

Foraging pattern of birds during the breeding season in thorn forest of Mudumalai wildlife sanctuary, Tamil Nadu, Southern India

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Abstract: Foraging pattern of birds in thorn forest was studied in Mudumalai Wildlife Sanctuary in 1995 and 1996 during January to April (dry spell) as most of the birds start breeding during this period, demands for energy are greatest and birds spend most of their time in foraging. This study examines the foraging pattern of birds in a 10 ha plot laid in the thorn forest. Information on foraging height, substrate, and method was collected. In total, 1386 observations were made on the above said three dimension for 33 species of birds. Cluster analysis of these three dimension shows that the most important factor dividing the bird community into foraging guilds related to the physical structure of the habitat followed by the foraging substrates and methods. In total, nine foraging heights, six foraging substrates, and nine foraging methods were identified for the bird species present in the study plot. All the birds overlapped considerably with other species at least in any one of the three dimensions. Niche overlap was observed high in the usage of height followed by foraging substrate and method. As the birds are evolved with special morphological adaptations to use particular foraging method and exploit particular substrate, overlap was less and specialization was more among birds in these two dimensions.

Resumen: Se estudió el patrón de forrajeo de las aves en el bosque espinoso del Santuario de Vida Silvestre Mudumalai en 1995 y 1996 de enero a abril (estación seca), puesto que la mayoría de las aves inician la reproducción durante este periodo, las demandas de energía son más grandes y las aves emplean la mayor parte del tiempo en el forrajeo. El estudio examina el patrón de forrajeo de aves en una parcela de 10 ha establecida en el bosque espinoso. Se recolectó información sobre la altura, sustrato y método de forrajeo. En total se hicieron 1386 observaciones en las tres dimensiones arriba mencionadas para 33 especies de aves. Un análisis de conglomerados de estas tres dimensiones muestra que el factor más importante que divide a la comunidad de aves en gremios de forrajeo está relacionado con la estructura física del hábitat, seguido por los sustratos de forrajeo y los métodos. En total, se identificaron nueve alturas de forrajeo, seis sustratos de forrajeo y nueve métodos de forrajeo para las especies presentes en la parcela de estudio. Al menos en una de las tres dimensiones todas las aves se superpusieron considerablemente con otras especies. Se observó un gran traslape de nicho en el uso de la altura, seguido del sustrato y del método de forrajeo. Dado que las aves han desarrollado adaptaciones morfológicas especiales para usar métodos particulares de forrajeo y explotar sustratos particulares, el traslape fue menor y la especialización mayor entre las aves en relación a estas dos dimensiones.

Resumo: O padrão de procura alimentar numa floresta espinhosa foi estudado no santuário de vida selvagem de Mudumalai em Tamil Nadu em 1995 e 1996 durante Janeiro a Abril (época seca) e que é o período em que a maior parte das aves iniciam a nidificação, em que as

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necessidades de energia são mais elevadas e em que gastam a maior parte do seu tempo procurando alimento. Este estudo examina o padrão de procura alimentar numa parcela de 10 ha demarcada na floresta espinhosa. A informação sobre a altura de colheita de alimentos, substrato e métodos foram colectados. No seu conjunto foram efectuadas 1386 observações em relação aos três parâmetros referidos para as 33 espécies de aves. Uma análise dos clusters destes três vectores mostrou que o factor mais importante de separação entre conjuntos de associações alimentares estavam relacionado com a estrutura física do habitat, seguido pelos substratos de recolha alimentar e métodos. Num total, nove Alturas de recolha alimentar, seis substratos alimentares e nove métodos de recolha alimentar foram identificados para as espécies de aves presentes na parcela de estudo. Todas as aves apresentavam considerável sobreposição com outras espécies, pelo menos numa das três dimensões. A sobreposição dos nichos foi observada ser elevada no uso da altura, seguida pelo substrato de recolho alimentar e método. Como as aves evoluíram com adaptações morfológicas especiais para usar um método de recolha alimentar próprio e explorar um substrato particular, a sobreposição foi menor e a especialização foi maior entre as aves nestas duas dimensões.

Key words: Birds, foraging height, foraging method, foraging pattern, foraging substrate, guild, Mudumalai, niche, thorn forest.

Introduction

Studies on foraging pattern mainly considered the method of exploiting the resources, as birds often exhibit differences in how they exploit resources. Some species, for instance, are generalists that will search for food at all heights and on a variety of substrates, while others show varying degrees of specialization. Species, therefore, differ in their response to changes in their habitat that may result from the influence of human activities. Logging, the establishment of plantations, and increased incidence of wildfire are examples of events initiated by people which can change the structure of vegetation and plant species composition of forests and thereby affect the survival of forest birds. Thus knowledge of key resources and how they are shared among members of the guild would give valuable inputs for the conservation management of species and their habitats. Although foraging guild has been well documented for European and North American bird species (e.g., Crome 1978; MacNally 1994; Recher *et al.* 1985), no such studies are available in India. However, in some community studies (Beehler *et al.* 1987; Daniels 1989; Johnsingh & Joshua 1994; Johnsingh *et al.* 1987; Sundramoorthy 1991) the foraging of birds was discussed based on the information given by Ali & Ripley (1987). In order to fill up the lacunae, an attempt was made to ex-

amine the foraging pattern of birds in a 10 ha plot laid in the tropical thorn forest of Mudumalai Wildlife Sanctuary.

Study area

The Mudumalai Wildlife Sanctuary (MWS) is located between 11°30 to 11°39 N and 76°27 and 76°43 E in the Nilgiris district, Tamil Nadu. It is situated at an average elevation of 1000 m. The climate is moderate, and temperatures vary from 14°-17°C during December-January to 29°-33°C during March-May. The annual rainfall varies from 600 mm to 2000 mm, which is received in two periods. The first is of high rainfall (June-August) from the south-west monsoon and the second brings low rainfall (September-November) from the north-east monsoon. The sanctuary is drained mainly by a perennial river Moyar and by various streams. Further details of the study area are given by Desai (1991).

