUNBIRD	0	0	0	6	93	1	0
STREAK-THROATED WOODPECKER	0	93	0	7	0	0	0
PLAIN FLOWERPECKER	0	0	46	40	14	0	0
INDIAN PEAFOWL	74	0	3	0	0	23	0
ASIAN PARADISE FLYCATCHER	0	0	12	0	0	0	88
GREENISH WARBLER	0	9	27	64	0	0	0
PURPLE-RUMPED SUNBIRD	0	0	5	7	87	1	0
PURPLE SUNBIRD	0	7	16	4	74	0	0
TAWNY-BELLIED BABBLER	0	0	14	85	0	1	0
RED-RUMPED SWALLOW	0	0	0	0	0	0	100
RED-VENTED BULBUL	2	12	4	12	0	71	0
RED-WHISKERED BULBUL	1	4	1	24	0	70	0
GREEN BEE-EATER	0	0	21	0	0	0	79
COMMON TAILORBIRD	3	0	35	58	0	5	0
PALE-BILLED FLOWERPECKER	0	0	15	21	64	0	0
WHITE-BROWED BULBUL	2	0	1	15	0	77	5
WHITE-BELLIED DRONGO	0	0	2	0	0	0	98
YELLOW-BILLED BABBLER	97	0	1	2	0	0	0
CHESTNUT-HEADED BEE-EATER	0	0	13	0	0	0	88
Substrate preference by Number of Bird Species	11	12	24	22	11	16	8

Table 5. Percentage of prey attack manoeuvres by different bird species in the tropical mixed dry deciduous forest, India.

Name of the Bird Species	Glean	hover	Pounce	Probe	Sally
BLACK BULBUL	100	0	0	0	0
BLACK-HOODED ORIOLE	83	0	17	0	0
BLOSSOM-HEADED PARAKEET	100	0	0	0	0
BLYTH'S REED WARBLER	100	0	0	0	0
MALABAR PARAKEET	100	0	0	0	0
BLUE-FACED MALKOHA	99	0	0	1	0
GREY JUNGLEFOWL	95	0	0	5	0
BLUE-WINGED LEAFBIRD	100	0	0	0	0
COMMON HOOPOE	74	0	0	26	0
COMMON IORA	100	0	0	0	0
JUNGLE BABBLER	100	0	0	0	0
JUNGLE MYNA	97	0	0	3	0
LARGE-BILLED LEAF WARBLER	100	0	0	0	0
BROWN-HEADED BARBET	100	0	0	0	0
VERNAL HANGING PARROT	100	0	0	0	0
LOTEN'S SUNBIRD	100	0	0	0	0
STREAK-THROATED WOODPECKER	71	0	0	29	0
PLAIN FLOWERPECKER	100	0	0	0	0
INDIAN PEAFOWL	67	0	0	33	0
GREENISH WARBLER	100	0	0	0	0
PURPLE-RUMPED SUNBIRD	100	0	0	0	0
PURPLE SUNBIRD	100	0	0	0	0
TAWNY-BELLIED BABBLER	100	0	0	0	0
RED-VENTED BULBUL	99	0	1	0	0
RED-WHISKERED BULBUL	100	0	0	0	0

Name of the Bird Species	Glean	hover	Pounce	Probe	Sally
COMMON TAILORBIRD	100	0	0	0	0
PALE-BILLED FLOWERPECKER	100	0	0	0	0
WHITE-BROWED BULBUL	95	0	0	0	5
YELLOW-BILLED BABBler	100	0	0	0	0
RED-RUMPED SWALLOW	0	100	0	0	0
ASHY DRONGO	24	0	0	0	76
BLACK DRONGO	0	0	0	0	100
ASIAN PARADISE FLYCATCHER	0	0	0	0	100
GREEN BEE-EATER	0	0	0	0	100
WHITE-BELLIED DRONGO	0	0	0	0	100
CHESTNUT-HEADED BEE-EATER	0	0	0	0	100

