FORAGING BEHAVIOUR OF THE NEAR THREATENED GREY-HEADED BULBUL *PYCNONOTUS PRIOCEPHALUS* IN RELATION TO SEASONS AND BREEDING STAGES

P. Balakrishnan [1,2]

[1]Wildlife Research and Conservation Trust, c/o Anupallavi, Chungathara P.O., Nilambur 679 334, Kerala, India.
[2]Address for Correspondence: Division of Conservation Biology, Jawaharlal Nehru Tropical Botanic Garden and Research Institute, Palode, Thiruvananthapuram 695 562, Kerala, India.
Email: baluperoth@gmail.com
doi: 10.17087/bnhs/2014/v111i1/56520

I studied the foraging behaviour and adaptive strategies of the Grey-headed Bulbul *Pycnonotus priocephalus*, an endemic species of the Western Ghats, India, in relation to seasons and reproductive stages in two tropical rainforest sites, Silent Valley National Park and Muthikkulam Reserve Forest, from 2002 to 2005 and 2012 to 2013. The species was recorded to use various foraging manoeuvres and food handling techniques, and was found to frequently use energy conserving manoeuvres and feeding techniques such as gleaning and gulping. There were significant differences in its foraging height and foraging tree use due to differential habitat selection during the breeding and non-breeding seasons. It showed plasticity in the foraging behaviour during the different reproductive stages. Its participation in mixed-hunting flocks during the local migratory phase (non-breeding season) seems to be an adaptive strategy to cope with resource competition and predation risks in a new and challenging habitat, which is in accordance with other studies on the flocking behaviour of tropical birds.

Key words: behavioural plasticity, foraging behaviour, Grey-headed Bulbul, mixed-species flocks, *Pycnonotus priocephalus*, Western Ghats

INTRODUCTION

Studies of foraging behaviour are central to explaining patterns in nature because survival and reproduction depend, ultimately, on an individual's success in acquiring and using energy from food resources (Hutto 1990). An understanding of the foraging manoeuvres, foraging height, and foraging site characteristics are also important in answering questions concerning co-existence and ecological segregation of similar species (Lack 1971). Moreover, information on the temporal changes in foraging strategies could be of vital importance for formulating strategies to conserve rare species. It has been widely demonstrated that food abundance and distribution are the primary determinants of foraging behaviour (reviewed in Morrison *et al.* 1990). Optimal foraging behaviour, however, may encompass other conflicting activities such as anti-predator behaviour that lead animals to trade food intake rate against other activities. Decision-making based on trade-offs may be influenced by the internal state of the animal (Krebs and Kacelnik 1991). Closely related birds nearly always show differences in the frequency of use of foraging manoeuvres (Root 1967). Theory and empirical evaluation of adaptations dictate that morphological features designed to perform one type of movement are unlikely to be well-designed for other types of movements (Moermond 1990).

Variations in foraging behaviour between sexes or during the seasons are well-known, and those associated with the stages of breeding cycle are pronounced (Brennan and Morrison 1990; Dobbs and Martin 1998; Sakai and Noon 1990). Moreover, behavioural and morphological traits that affect foraging efficiency would be adapted in part to the diet available during the periods when food limits survival or reproduction (Martin and Karr 1990). Thus, knowledge of partitioning of a species' foraging niche by sex or season is essential to increase our understanding of its life history.

Multi-species foraging flocks are a widespread phenomenon in both tropical and temperate forests. Two principal selective advantages thought to favour the evolution of mixed-species flocking behaviour are decreased predation and increased foraging efficiency (Chen and Hsieh 2002; Jullien and Thiollay 1998; Sridhar *et al*. 2009). However, it can also lead to increased intraspecific competition, particularly when food is a limiting factor (Milinski and Parker 1991). Numerous studies on mixed-species flocks have been conducted in the tropics (see Chen and Hsieh 2002; Jullien and Thiollay 1998; Sridhar *et al*. 2009 for reviews). Many endemic species of the Western Ghats of India are known to participate in mixed-species flocks (Goodale *et al*. 2009), but there is lack of detailed information on the flock feeding strategies of these species.