The study was carried out in a 10 ha plot laid in the tropical thorn forest which is dominated by species such as *Acacia* spp. (including *A. chundra*, *A. leucopholea*, and *A. ferruginea*), *Anogeissus latifolia*, *Zizyphus* spp., *Sapindus emarginatus*, *Phyllanthus emblica*, *Erythroxylum monogynum*, *Cassia fistula*, and *Capparis* spp. In recent years, considerable increase in the human population in and around the thorn forest of this Sanctuary has dras-

tically altered the vegetation largely by woodcutting and hence, knowledge of crucial microhabitats available in/on the plants is an urgent need. Thus, we selected this study area and used the foraging pattern for the identification of crucial microhabitats for birds.

Methods

Foraging records were collected at the study site in 1995 and 1996 during January to April (dry spell) as most of the birds start breeding during this period, demands for energy are greatest and birds spend most of their time in foraging (Cody 1974). Most of the records were collected within the first four hours after sunrise. For rarer species additional observations were made throughout the day. Only one foraging record (initial record) was taken from any individual encountered as done by MacNally (1994). No observation was made for the swallows, swifts and raptors. Mixed flocks were avoided to study the foraging patterns as it affects the independence of foraging behaviour of each species. For each foraging attempt microhabitat details such as the height above ground level, substrate and species of plant on which the prey was, and foraging method were recorded.

Foraging height

Foraging attempts were assigned to 12 height categories: 0 m (ground), and at every 1 metre in-

terval up to 10, and >10 m based on the general physiognomy of the vegetation (Gokula *et al.* 1999). Some prominent trees were selected and marked with heights and were used for reference.

Foraging substrate

A substratum is the material from which food is taken by the birds. Substrates were classified as (1) ground - including debris, litter and grass; (2) trunk/main branches - the main axes of trees; (3) foliage - leaves including leaf-blades and petioles; (4) twigs - small branches to which leaves were attached (5) flower and fruits, and (6) air. Among these, the nectar/seed/fruit category represents the food taken by the birds. As other five categories are meant purely for insectivorous birds, to separate the non-insect feeders from the insect feeders, the nectar/seed/fruit category was included as one substrate.

Foraging methods

Foraging methods of insectivorous birds were broadly categorized as follows: (1) glean: a stationary food item is picked from its substrate by a standing or hopping bird; (2) probe : as glean, only the bird's beak penetrates or lifts the substrate to locate concealed food; (3) pounce : a bird flies from a perch and grabs the food item as it lands on the substrate which is similar to flycatcher-gleaning; and (4) sally or flycatching : a bird fly into air to catch flying prey. To cluster or segregate the spe-

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

No.	Activity (description)
1.	Abovecanopy-sally (Sally to airborne insects in or above the main canopy)
2.	Belowcanopy-sally (Sally from perched position to airborne insects below the main canopy)
3.	Bush-sally (Sally to airborne insects from the bushes)
4.	Ground-sally (Sally to airborne insects from the ground)
5.	Leaf-glean (Gleaning of perched prey from leaves of trees)
6.	Twig-glean (Gleaning of perched prey from twigs of trees)
7.	Fallen-log-gleaning (Searching fallen logs)
8.	Bush-gleaning (Gleaning of perched prey from bush)
9.	Bark-tear (Searching for prey by tearing the bark)
10.	Wood-probing (Probing the bark)
11.	Litter-search (Scratch and search through litter for insects)
12.	Wood-search (Gleaning of perched prey from trunks or main branches)
13.	Ground-pounce (Attack on grounded prey from perched position)
14.	Ground-search (Searching ground for insects)
15.	Arboreal-granivory (Consumption of seeds in trees)
16.	Ground-granivory (Consumption of seeds in ground)
17.	Fruit-exploiting (Consumption of fruits)
18.	Flower-exploiting (Consumption of pollen and nectar or blossoms)

cies on a micro level, the sally and glean were classified further into finer levels based on the vegetation. The method "sally" was further classified into four types and "gleaning" into five categories based on the location of the prey (Table 1). In order to separate the non-insect feeders from the insect feeders, methods were classified based on the food items (nectar/seed/fruit) rather than method adopted. Moreover, the fruit/nectar classification was used to record all frugivores and nectarivores behaviour since the use of plants by omnivorous birds was only of relevance in comparison to their insectivorous behaviour. In total, 18 categories were used to collect information on foraging (Table 1) which encompasses the behaviours described by Crome (1978) and expanded by Holmes *et al.* (1979) and MacNally (1994). For the purposes of getting sufficient sample size, the information was pooled irrespective of years. As thirty independent observations are recommended to represent the behaviour of a bird accurately (Morrison 1984), all species were used for analysis.

Statistical analyses

Specialist-Index *J*

The foraging specialization of each foraging dimension (height, method, and substrate) was analyzed using the Shannon-Weaver index (1949) $H = -\sum p_i \ln p_i$ (Where H = diversity and p_i = the proportion of observation in subset i). These values were then converted to a standardized range using the formula $J = H/H_{\max}$ (Where J = specialization and H_{\max} = the H value obtained when the observations are distributed equally across all subsets of the foraging dimension) followed by Crome (1978) and Recher *et al.* (1985). J values range between one to zero, with foraging specialization increasing as J falls.

Niche overlap

The degree of species overlap in niche utilization for the different categories recorded (i.e. foraging method, substrate and foraging height) has been quantitatively expressed using Horn's (1966) equation:

$$R_0 = \frac{(x_1 + y_1) \log (x_1 + y_1) - x_1 \log x_1 - y_1 \log y_1}{(X + Y) \log (X + Y) - X \log X - Y \log Y}$$

where X and Y are the total number of observations for species, for the particular category, and x_i

and y_i are the number of occurrences made in the i 'th subdivision within each category for X and Y , respectively.