5.3. Foraging Methods

Birds such as gleaner (88%), sallier (10%), prober (1%), pouncer and hoverer (1%) were recorded from this forest (Table 5). Twenty-nine species were recorded as gleaner, of which 24 species predominantly used (100%) gleaning. Six species such as Asian Paradise Flycatcher, White-bellied Drongo, Green Bee-eater, Black Drongo, Ashy Drongo and Chestnut-headed Bee-eater used sallying to obtain their prey. Except Ashy Drongo, all other birds of this guild used sally as the only prey attacking manoeuvre. Red-rumped Swallow was recognized as hoverer or aerial capture, which used this method alone as the prey-attacking manoeuvre.

Prey attack manoeuvre by gleaners: Since gleaning formed the major method adopted by the birds of tropical mixed dry deciduous forest, India, it's usage was further bifurcated into eight types (Table 6). In total, gleaning of flower (21%), fruit (21%) and twig (21%) formed 63% of gleaning. Gleaning on

ground (18%) and leaf (11%) was comparatively less, while on trunk (4%) and stem (4%) it was very little.

Flower Gleaning: Six species exploited the flowers by gleaning for nectar. Vernal Hanging Parrot alone used only this method for feeding. Loten's Sunbird, Purple-rumped Sunbird and Purple Sunbird used this method predominantly while Pale-Billed Flowerpecker and Jungle Myna used this method frequently (Table 6). *Fruit Gleaning:* Malabar Parakeet, Blossom-headed Parakeet frequently used this method along with flower gleaning. Brown-headed Barbet, White-browed Bulbul, Red-vented Bulbul and Red-whiskered Bulbul also used this method along with other methods. *Ground Gleaning:* Yellow-billed (White-headed) Babbler, Grey Junglefowl, Jungle Babbler, Indian Peafowl and Common Hoopoe formed the ground gleaner to get their prey from ground and overlap with litter gleaning.

Table 6. Percentage of Prey Attack Manoeuvres by different types of Gleaner Bird Species in the Tropical Mixed Dry Deciduous Forest, India.

Name of the bird species	Flower Gleaner	Fruit Gleaner	Ground Gleaner	Leaf Gleaner	Litter Gleaner	Trunk Gleaner	Stem Gleaner	Twig Gleaner
LARGE-BILLED LEAF WARBLER	0	0	0	90	0	0	0	10
BLYTH'S REED WARBLER	0	0	0	56	0	0	0	44
STREAK-THROATED WOODPECKER	0	0	0	0	0	65	25	10
COMMON IORA	0	0	0	28	0	0	0	72
GREENISH WARBLER	0	0	0	27	0	0	9	64
COMMON HOOPUE	0	0	46	0	46	4	0	4
JUNGLE BABBler	0	0	55	0	26	0	2	17
GREY JUNGLEFOWL	0	0	74	3	22	0	0	0
TAWNY-BELLIED BABBler	0	1	0	14	0	0	0	85
BLACK-HOODED ORIOLE	0	3	0	0	0	9	50	38
COMMON TAILORBIRD	0	5	3	35	0	0	0	58
BLUE-FACED MALKOHA	0	23	7	10	16	0	8	36
BLACK BULBUL	0	32	0	0	0	0	2	66
INDIAN PEAFOWL	0	33	54	4	8	0	0	0
RED-WHISKERED BULBUL	0	70	1	1	0	0	4	24
RED-VENTED BULBUL	0	71	1	4	0	0	12	12
BROWN-HEADED BARBET	0	87	0	6	0	0	6	0
YELLOW-BILLED BABBler	1	0	93	1	4	0	0	2
WHITE-BROWED BULBUL	1	81	2	1	0	0	0	16
MALABAR PARAKEET	2	98	0	0	0	0	0	0
BLOSSOM-HEADED PARAKEET	11	89	0	0	0	0	0	0
PLAIN FLOWERPECKER	16	0	0	45	0	0	0	39
JUNGLE MYNA	54	6	40	0	0	0	0	0
PALE-BILLED FLOWERPECKER	67	0	0	14	0	0	0	19
PURPLE SUNBIRD	74	0	0	16	0	0	7	4
PURPLE-RUMPED SUNBIRD	88	0	0	5	0	0	0	7
LOTEN'S SUNBIRD	93	1	0	0	0	0	0	6
VERNAL HANGING PARROT	100	0	0	0	0	0	0	0

Leaf Gleaning: Large-billed Leaf Warbler, Blyth's Reed Warbler and Plain Flowerpecker used this method with twig and flower gleaning.