I carried out a study on the foraging behaviour and adaptive strategies of Grey-headed Bulbul *Pycnonotus priocephalus*, one of the 16 range-restricted bird species of the Western Ghats in relation to seasons and breeding stages. This species is listed as a Near Threatened species (BirdLife International 2014) owing to habitat loss and complex life

history characteristics (Balakrishnan 2007, 2011). It has a very limited distribution in the heavy rainfall areas along the south-western region of India, from Belgaum and Goa south through Kerala, and east to the Nilgiris and Palnis, western Mysore and Coorg; from the plains to *c*.1,000 m, rarely to 1,800 m; optimum zone between 600 m and 900 m (Ali and Ripley 1987). Recent studies show a distinct patchy distribution of the species within the breeding sites and regular seasonal migration at the end of the breeding season (Balakrishnan 2007). The species is known to feed on fruits of several plant species, which include many canopy and sub-canopy trees, shrubs, lianas, and epiphytes, and insects (Ali and Ripley 1987; Balakrishnan 2007).

STUDY AREA

The study was undertaken during 2002–2005 and 2012–2013 in Silent Valley National Park (89.52 sq. km; 11º 00′–11º 15′ N; 76º 15′–76º 35′ E; 658–2,383 m above msl) and Muthikkulam Reserve Forest (63.83 sq. km; 10º 56′–10º 59′ N; 76º 41′–76º 45′ E; 610–2,065 m above msl) in the Western Ghats, both the sites separated by an area about 30 sq. km of human-modified landscape. The vegetation of both the study sites is dominated by west coast tropical evergreen forest, followed by southern montane wet temperate forest with grasslands restricted mainly to the higher slopes and hill tops. Silent Valley receives comparatively higher rainfall during the south-west monsoon (>6,000 mm/yr) than Muthikkulam (4,500 mm/yr). All the breeding season data were collected from Silent Valley, and data for non-breeding season and mixed-hunting flocks were from Muthikkulam, due to the complete absence of the study species in the former site consequent to the altitudinal migration during June to December. Further descriptions of the two study areas are available elsewhere (Balakrishnan 2007; Basha 1999; Nair and Balasubramanyan 1985).

METHODS

Foraging behaviour

The foraging behaviour of the Grey-headed Bulbul was studied by the methods described by Remsen and Robinson (1990), the observations recorded while walking slowly through existing trek paths and animal trails. For each foraging observation, the foraging manoeuvre, substrate used (twig, leaf, flower, and air), height of the foraging location, species and height of the foraging tree, the horizontal position of the bird in the canopy (nine categories: three vertical and and three horizontal), and foliage density at the foraging site (calculated as percentage cover within a one meter radius around the bird) were recorded. The relative foraging height was calculated as the foraging height relative to the height of the tree (foraging height of bird/tree height). The fruits consumed were identified by direct observations. Attempts to identify arthropod component of the diet were not successful due to poor visibility in the rainforest canopies.

Foraging manoeuvres and food handling techniques were again categorized based on Remsen and Robinson (1990). The major near-perch manoeuvres were classified as: (i) *glean* [pick food items from a nearby substrate (including from the ground) that can be reached without full extension of legs or neck, with no acrobatic movements involved]; (ii) *reach* (extend completely the legs or neck upwards, outwards, or downwards to reach food); (iii) *hang* (use legs and toes to suspend the body below the feet to reach food that cannot be reached from any other perched position); and (iv) *lunge* (manoeuvres in which the food item is beyond *reach*, and rapid leg movements rather than flight are used to reach and obtain the food item). Aerial manoeuvres were grouped as: (i) *sally* (to fly from a perch to obtain a food item and then return to a perch), and (ii) *leap* (launch into the air to reach a food item too far for a *reach* but too close for a *sally*. This differs from *sally* in that the upward thrust seems to come mostly from leg movements rather than wing movements).

The major food handling techniques recorded were classified as: (i) *gulp* (to swallow upon capture/contact without any noticeable manipulation other than being held briefly in the bill), (ii) *engulf* (to capture and swallow in one continuous motion without being held by the bill), and (iii) *bite* (to bite and remove a section of the food item).

Breeding birds were observed to study the heterogeneity in foraging behaviour within the breeding season (mid January to mid May), the reproductive stages categorized as pre-incubation, incubation, brooding, and post-brooding.