Cluster analysis

To compare foraging behaviour, substrate use, and height use between species, cluster analyses were performed on a data matrix (species x characteristics), following Holmes *et al.* (1979). The analysis used the unweighted pair clustering method with arithmetic average (UPGMA) and Euclidian distance coefficients (Legendre & Legendre 1983; Rohlf 1987). The SPSS software (Norusis 1990) was used for the data analyses.

Results

A total of 1386 observations were made on 33 bird species (Table 2).

Foraging height

Of the 12 height categories in the thorn forest, nine such as ground, 0-1 m, >1-2 m, >2-3 m, >3-4 m, >4-5 m, >5-6 m, >6-7 m and >7-8 m were utilized by 33 bird species (Table 3). Although most species foraged over a broad range of heights, they were grouped according to the layer of vegetation in which the majority of their foraging was recorded.

Foraging height was apportioned between 3 layers of strata: ground (0 m), shrub/short trees (0-2 m) and tree (>2 m). Ten species foraged mainly on or near the ground. The shrub/short tree layer (0-2 m) was utilized by seven species. Of the seven species, only warblers such as Grey-breasted Prinia and Blyth's Reed Warbler constantly used this layer while others showed variation in their height usage. The tree layer (>2 m) was used by 16 bird species. Within the tree layer, higher percentage of foraging manoeuvres were recorded only in 2-3 m and 5-6 m categories, which can be considered as lower canopy and middle canopy respectively. For the avian community as a whole, a higher percentage (48.8%) of foraging manoeuvres were recorded in the tree layers (>2 m).

Foraging substrate

Six substrates namely air, ground, twigs, trunk/main branches, foliage, and nectar/seed/fruits were recognized in the thorn forest (Table 4).

Table 2. Number of foraging records made in thorn forest of Mudumalai wildlife Sanctuary.

No.	Species name	Number of observations	
1.	Grey junglefowl	<i>Gallus sonneratii</i>	30
2.	Spotted Dove	<i>Sterptopelia chinensis</i>	38
3.	Vernal Hanging Parrot	<i>Loriculus vernalis</i>	32
4.	Green Bee-eater	<i>Merops orientalis</i>	35
5.	Common Hoopoe	<i>Upupa epops</i>	34
6.	Brown-headed Barbet	<i>Megalaima zeylanica</i>	32
7.	Lesser Yellownape	<i>Picus chlorolophus</i>	33
8.	Black-rumped Flameback	<i>Dinopium benghalense</i>	34
9.	Yellow-crowned Woodpecker	<i>Dendrocopos mahrattensis</i>	31
10.	Bay-backed Shrike	<i>Lanius vittatus</i>	37
11.	Black-hooded Oriole	<i>Oriolus xanthornus</i>	32
12.	White-bellied Drongo	<i>Dicrurus caeruleus</i>	32
13.	Brahminy Starling	<i>Sturnus pagodarum</i>	44
14.	Scarlet Minivet	<i>Pericrocotus flammeus</i>	36
15.	Small Minivet	<i>Pericrocotus cinnamomeus</i>	48
16.	White-bellied Minivet	<i>Pericrocotus erythropygus</i>	30
17.	Common Iora	<i>Aegithina tiphia</i>	34
18.	Red-vented Bulbul	<i>Pycnonotus cafer</i>	69
19.	Yellow-eyed Babbler	<i>Crysomma sinense</i>	66
20.	Yellow-billed Babbler	<i>Turdoides affinis</i>	103
21.	White-browed Fantail	<i>Rhipidura aureola</i>	34
22.	Paradise Flycatcher	<i>Terpsiphone paradisi</i>	33
23.	Grey-breasted Prinia	<i>Prinia hodgsonii</i>	64
24.	Indian Tailor Bird	<i>Orthotomus sutorius</i>	33
25.	Blyth's Reed Warbler	<i>Acrocephalus dumetorum</i>	36
26.	Greenish Warbler	<i>Phylloscopus trochiloides</i>	46
27.	Indian Robin	<i>Saxicoloides fulicata</i>	31
28.	Great Tit	<i>Parus major</i>	43
29.	Chestnut-bellied Nuthatch	<i>Sitta castanea</i>	60
30.	Plain Flowerpecker	<i>Dicaeum concolor</i>	38
31.	Oriental White-eye	<i>Zosterops palpebrosus</i>	58
32.	Chestnut-shouldered	<i>Petronia Petronia xanthocollis</i>	43
33.	Common Rosefinch	<i>Carpodacus erythrinus</i>	37
	Total		1386

Air

Five species, namely Paradise Flycatcher, Common Bee-eater, White-bellied Drongo, White-browed Fantail, and Scarlet Minivet fed predominantly from air. No absolute usage (100%) of air as substrate was found in any one of the bird species.

Ground

Among the six substrates, ground was predominantly used by more number of birds (8) of which Grey Junglefowl, Indian Robin, Common Hoopoe, and Spotted Dove used only this substrate, while the Chestnut-shouldered Petronia and Tailor Bird used this substrate less frequently than the others. Both insectivores and granivores used this substrate.

Twigs

Only four species namely Greenish Warbler, Yellow-eyed Babbler, White-bellied Minivet and Common Iora largely exploited their prey from twigs. No absolute usage of this substrate by any one of the birds was found in this category. Foliage was used after twigs by all the species of this guild. The Common Iora used equally both twigs and foliage.

Trunk/Main branches

Chestnut-bellied Nuthatch and Woodpeckers largely obtained their prey from the trunk/main branches. In addition to this substrate, Lesser Yellownape utilized ground also for obtaining the insects.

Table 3. Height distribution of birds in thorn forest (% of prey attacks).