Trunk Gleaning: Streak-throated Woodpecker alone used this type of feeding along with gleaning on stem and twig.

Stem Gleaning: Black-hooded Oriole was the only bird species, which used this method. This species also used fruit, trunk and twig as substrate for collecting food.

Twig Gleaning: Common Iora, Greenish Warbler, Tawnybellied Babbler, Black Bulbul, Common Tailorbird and Blue-faced Malkoha were recognized as twig gleaners (Table 6).

5.4. Position in the Canopy

Majority of the canopy layers used for foraging of bird species were edge edge (23%) followed by ground (18%) and middle lower (17%). Five major canopy layers out of 10 categories were distinctly used by 36 bird species in the tropical mixed dry deciduous forest, India. The major canopy positions foraged were Edge edge, center middle, center edge, middle edge and the birds used ground or air also (Table 7).

5.4.1. Ground/Air (Under/over Canopy)

Bird species such as Grey Junglefowl, Red-rumped Swallow, Yellow-billed Babbler, Common Hoopoe, Jungle Babbler, Indian Peafowl, Green Bee-eater, Jungle Myna, Chestnut-headed Bee-Eater and Blue-faced Malkoha occupied this for its prey. Grey Junglefowl and Red-rumped Swallow depend only on these strata and the other bird species extends overlap with other layers in the canopy (Table 7).

5.4.2. Center Center (Lower Canopy)

Bird species perched on the middle main axis of the plant canopy were Streak-throated Woodpecker, Black-hooded Oriole and Tawny-bellied Babbler. They also feed on the edge edge and middle middle canopy. No species was restricted to any particular layer alone.

5.4.3. Middle Edge (Middle Canopy)

Bird species feeding on the upper canopy was White-bellied Drongo which feeds on the upper and middle canopy. *Center edge (upper canopy):* Birds perched for preying over the upper canopy was Common Tailorbird. *Edge edge (upper canopy):* Twenty-one bird species (Table 7) were feeding on the upper canopy of the plant. Asian Paradise flycatcher and Common Tailorbird exploited food from other canopies too.

5.5. Specialists

Among the four dimensions, number of specialists ($J'=0$) was more in the substrates (2) method (2) and canopy (1) followed by height (Table 8). Grey Jungle Fowl, Vernal Hanging Parrot and Red-rumped Swallow are specialists as their J' values were zero. On the contrary, generalists were Blue-faced Malkoha, Common Tailorbird and Chestnut-headed Bee-eater (Table 8).

5.6. Niche Overlap

Niche overlap was calculated with foraging height (12 categories), foraging manoeuvre (20 categories), canopy (10 categories) and foraging substrate (7 categories). Among the foraging dimensions the highest mean niche overlap among the species was found in method (White-browed Bulbul) followed by canopy, height and the lowest in foraging method (Redrumped Swallow).

Height: Blue-faced Malkoha and Purple-rumped Sunbird had the highest mean niche overlap (0.75) while the lowest (0.36) was found in Yellow-billed Babbler (Table 9). *Method:* The mean niche overlap in feeding method was highest in the White-browed Bulbul (0.83) and lowest (0.14) in the Red-rumped Swallow (Table 9). *Canopy:* The highest mean niche overlap was found in Brown-headed Barbet (0.82) and lowest was in Yellow-billed Babbler (0.42). *Substrate:* The highest mean niche overlap was in Common Tailorbird (0.63) and the lowest was in Yellow-billed Babbler (Table 9).