Participation in mixed-hunting flocks

Mixed-species flocks are defined after Stotz (1993) as “associations between two or more species moving in the same direction for at least 5 min”. The Grey-headed Bulbul participated in mixed-hunting flocks only during the non-breeding season. Once a mixed-hunting flock with the Grey-headed Bulbul was located, it was followed for up to an hour or till it disappeared from sight. For each flock, I recorded the number of species and their individual numbers. To minimize duplication of observations, I excluded multiple flocks encountered in the same area. For each foraging individual, data were collected on the foraging behaviour, foraging positions, substrate, and food plants. To determine the foraging diversity of the major participants of mixed-

hunting flocks, I recorded a single foraging event for each bird in the flock. The foraging niche-breadth of mixed-flock participants was calculated following Levins (1968): $\beta = 1 / \sum P_i^2$. The foraging niche-overlap (Pianka 1973) between the Grey-headed Bulbul and other flock participants was calculated by the formula $ø_{ij} = \sum P_{ij} P_{ik} / \sqrt{\sum P^2_{ij} P^2_{ik}}$, where $ø_{ij}$ = Pianka's measure of niche overlap between species j and species k, P_{ij} = proportion resource *i* is of the total resource used by species j, and P_{ik} = proportion resource *i* is of the total resource used by species k.

To understand the advantages of flock participation on foraging behaviour, I compared the foraging intensity (feeding rate/minute) of solitary non-breeders in the non-breeding site (Muthikkulam) with those foraging in mixed-species flocks from the same study site. The feeding rates were assessed during focal sampling of two-minutes duration. Foraging samples where interactions between the bird species occurred (e.g., chases) were omitted. The influence of prey-density on the feeding rate was not considered since both the feeding samples were collected during same period and from the same site.

RESULTS

Foraging manoeuvre

Based on the 1,827 foraging records of the Grey-headed Bulbul, the species was recorded to mostly forage in pairs (89%), and rarely in flocks. The diet comprises fruits (65.57%), invertebrates (34.26%), and the remaining nectar. Gleaning was the most preferred foraging manoeuvre (70.17%), followed by reach (14.01%), hang (9.30%) and sally (5.58%). Of the different techniques used to catch insects, gleaning was the most used manoeuvre (Chi-square test: $\chi^2 = 482.23$; $df = 4$; $n = 626$; $P < 0.001$). Gulping was the most used food handling technique. The Grey-headed Bulbul handled smaller fruits, arthropods, and lepidopteran larvae by either gulping or engulfing, while larger fruits of *Persea macrantha*, *Leea indica*, *Litsea floribunda*, *Syzygium* spp., and *Symplocose racemosa*, and larger insects were pecked and eaten.

Foraging locations

The mean foraging height was 4.49 ±2.52 m (range: 1–20 m) and the mean height of trees used for foraging was 5.78 ±3.30 m (range: 1–22 m). The birds foraged more in the upper (36.20%) and middle edges (23.44%) of the canopy. Foraging at the edges was significantly higher than in the inner areas of the canopy (Chi-square test: $\chi^2 = 1162.46$; $df = 5$; $n = 1826$; $P < 0.01$). The average foliage density at the point of observations was 33.76 ±18.37% (range: 2–80%).

Seasonal variation in foraging during the breeding and non-breeding seasons

Overall, there were no marked changes in the diet of Grey-headed Bulbul during the breeding and non-breeding seasons. Fruits were the most preferred food during breeding (66.09%) and non-breeding seasons (63.95%), followed by invertebrates (33.69% and 36.05% respectively), the remaining nectar. However, the fruit species consumed varied between the seasons. *Symplocos cochinchinensis*, *Antidesma menasu*, *Clerodendrum viscosum*, *Syzygium cumini*, and *Litsea floribunda* were the more preferred fruits during the breeding season, and *Maesa indica*, *Callicarpa tomentosa*, *Leea indica*, and *Lantana camara* during the non-breeding season.

Foraging manoeuvres and food handling techniques were consistent during the breeding and non-breeding seasons (Fig. 1). There were significant differences in the height of trees used for foraging (mean ± S.E: 6.41 ±3.39 m *vs* 3.81 ±1.98 m; Mann-Whitney *U*-test: $z = -16.36$; $P < 0.001$) and the foraging height (mean ± S.E: 5.01 ±2.60 m *vs* 2.88 ±1.29 m; Mann-Whitney *U*-test: $z = -18.01$; $P < 0.001$) between the breeding ($n = 1,386$) and non-breeding ($n = 441$) seasons. During the breeding season, birds foraged more in