Guild/Species name	Foraging heights (m)									
	G	1	2	3	4	5	6	7	8	H
<i>Ground</i>										
Indian Robin	100	-	-	-	-	-	-	-	-	-
Common Hoopoe	100	-	-	-	-	-	-	-	-	-
Grey Junglefowl	100	-	-	-	-	-	-	-	-	-
Spotted Dove	100	-	-	-	-	-	-	-	-	-
Yellow-billed Babbler	94	6	-	-	-	-	-	-	-	0.22
Chestnut-shouldered Petronia	74	-	5	12	9	-	-	-	-	0.84
Tailor Bird	58	6	33	3	-	-	-	-	-	0.96
Bay-backed Shrike	56	4	33	7	-	-	-	-	-	1.01
Brahminy Starling	43	-	11	32	-	14	-	-	-	1.25
White-browed Fantail	46	9	15	6	12	-	12	-	-	1.60
<i>Shrub/short trees</i>										
Grey-breasted Prinia	-	100	-	-	-	-	-	-	-	-
Blyth's Reed Warbler	3	97	-	-	-	-	-	-	-	0.13
Paradise Flycatcher	4	22	74	-	-	-	-	-	-	0.69
Yellow-eyed Babbler	-	44	56	-	-	-	-	-	-	0.69
Oriental White-eye	-	7	29	26	5	10	5	-	18	1.74
Chestnut-bellied Nuthatch	20	17	50	-	-	13	-	-	-	1.23
Red-vented Bulbul	4	-	42	28	-	3	22	1	-	1.23
<i>Trees</i>										
Great Tit	5	-	12	65	9	9	-	-	-	1.12
White-bellied Drongo	9	-	27	59	5	-	-	-	-	1.02
Lesser Yellownappe	33	3	15	42	7	-	-	-	-	1.29
Lesser Goldenbacked Woodpecker	12	9	-	38	21	12	8	-	-	1.63
Small Minivet	-	-	6	35	19	25	15	-	-	1.49
Common Iora	-	-	18	35	32	9	6	-	-	1.42
White-bellied Minivet	-	-	-	-	60	40	-	-	-	0.67
Plain Flowerpecker	-	-	-	14	50	29	7	-	-	1.17
Yellow-crowned Woodpecker	-	-	23	35	42	-	-	-	-	1.07
Scarlet Minivet	-	-	-	11	36	17	25	11	-	1.50
Black-hooded Oriole	-	-	-	-	23	32	32	13	-	1.34
Rosefinch	-	-	-	-	-	-	100	-	-	-
Brown-headed Barbet	-	-	-	-	-	14	77	9	-	0.69
Green Bee-eater	20	-	14	14	-	14	38	-	-	1.52
Vernal Hanging Parrot	-	-	-	6	6	6	48	34	-	1.24
Greenish Warbler	-	-	-	-	-	26	48	26	-	1.05

Foliage

Warblers namely Blyth's Reed Warbler and Grey-breasted Prinia exploited only foliage (100%) while the other species predominantly used foliage to obtain their prey. The warblers used only foliage of shrubs while others used foliage of the trees.

Nectar/Seed/Fruit

Seven species formed this guild and of which Vernal Hanging Parrot, Plain Flowerpecker and Rosefinch (100%) used only this substrate. Other four bird species also used this substrate predominantly.

Foraging methods

Based on the 18 foraging techniques employed by the birds, 9 major methods were possibly distinguished for the birds in the thorn forest. At least one bird species was found predominantly using any one of the nine major methods. The major prey attack manoeuvres used by birds in thorn forest were sallying, pouncing, foliage-gleaning, wood-gleaning, wood-probing, ground animal-exploiting (carnivore), nectar-gleaning, fruit-gleaning and grain or seed-gleaning (Table 5).

Table 4. Percent use of substrate by birds in the thorn forest.

Species	Air	Ground	Twigs	Trunk/Main branches	Foliage	Nectar/Seed/Fruits
<i>Air</i>						
Paradise Flycatcher	96	4	-	-	-	-
Green Bee-eater	91	9	-	-	-	-
White-bellied Drongo	91	9	-	-	-	-
White-browed Fantail	88	9	-	-	3	-
Scarlet Minivet	61	-	-	-	39	-
<i>Ground</i>						
Grey Junglefowl	-	100	-	-	-	-
Indian Robin	-	100	-	-	-	-
Common Hoopoe	-	100	-	-	-	-
Spotted Dove	-	100	-	-	-	-
Yellow-billed Babbler	3	94	3	-	-	-
Bay-backed Shrike	7	93	-	-	-	-
Chestnut-shouldered Petronia	-	74	-	-	-	26
Tailor Bird	-	60	13	-	27	-
<i>Twigs</i>						
Greenish Warbler	-	-	83	-	17	-
Yellow-eyed Babbler	-	-	74	-	26	-
White-bellied Minivet	-	-	65	-	35	-
Common Iora	-	-	50	-	50	-
<i>Trunk/Main branches</i>						
Yellow-crowned Woodpecker	-	-	-	100	-	-
Black-rumped Flameback	-	-	-	100	-	-
Chestnut-bellied Nuthatch	-	-	-	100	-	-
Lesser Yellownappe	-	34	-	66	-	-
<i>Foliage</i>						
Blyth's Reed Warbler	-	3	-	-	97	-
Grey-breasted Prinia	-	-	-	-	100	-
Black-hooded Oriole	18	-	-	-	82	-
Great Tit	-	2	14	26	58	-
Small Minivet	19	-	19	-	62	-
<i>Nectar/seed/fruits</i>						
Vernal Hanging Parrot	-	-	-	-	-	100
Plain Flowerpecker	-	-	-	-	-	100
Rosefinch	-	-	-	-	-	100
Red-vented Bulbul	-	4	-	-	-	96
Oriental White-eye	-	-	29	-	7	64
Brown-headed Barbet	-	-	-	-	41	59
Brahminy Starling	-	43	-	-	-	57

Sallying

Five bird species were recognized as salliers. No absolute use of this method was found in any one of the birds. Except Scarlet Minivet, pounce was used as next major manoeuvre by the members of this guild.

Pouncing

Only Bay-backed Shrike and Indian Robin were recognized as pouncers in the thorn forest. Ground-carnivory was the second dominant method used by the pouncers in the thorn forest.

Foliage-gleaning

Five bird species formed this guild. The warblers (Grey-breasted Prinia and Blyth's Reed Warbler) used this method fully (100%) while the Great Tit, Black-hooded Oriole, and Small Minivet used mainly this method along with sallying or wood-gleaning.