Table 7. Percentage of Ten Foraging Canopy Layers preferred by different bird species in the Tropical Mixed Dry Deciduous Forest, India.

Name of the bird species	Ground/ Air	Centre lower	Centre middle	Centre edge	Middle lower	Middle middle	Middle edge	Edge lower	Edge middle	Edge edge
GREY JUNGLEFOWL	100	0	0	0	0	0	0	0	0	0
STREAK-THROATED WOODPECKER	0	7	75	0	0	11	0	0	7	0
RED-RUMPED SWALLOW	100	0	0	0	0	0	0	0	0	0
JUNGLE BABBLER	81	2	4	0	0	10	0	0	2	1
INDIAN PEA FOWL	77	0	0	0	0	0	0	6	6	11
GREEN BEE-EATER	71	0	0	0	0	2	0	0	0	26
YELLOW-BILLED BABBLER	97	0	2	0	0	0	1	1	0	1
ASHY DRONGO	18	0	0	0	0	15	3	9	21	33
ASIAN PARADISE FLYCATCHER	9	2	9	1	10	10	4	16	18	22
BLUE-WINGED LEAFBIRD	0	0	0	1	0	3	10	0	40	46
BLACK-HOODED ORIOLE	0	2	56	2	0	27	0	2	0	10
COMMON HOPOE	91	0	0	3	0	0	0	0	6	0
LARGE-BILLED LEAF WARBLER	0	0	2	3	0	16	15	6	29	29
BLACK DRONGO	10	1	5	4	0	3	5	8	23	40
TAWNY-BELLIED BABBLER	0	3	32	4	1	14	7	0	10	30
WHITE-BELLIED DRONGO	11	0	1	4	0	10	17	4	29	25
BLUE-FACED MALKOHA	24	0	20	5	0	23	5	3	7	12

Name of the bird species	Ground/ Air	Centre lower	Centre middle	Centre edge	Middle lower	Middle middle	Middle edge	Edge lower	Edge middle	Edge edge
JUNGLE MYNA	39	0	0	7	1	8	11	0	28	6
BLYTH'S REED WARBLER	0	0	5	7	2	16	16	5	17	31
GREENISH WARBLER	0	0	8	8	0	17	10	3	31	23
PALE-BILLED FLOWERPECKER	0	0	2	10	0	9	21	3	11	45
RED-WHISKERED BULBUL	1	0	7	11	1	2	19	6	13	39
BLOSSOM-HEADED PARAKEET	0	0	0	12	0	0	21	0	0	67
COMMON IORA	0	0	4	13	1	18	10	3	20	31
PLAIN FLOWERPECKER	0	0	4	14	0	7	6	1	19	49
WHITE-BROWED BULBUL	2	0	5	17	0	10	8	1	16	40
MALABAR PARAKEET	0	0	4	18	0	0	9	0	9	59
LOTEN'S SUNBIRD	0	0	1	18	0	4	11	0	10	56
PURPLE SUNBIRD	0	0	5	18	2	11	12	4	23	26
BROWN-HEADED BARBET	0	0	3	19	0	10	16	3	13	35
PURPLE-RUMPED SUNBIRD	0	0	1	22	1	2	11	4	11	49
COMMON TAILORBIRD	3	5	15	23	5	5	8	8	13	18
CHESTNUT-HEADED BEE-EATER	29	0	0	25	0	0	11	5	25	5
RED-VENTED BULBUL	2	0	4	26	0	1	10	1	9	47
VERNAL HANGING PARROT	0	0	2	26	0	0	32	2	4	34
BLACK BULBUL	0	0	0	35	0	19	9	1	0	35
Total	765	22	276	356	712	283	318	105	470	981
Total in %	18	1	6	8	17	7	7	2	11	23

Table 8. Extent of specialization (J') by different bird species in foraging substrate, foraging canopy, foraging method and foraging height in the tropical mixed dry deciduous forest, India (J' values range from 0.01 and specialization increases as J' decreases; Specialists are indicated in bold numbers).