Wood-gleaning

The number of bird species forming the wood-gleaning guild was more than the other groups. Woodpeckers, Greenish Warbler, and Nuthatch

Table 5. Percent prey attack manoeuvres by birds in thorn forest.

Species	Sallier	Pouncer	Foliage-gleaner	Wood-gleaner	Wood-prober	Ground-carnivore	Nectar gleaning	Fruit gleaning	Grain gleaning
Sallier									
Paradise Flycatcher	96	4	-	-	-	-	-	-	-
White-bellied Drongo	91	9	-	-	-	-	-	-	-
Green Bee-eater	91	9	-	-	-	-	-	-	-
White-browed Fantail	88	9	3	-	-	-	-	-	-
Scarlet Minivet	61	-	39	-	-	-	-	-	-
Pouncer									
Bay-backed Shrike	7	82	-	-	-	11	-	-	-
Indian Robin	-	52	-	-	-	48	-	-	-
Foliage-gleaner									
Grey-breasted Prinia	-	-	100	-	-	-	-	-	-
Blyth's Reed Warbler	-	-	97	-	-	3	-	-	-
Black-hooded Oriole	18	-	82	-	-	-	-	-	-
Small Minivet	19	-	62	19	-	-	-	-	-
Great Tit	-	-	58	40	-	2	-	-	-
Wood-gleaner									
Chestnut-bellied Nuthatch	-	-	-	100	-	-	-	-	-
Greenish Warbler	-	-	17	83	-	-	-	-	-
Yellow-eyed Babbler	-	-	26	74	-	-	-	-	-
Yellow-crowned Woodpecker	-	-	-	68	32	-	-	-	-
White-bellied Minivet	-	-	35	65	-	-	-	-	-
Lesser Yellownappe	-	-	-	36	30	34	-	-	-
Wood-prober									
Lesser Goldenbacked Woodpecker	-	-	-	8	92	-	-	-	-
Ground-carnivore									
Common Hoopoe	-	-	-	-	-	100	-	-	-
Yellow-billed Babbler	3	-	-	3	-	94	-	-	-
Tailor Bird	-	24	27	13	-	36	-	-	-
Nectar gleaning (N)									
Plain Flowerpecker	-	-	-	-	-	-	100	-	-
Vernal Hanging Parrot	-	-	-	-	-	-	100	-	-
Oriental White-eye	-	-	7	29	-	-	64	-	-
Fruit gleaning (F)									
Red-vented Bulbul	-	-	-	-	-	4	3	93	-
Brown-headed Barbet	-	-	41	-	-	-	-	59	-
Brahminy Starling	-	-	-	-	-	-	-	57	43
Grain gleaning (G)									
Chestnut-shouldered Petronia	-	-	-	-	-	-	-	-	100
Spotted Dove	-	-	-	-	-	-	-	-	100
Rosefinch	-	-	-	-	-	-	-	-	100
Grey Junglefowl	-	-	-	-	-	-	-	-	100
* Common Iora	-	-	50	50	-	-	-	-	-

were recognized as wood-gleaners. Only Chestnut-bellied Nuthatch used this manoeuvre (100%) absolutely while woodpeckers used this method predominantly.

Wood-probing

Only the Black-rumped Flameback frequently used this method along with wood-gleaning.

Ground carnivore

Common Hoopoe, Yellow-billed Babbler and Tailor Bird formed this guild, of which the Common Hoopoe used only this method.

All the above mentioned methods are applied to get the invertebrate prey. In the case of nectar/seed/fruits as food the method applied is glean but it will overlap with insect gleaners. Hence, they are treated separately as nectar-gleaning, fruit-gleaning and seed-gleaning.

Nectar-gleaning

The Plain Flowerpecker, Vernal Hanging Parrot and Oriental White-eye were the species coming under this group; the first two used only this method (100%) while the Oriental White-eye employed wood-and foliage-gleaning methods also.

Fruit-gleaning

Three species formed this group of which only the Red-vented Bulbul used it mostly. Brown-headed Barbet and Brahminy Starling used this method less frequently. In addition to fruit-exploiting, the Barbet used foliage-glean (41%) while the Myna used seed-exploiting (43%).

Seed-gleaning

All the members in this group (Chestnut-

shouldered Petronia, Spotted Dove, Rosefinch, Grey Jungle Fowl) used only this method. Among these, the Spotted Dove and Junglefowl took their food only from the ground and the other two mostly from the tree. The Common Iora, although basically a gleaner was found difficult to fit in any one of the nine groups as they used foliage-gleaning and wood-gleaning manoeuvres equally (50%).

Niche overlap

One way of measuring the extent to which foraging activities of the various species overlap, is by calculating the overlap values. This was done with respect to (a) foraging height (12 categories), (b) foraging manoeuvres (18 categories), and foraging substrate (6 categories). Overlap between spe-

Table 6. Mean niche overlap for each bird species in thorn forest (High values are in bold type).