Name of the bird species	Foraging Substrate J'	Foraging Canopy J'	Foraging Method J'	Foraging Height J'
GREY JUNGLEFOWL	0.09	0.00	0.52	0.00
INDIAN PEA FOWL	0.45	0.37	0.89	0.56
BLOSSOM-HEADED PARAKEET	0.17	0.40	0.15	0.11
MALABAR PARAKEET	0.06	0.58	0.05	0.44
VERNAL HANGING PARROT	0.00	0.64	0.00	0.33
BLUE-FACED MALKOHA	1.00	0.88	1.00	0.85
CHESTNUT-HEADED BEE-EATER	0.26	0.75	0.65	1.00
GREEN BEE-EATER	0.35	0.32	0.41	0.26
COMMON HOOPOE	0.24	0.17	0.92	0.70
STREAK-THROATED WOODPECKER	0.18	0.39	0.22	0.11
REDRUMPED SWALLOW	0.00	0.00	0.00	0.22
BLACK-HOODED ORIOLE	0.49	0.56	0.78	0.52
BLACK DRONGO	0.05	0.82	0.72	0.89
ASHY DRONGO	0.37	0.76	0.68	0.71
WHITE-BELLIED DRONGO	0.06	0.83	0.74	0.78
JUNGLE MYNA	0.66	0.75	0.57	0.56
COMMON IORA	0.41	0.84	0.37	0.33
BLUE-WINGED LEAFBIRD	0.78	0.52	0.68	0.52
RED-WHISKERED BULBUL	0.55	0.82	0.49	0.81
RED-VENTED BULBUL	0.64	0.68	0.58	0.67
WHITE-BROWED BULBUL	0.51	0.79	0.45	0.33
BLACK BULBUL	0.63	0.63	0.56	0.54
TAWNY-BELLIED BABBLER	0.31	0.80	0.28	0.26
JUNGLE BABBLER	0.39	0.35	0.64	0.26
YELLOW-BILLED BABBLER	0.09	0.08	0.17	0.15
ASIAN PARADISE FLYCATCHER	0.25	0.98	0.62	0.52
COMMON TAILORBIRD	0.63	1.00	0.56	0.33
BLYTH'S REED WARBLER	0.47	0.21	0.41	0.54
LARGE-BILLED LEAF WARBLER	0.22	0.78	0.20	0.56
GREENISH WARBLER	0.59	0.82	0.51	0.56
BROWN-HEADED BARBET	0.32	0.80	0.28	0.85
PALE-BILLED FLOWERPECKER	0.61	0.73	0.54	0.70
PLAIN FLOWERPECKER	0.67	0.70	0.60	0.67
PURPLE-RUMPED SUNBIRD	0.33	0.68	0.28	0.33
LOTEN'S SUNBIRD	0.19	0.60	0.16	0.63
PURPLE SUNBIRD	0.55	0.86	0.49	0.81
Number of specialists	2	2	2	1
Number of generalist	1	1	1	1

Table 9. Mean niche overlap for different bird species in foraging height, foraging substrate, foraging canopy and foraging method in the tropical mixed dry deciduous forest, India (niche overlap ranges from 0.01 and high niche overlap is indicated in bold numbers).