Species name	Niche overlap			
	Foraging Height	Foraging method	Foraging Substrate	Overall
Chestnut-shouldered Petronia	0.58	0.30	0.43	0.44
Lesser Yellownappe	0.62	0.34	0.35	0.44
Yellow-eyed Babbler	0.41	0.39	0.34	0.38
Yellow-billed Babbler	0.47	0.26	0.40	0.38
Oriental White-eye	0.57	0.37	0.39	0.44
White-bellied Minivet	0.39	0.40	0.35	0.38
White-browed Fantail	0.66	0.35	0.34	0.45
White-bellied Drongo	0.55	0.32	0.32	0.40
Tailor Bird	0.57	0.41	0.49	0.49
Spotted Dove	0.45	0.28	0.36	0.36
Small Minivet	0.57	0.43	0.43	0.47
Scarlet Minivet	0.53	0.39	0.38	0.43
Red-vented Bulbul	0.58	0.28	0.32	0.39
Rosefinch	0.33	0.23	0.28	0.28
Paradise Flycatcher	0.45	0.24	0.29	0.32
Plain Flowerpecker	0.49	0.27	0.28	0.35
Yellow-crowned Woodpecker	0.51	0.30	0.21	0.34
Brown-headed Barbet	0.41	0.36	0.40	0.39
Vernal Hanging Parrot	0.46	0.27	0.28	0.34
Black-rumped Flameback	0.62	0.27	0.21	0.37
Indian Robin	0.45	0.31	0.36	0.37
Common Hoopoe	0.45	0.26	0.36	0.36
Grey Junglefowl	0.45	0.28	0.36	0.36
Great Tit	0.55	0.44	0.43	0.47
Grey-breasted Prinia	0.28	0.25	0.33	0.29
Greenish Warbler	0.41	0.38	0.32	0.37
Chestnut-bellied Nuthatch	0.56	0.28	0.21	0.35
Common Iora	0.57	0.41	0.37	0.45
Green Bee-eater	0.63	0.30	0.32	0.42
Brahminy Starling	0.61	0.31	0.42	0.45
Black-hooded Oriole	0.47	0.38	0.38	0.41
Bay-backed Shrike	0.58	0.31	0.39	0.43
Blyth's Reed Warbler	0.31	0.26	0.33	0.30
Mean SE	0.50 ± 0.01	0.32 ± 0.01	0.35 ± 0.01	0.39 ± 0.01

cies was calculated for each habitat and mean overlap of each species with others is presented. The results suggested that all the bird categories in this study overlapped with others in at least one foraging dimension (Table 6). Among the three dimensions (foraging height, foraging method, and foraging substrate), highest mean overlap for the whole avian community was found in the foraging height (0.50) while lowest was in foraging method (0.32).

Specialist index

Of the three dimensions, specialization was more in the substrates (12) followed by method (7)

and height (6) categories (Table 7). Bird species such as Spotted Dove, Rosefinch, Common Hoopoe, Grey Jungle Fowl, and Grey-breasted Prinia can be considered as specialists as their J values were 0 in all the three dimensions.

Determination of foraging guilds

The relationships among the 33 bird species based on the substrates and foraging methods, are summarized in the cluster diagram (Fig. 1). Species were separated into a number of distinct groups whose members exploit food resources in similar substrates, methods, and heights, and can

Table 7. Extent of specialization by birds in foraging method and foraging height as shown by J values in thorn forest. J values range from 0-1, and specialization increases as J falls. (Specialists are in bold type).

Species name	Foraging Height		Foraging Method		Foraging substrate	
	H	J	H	J	H	J
Chestnut-shouldered Petronia	0.84	0.34	0.57	0.20	0.57	0.32
Lesser Yellowname	1.29	0.52	1.10	0.38	0.63	0.35
Yellow-eyed Babbler	0.69	0.28	0.57	0.20	0.57	0.32
Yellow-billed Babbler	0.22	0.09	0.26	0.09	0.27	0.15
Oriental White-eye	1.74	0.70	0.83	0.29	0.83	0.46
White-bellied Minivet	0.67	0.27	0.65	0.22	0.65	0.36
White-browed Fantail	1.60	0.64	1.14	0.39	0.43	0.24
White-bellied Drongo	1.02	0.41	0.69	0.24	0.30	0.17
Tailor Bird	0.96	0.38	1.32	0.46	0.91	0.51
Spotted Dove	-	0.00	-	0.00	-	0.00
Small Minivet	1.49	0.60	0.92	0.32	0.93	0.52
Scarlet Minivet	1.50	0.60	1.05	0.36	0.67	0.37
Red-vented Bulbul	1.35	0.54	0.31	0.11	0.17	0.09
Rosefinch	-	0.00	-	0.00	-	0.00
Paradise Flycatcher	0.69	0.28	0.18	0.06	0.17	0.09
Plain Flowerpecker	1.17	0.47	-	0.00	-	0.00
Yellow-crowned Woodpecker	1.07	0.43	0.63	0.22	-	0.00
Brown-headed Barbet	0.69	0.28	0.68	0.23	0.68	0.38
Vernal Hanging Parrot	1.24	0.50	-	0.00	-	0.00
Black-rumped Flameback	1.63	0.65	0.29	0.10	-	0.00
Indian Robin	-	0.00	0.69	0.24	-	0.00
Common Hoopoe	-	0.00	-	0.00	-	0.00
Grey Junglefowl	-	0.00	-	0.00	-	0.00
Great Tit	1.12	0.45	1.27	0.44	1.01	0.56
Grey-breasted Prinia	-	0.00	-	0.00	-	0.00
Greenish Warbler	1.05	0.42	0.46	0.16	0.46	0.25
Chestnut-bellied Nuthatch	1.23	0.49	0.50	0.17	-	0.00
Common Iora	1.42	0.57	0.69	0.24	0.69	0.39
Green Bee-eater	1.52	0.61	0.91	0.31	0.30	0.17
Brahminy Starling	1.25	0.50	0.68	0.23	0.68	0.38
Black-hooded Oriole	1.34	0.54	0.47	0.16	0.47	0.26
Bay-backed Shrike	1.01	0.40	0.59	0.20	0.25	0.14
Blyth's Reed Warbler	0.13	0.05	0.13	0.04	-	0.00
Number of specialists	6		7		12	

H = Diversity index, J = Specialist index

thereby be considered as guilds. Two distinct guilds were arbitrarily recognized from the cluster diagram (Fig. 1) as follows : Guild I contains birds that foraged extensively on or near ground. This was further divided into 3 guilds based on the foraging method: ground-granivore, ground-carnivore, and pouncers. Guild II consists of birds that predominantly obtained their prey from the air and plant species (tree/shrub). Within this guild, there were three major group of birds such as nectar/fruit/seed-gleaners, salliers, and gleaners. The group gleaners were further divided into 3 groups based on their use of substrate: wood-gleaners, bush-gleaners, and foliage-gleaners.

Based on the observational data, birds that foraged in similar ways or height or substrate for food were grouped in a schematic way (Fig. 2). The schematic portrayal of the grouping relies on foraging behaviour, foraging height, and foraging substrate differences to associate species. Among the 33 species, 23 were insectivores followed by

nectar/fruit-eaters (6 species) and granivores (4 species). More number of species (3 of 4) in the granivore group largely obtained their food (seeds) from the ground while more number of species (18 of 23) in the insectivorous group largely obtained their food (insect) from above ground level. Within the insectivores (above ground group), the number of species which obtained their food from wood was more than from other substrates (foliage and air). Only two species of warblers used foliage of shrubs for procuring their food.

Discussion

Among the birds, there are four major groupings based on the food eaten: insectivores, nectarivores, granivores, and frugivores (Fig. 2). The height and height-related characteristics separate

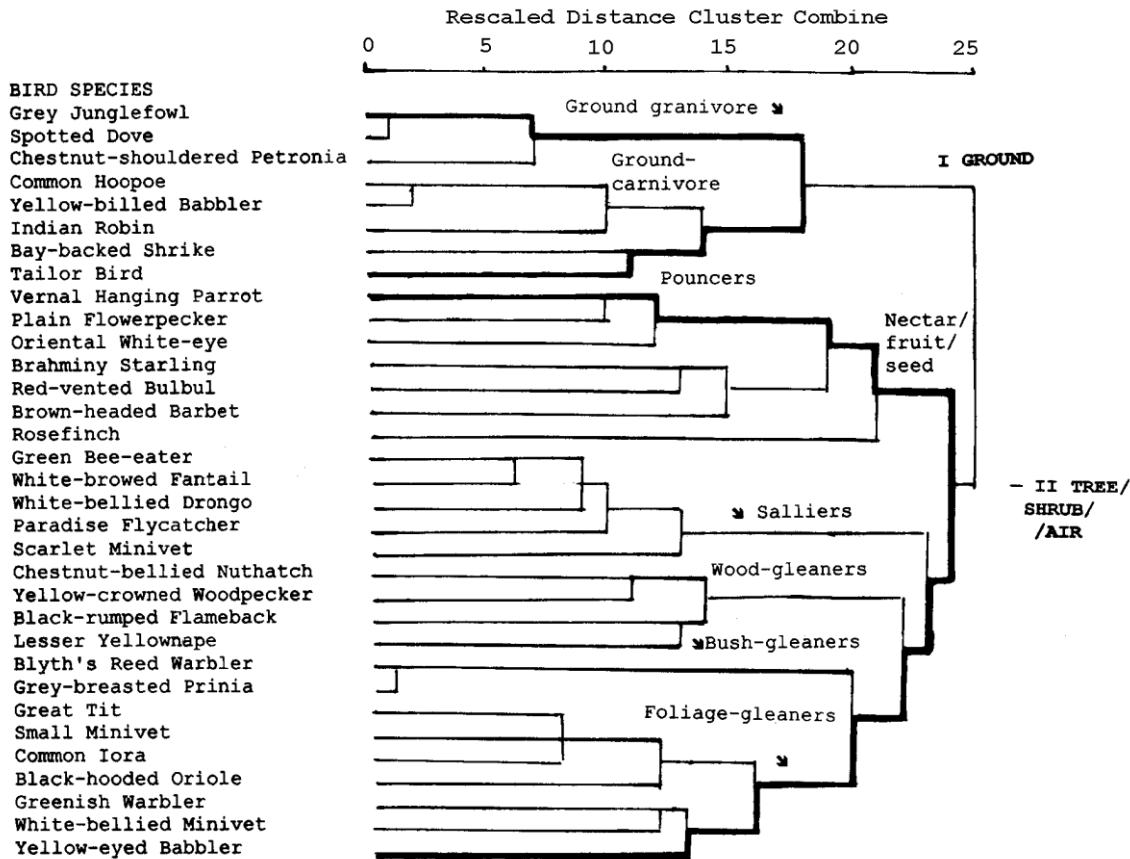


Fig. 1. Interspecific relationships of 33 bird species, based on multivariate analyses of foraging method, foraging substrate and foraging height use.