Name of the Bird species	Niche overlap				
	Foraging Height	Foraging Substrate	Foraging Canopy	Foraging Method	All dimensions
ASHY DRONGO	0.68	0.54	0.80	0.56	0.67
BLACK BULBUL	0.59	0.58	0.71	0.82	0.63
BLACK DRONGO	0.66	0.43	0.81	0.26	0.63
BLACK-HOODED ORIOLE	0.69	0.54	0.61	0.77	0.61
BLOSSOM-HEADED PARAKEET	0.54	0.51	0.73	0.82	0.59
BLYTH'S REED WARBLER	0.66	0.51	0.79	0.82	0.65
MALABAR PARAKEET	0.71	0.36	0.72	0.82	0.59
BLUE-FACED MALKOHA	0.75	0.61	0.76	0.82	0.70
GREY JUNGLEFOWL	0.38	0.42	0.43	0.82	0.41
BLUE-WINGED LEAFBIRD	0.66	0.57	0.71	0.81	0.64
COMMON HOPOE	0.53	0.52	0.58	0.75	0.54
COMMON IORA	0.73	0.45	0.78	0.82	0.65
JUNGLE BABBLER	0.51	0.42	0.53	0.82	0.48
JUNGLE MYNA	0.61	0.50	0.73	0.82	0.61
LARGE-BILLED LEAF WARBLER	0.71	0.44	0.76	0.82	0.63
BROWN-HEADED BARBET	0.73	0.55	0.82	0.82	0.69
VERNAL HANGING PARROT	0.49	0.46	0.74	0.82	0.56
LOTEN'S SUNBIRD	0.70	0.46	0.76	0.82	0.64
STREAK-THROATED WOODPECKER	0.70	0.51	0.57	0.74	0.59
PLAIN FLOWERPECKER	0.70	0.59	0.79	0.82	0.69
INDIAN PEA FOWL	0.56	0.55	0.65	0.73	0.59
ASIAN PARADISE FLYCATCHER	0.63	0.43	0.77	0.26	0.60
GREENISH WARBLER	0.69	0.51	0.77	0.82	0.65
PURPLE-RUMPED SUNBIRD	0.75	0.42	0.74	0.82	0.63
PURPLE SUNBIRD	0.72	0.54	0.80	0.82	0.68
TAWNY-BELLIED BABBLER	0.49	0.51	0.73	0.82	0.57
REDRUMPED SWALLOW	0.53	0.36	0.49	0.14	0.46
RED-VENTED BULBUL	0.68	0.52	0.77	0.82	0.65
RED-WHISKERED BULBUL	0.74	0.54	0.80	0.82	0.69
GREEN BEE-EATER	0.64	0.47	0.66	0.26	0.59
COMMON TAILORBIRD	0.68	0.63	0.78	0.82	0.69
PALE-BILLED FLOWERPECKER	0.74	0.54	0.78	0.82	0.68
WHITE-BROWED BULBUL	0.66	0.47	0.80	0.83	0.64
WHITE-BELLIED DRONGO	0.69	0.40	0.80	0.27	0.63
YELLOW-BILLED BABBLER	0.36	0.35	0.42	0.82	0.38
CHESTNUT-HEADED BEE-EATER	0.71	0.47	0.73	0.26	0.63

All dimensions: All the dimensions together when combined, Yellow-billed Babbler showed the lowest overlap (0.38) and Blue-faced Malkoha (0.70) showed the highest overlap among the 36 species (Table 9).

5.7. Foraging Guilds

Species were separated into a number of distinct groups whose members exploit food resources from similar substrates or height using similar methods and thereby considered as guilds. The guild formed in the tropical mixed dry deciduous forest, India based on the use of substrates, methods, canopy and height, their relationships among the 36 bird species are summarized in the cluster diagram (Figure 2). Two distinct major guilds (gleaner and sallier) were

arbitrarily recognized from the cluster diagram (Figure 2). The gleaner was further consisted of three distinct guilds based on the substrates of gleaning, namely 1. Fruit, 2. Flower, 3. Ground and 4. Stem (trunk and twigs).

Guild I consisted of birds that glean their prey on fruit (Frugivore). Guild II consisted of birds that glean their food from the flower (Nectarivore). The guild III consisted of birds that largely obtained their food mainly insects or other invertebrates from all strata (ground, plant and air) (Figure 2). Within this guild, two major groups were obvious such as purely insectivore and omnivore. This was bifurcated again into five groups based on the substrates: ground, twigs and leaf, main trunk and air.

Figure 2. Dendrogram showing interspecific relationships of 36 bird species based on multivariate analyses of foraging method, substrate and height use in the tropical mixed dry deciduous forest, India.

Based on the observational data, birds foraged in similar ways or exploited the same resources for foods were grouped in a schematic representation (Figure 3). The schematic portrayal of the groupings relies on the foraging behavior, foraging height, canopy and foraging substrate differences to associate species. Of the 36 species, major group of birds was of insectivores, which comprised of 24 bird species followed by nectarivores such as Vernal Hanging Parrot, Loten's Sunbird, Purple-rumped Sunbird, Pale-billed Flowerpecker and Jungle Myna. Frugivore guild comprised of (fruit, flower, insect and grain feeder) Red-whiskered Bulbul, Red-vented Bulbul, White-browed Bulbul, Malabar Parakeet, Brown-headed Barbet and Blossom-headed Parakeet. Insectivores largely obtain their food from plants or from air

by sally (Red-rumped Swallow). Among the plant forms, the number of species, which obtained their food from twig and leaf were more than that depending on other substrates such as main trunk and secondary branches. Six bird species sallying from four different positions in the canopy were distinguished as insectivore's viz. Chestnut-headed Bee-eater, White-bellied Drongo, Ashy Drongo, Paradise Flycatcher and Green Bee-eater (Figure 3). Other insectivores guild, feeding from plants were Streak-throated Woodpecker, Black-hooded Oriole, Tawny-bellied Babbler, Common Tailorbird, Common Iora, Greenish Warbler, Blyth's Reed Warbler, Blue-winged Leafbird, Plain Flowerpecker, Large-billed Leaf Warbler and Blue-faced Malkoha.

Figure 3. Schematic diagram of foraging guild of birds in the tropical mixed dry deciduous forest India.

5.8. Plant Community in the Tropical Mixed Dry Deciduous Forest

Vegetation profile of mixed dry deciduous forest consisted mostly of tree species of 2-6m height (Figure 4) and the upper stratum was thinned out with a few tall trees such as *Ficus* sp., *Tamarindus indica*, *Acacia polyacantha*, *Albizia*

amara, *Canthium dicoccum*, *Celtis philippensis* and *Commiphora caudata*. Shrubs formed the lower stratum at 0-2m. and it occupied a predominant place from ground to 1m height in mixed dry deciduous forest. Moreover the number of shrub species are higher (45) than the tree species (27). Higher foliage profile layers harbour more bird species [19] was true in this habitat as studied by [20].

Figure 4. Vegetation profile of mixed dry deciduous forest.

6. Discussion

Tree layers found to be a distinctive foraging environment for birds in the tropical mixed dry deciduous forest, India followed by shrubs/short tree layers due to the availability of high foliage layer in the trees and more foliage overlap between short trees and shrubs. Successful foraging by avian predators is influenced largely by prey availability, which encompasses not only the density of prey but also its vulnerability to capture [21]. An interesting observation was this forest comprised of two guilds namely gleaners and salliers. Feeding methods are more specialised in each species. Species generalised in feeding tend to vary in feeding technique, substrate choice, canopy and height when the type of food varies. Yet another interesting observation was large scale utilization of layers at different height such as 0.1-2m and 3-6m. This might perhaps be due to the foliage of majority of the trees in the tropical mixed dry deciduous forest of India are spread between 3-6m height which formed the upper stratum and shrubs of 0-2m height formed the lower stratum and that gives more opportunity to birds for exploitation. Moreover the number of shrub species are higher than the tree species. The availability of various plant forms such as shrubs, short trees and trees in these habitats not only increases the vertical and horizontal foliage layering and complexity, but also provides many supporting substrates. So majority of birds in this habitat used these strata for foraging. Foraging birds require a large number of small preys to maintain resting metabolic rates [22]. Information on the foraging height, attack maneuvers; substrate and foliage density was collected independently for each foraging bird [23].