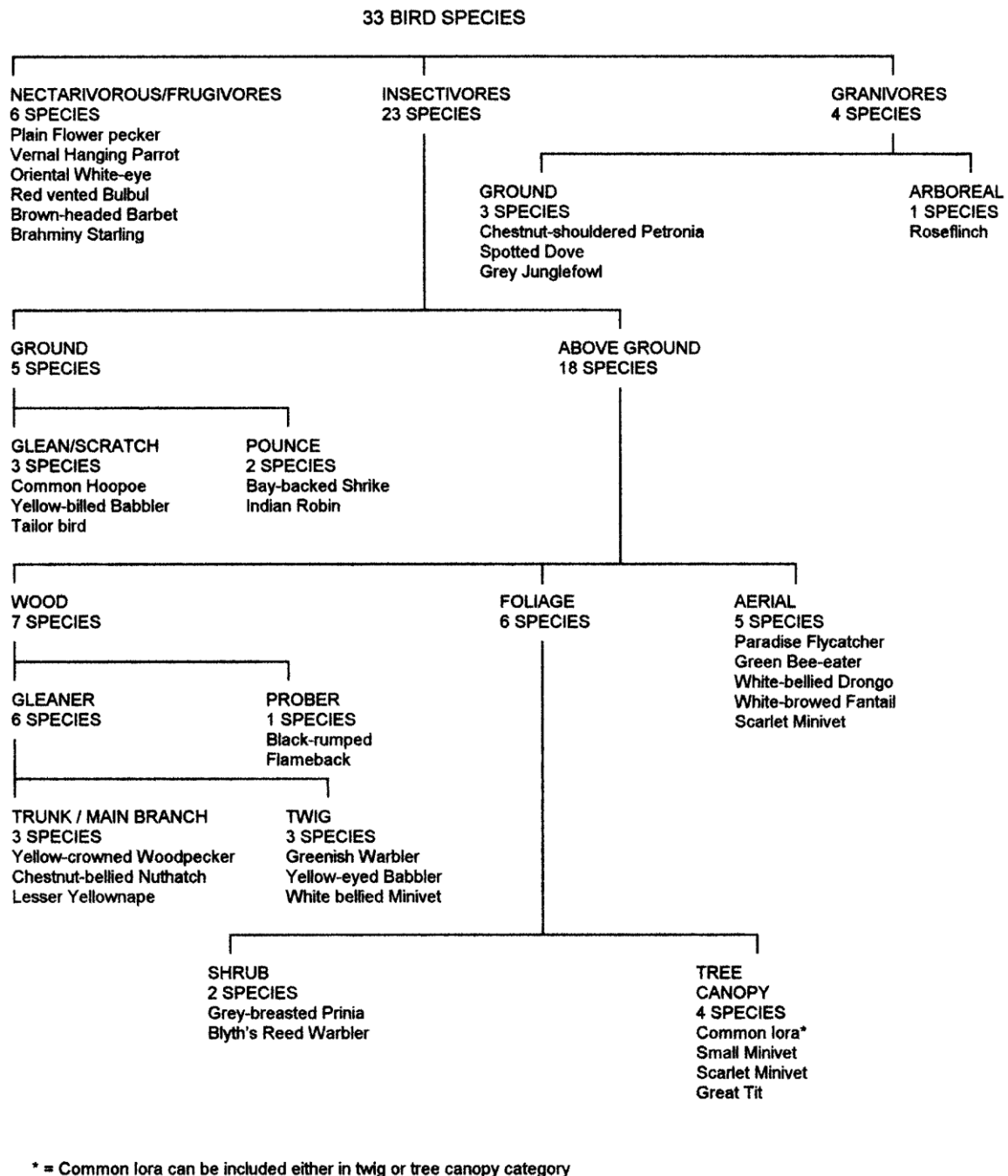


Fig. 2. A hierarchial cluster of 33 bird species found in the thorn forest based on observational data.

the ground foragers from all other species. There are, therefore, three distinct foraging environments (forest floor, plant and air) at thorn forest. The plant (shrubs and trees) surface provides microhabitats such as foliage and wood. Each of these regions (environments and microhabitats) is exploited by the bird species that have the special

ized morphology and behaviour necessary for foraging there. Distinction of ground and above-ground (air, shrubs, and trees) emphasizes the importance of foraging opportunities on these environments. The availability of various plant forms (shrubs, short trees, trees) in this habitat not only increases dimensions of the vertical habitat and,

as a consequence, the foliage layering and complexity, but also provides supporting substrates (twigs, trunk/main branches, and foliage). The proportion of foliage at different heights is also a function of the branching structure of the plant forms. As branches of most of the short tree species in the thorn forest are pendant or branching downwards, it overlaps with the shrub foliage. Thus, no distinction could be between shrubs and short trees in this habitat type.

In general, five substrates such as air, ground wood (twigs and trunk/main branches), foliage, and nectar/seed/fruit were recognized in the thorn forest. It can be further reduced into air, ground and plant of which, larger number of bird species fall under the plant-guild because plant offers a greater variety of microhabitats (trunk, branches, twigs, foliage) to find suitable food in this habitat.

In total, birds in the study area chiefly used nine methods to obtain the food. In the present study, closely related species used the same basic searching methods indicating the importance of phylogenetic and evolutionary process in determining the patterns (Robinson & Holmes 1982). However, adaptive radiation in certain groups provides facilities for them to diverse resource utilization using different methods. In most of the cases, guild was formed by a group of birds which are similar in their morphological adaptation. For example, all the woodpeckers were chiefly wood-gleaning and mostly on the trunk/main branches. But, species with different morphologies also utilize the same general searching mode and take the similar types of prey, suggesting that morphology does not necessarily predetermine the foraging behaviour or diet, as has been inferred by insectivorous birds (Ricklefs & Travis 1980). Therefore, it may be concurred with Hutto (1981) that morphological analyses will never provide a complete characterization of the food exploitation patterns and ecological relations of co-occurring bird species.

Resource partitioning reduces the effect of competition by decreasing the amount of overlap between the competing species (Wiens 1989). So, the incidence of overlap amongst potential competitors may be used to assess the extent of resource partitioning on the niche dimensions measured. All the birds in these habitats overlapped with others but only to a smaller extent. Although some species had higher overlap in one dimension, they had very little overlap in the other dimensions. However, it can be said that partitioning of

foraging dimensions among birds occurred in the thorn forest as reported earlier of bird communities of various places (Recher *et al.* 1985).

Niche overlaps are shaped by several factors (Cody 1974; MacArthur 1968). In this study in all three dimensions (foraging height, foraging method and foraging substrate), for the avian community as a whole, highest mean niche overlap was found in the use of foraging height followed by foraging substrate and the least in the foraging method. The birds are evolved with special morphological adaptations to use specific method and exploit particular substrates for their prey and hence morphology of birds may constrain the usage of foraging method and substrates (Alatalo 1981, 1982; Rolando & Robotti 1985). It may be the reason for birds showing low niche overlap value in these two categories. High value in the height dimension can be attributed to the distribution of different food items (insects, fruits, seeds and flowers) particularly at certain height category. For example, both seeds and insects were available in the ground layer and similarly, insects were available close to a height where flowers, fruits, and seeds were available. In general, the shape of the niche overlap (low or high) shown by birds can be attributed to the availability of food resources, morphology of species and competition as suggested by Alatalo (1981, 1982), Rolando & Robotti (1985) and Szekely (1985).

Among the three dimensions, there was more number of specialists in the substrate category. Organisms may specialize because only when resources are available in restricted or particular environment, or otherwise morphology of organisms influence diets (Rolando & Robotti 1985). Among the dimensions (foraging height, foraging method and foraging substrate), prey largely depends on the substrate and thus, substrate determines what sort of prey it can support. The birds are evolved with special morphological adaptations to exploit the particular substrates for particular prey and hence, specialists were more in the substrates.

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