Three major substrates namely ground, plant and air were recognized. Of which, more bird species fell under the plant guild because plant offers a great variety of microhabitats (trunk, branches, twigs, foliage, flower and fruit) to find their suitable and favourable food. Foliage and twigs were utilized by more number of birds because branches with leaves offer a great variety of places to find food along with concealment. Moreover most of the trees in this habitat withered their dryleaves and emerging of new leaves tookplace during winter, thus increasing the opportunity of searching and finding their prey or vicinity of the prey

becomes more. In total, bird species used 12 methods to obtain food from the tropical mixed dry deciduous forest of India. Searching patterns are largely a function of the morphological and perceptual traits of each species, which allow the birds to move through the foliage to locate, detect and capture prey in specific ways. Similar study was reported in thorn forest [5] of Mudumalai Wildlife Sanctuary, India. Information on the foraging height, attack maneuvers; substrate and foliage density was collected independently for each foraging bird [23].

The availability of diverse food items may vary between habitats [20] and hence birds that feed on variety of foods (e.g., insects, seed, nectar and fruit) may change their manoeuvre according to the habitat. Moreover, changes in the foraging manoeuvres may be a strategy to avoid competition. Hence it is likely that the combination of factors such as availability of food, habitat structure and interspecific competition are responsible for the variations in the foraging behaviour of birds observed in this forest. Predation of two adult birds was recorded during the study period. Also, predation of fledglings of almost all the breeding birds was observed. Interspecific competition also can alter foraging behavior of Warblers and Babblers [24], [25], [26]. Thus, changes in the foraging manoeuvre may be a strategy to avoid competition. Hence, it is likely that the combination of factors such as availability of food, habitat structure and interspecific competition are responsible for the changes. Foraging behavior and foraging success of the reddish egret were studied by [27] focusing on whether their foraging behavior or success varied with age, color morph, group size and habitat measures.

In this study, closely related species used the same basic foraging method indicating the importance of phylogeny in determining the feeding patterns of birds [28], [4]. Resource partitioning reduces the effect of competition by decreasing the amount of overlap between the competing species [2]. Partitioning of foraging dimensions among birds could occur in this habitat as reported earlier for bird communities of various places and habitats [6], [29], [5], [20]. Foraging behavior and foraging success of the reddish egret were studied by [27] focusing on whether their foraging behavior or success varied with age, color morph, group size and habitat measures.

Many species fed from different strata and positions in the canopy overlapping with others where specialists such as the Yellow-billed Babbler fed by only gleaning and that too from ground thus sharing high specialization or preference and thus having very little overlap with other species. When food availability is high they feed on the outer part of tree canopies in this study as found by Diaz *et al.* [30] in Tits. Birds selected foraging sites with a higher mean prey density than at random sites [31].

Some species of water birds have been found to forage at the interface of open water and vegetation [32], [33], [34].

Bird species evolved with specialization for a particular type of habitat or substrate or prey that resulted in a specialist for a particular habitat. Greenberg [35], [36] investigated

Warblers' response to different substrate and inferred that the species that had a diverse foraging behavior were conservative in their use of substrates. Thus it can be inferred that niche overlap can be attributed to the availability of food resources, morphology of species and competition as suggested by Alatalo [24], Rolando and Robotti [37], Szekely [38] and Gokula and Vijayan [5]. Successful foraging by avian predators is influenced largely by prey availability, which encompasses not only the density of prey but also its vulnerability to capture [21].

7. Conclusion

Foraging data were collected early in the morning during the study period. In total, 36 species were observed from the mixed dry deciduous forest. Various foraging dimensions such as method, substrate, height and position in the canopy were analyzed. Foraging attempts were assigned to 12 height categories, seven substrate categories, 9 positions in the canopy and 20 foraging methods. Thirteen species shared change in the use of substrate while only five species changed the method used. Five bird species were considered as specialists as their J' values were zero. In four dimensions highest mean niche overlap is found in the use of foraging height. There are two major guilds, namely gleaners and salliers and gleaners are grouped into four major guilds. There are four major groupings among the bird species based on the food eaten such as insectivores, nectarivores, frugivores and omnivores. The plant (shrubs and trees) surface provides microhabitats such as foliage, twig, flower, fruit, secondary branches and trunk and the proportion of foliage use at different heights is higher. Specialization of species and their niche overlap with others are analysed. Foraging method is specialized being constrained by morphology in many species while substrates and strata are used opportunistically depending on the environment.

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