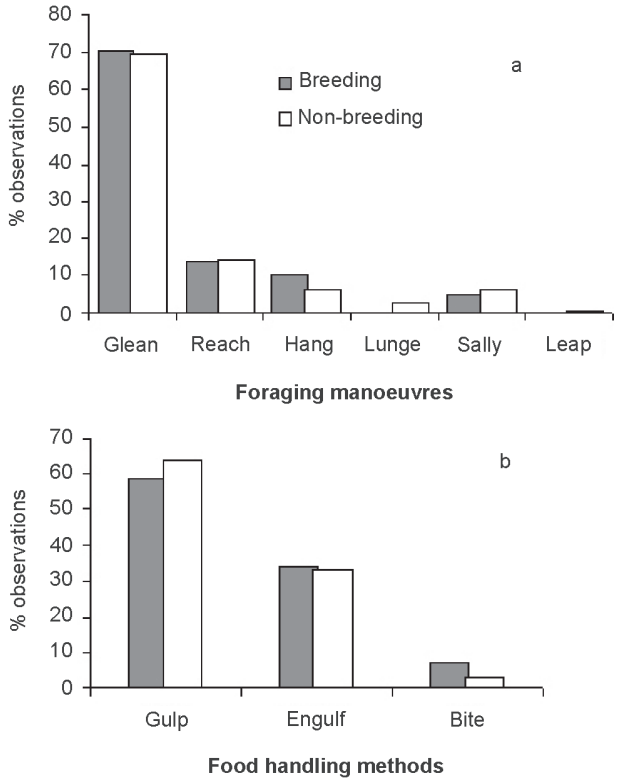

Fig. 1: (a) Foraging manoeuvres and (b) food handling methods of Grey-headed Bulbul during the breeding (n = 1,386) and non-breeding (n = 441) seasons

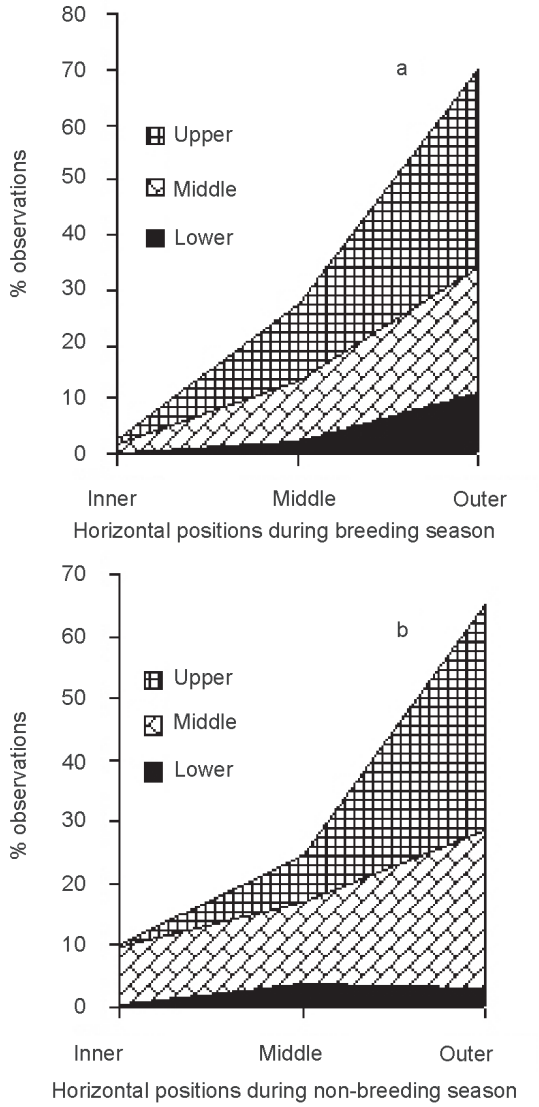

Fig. 2: Horizontal position use in canopy by the Grey-headed Bulbul during the (a) breeding and (b) non-breeding seasons

the upper canopy, while it was more in the understorey shrubs during the non-breeding season, but there was no significant difference in the relative foraging heights (relative to the height of the foraging tree) between the breeding and non-breeding seasons (Mann-Whitney *U*-test: $z = -0.777$; $P = 0.437$). Foraging at the edges was significantly higher than in the inner canopy during both the breeding (Chi-square test: $\chi^2 = 955.94$; $df = 2$; $n = 1{,}384$; $P < 0.01$) and non-breeding seasons (Chi-square test: $\chi^2 = 203.08$; $df = 2$; $n = 440$; $P < 0.01$; Fig. 2).

Annual variation in foraging

There was no significant annual variation in the foraging height use (ANOVA: $F_{2,1382} = 2.783$, $P = 0.062$), but the height of foraging trees (ANOVA: $F_{2,1382} = 21.004$, $P < 0.001$) and the relative foraging heights ($F_{2,1382} = 86.900$, $P = 0.001$) varied between the years (2003–2005) during the breeding seasons (Table 1). In contrast, the yearly variations in all these three parameters were prominent during the non-breeding seasons (ANOVA: $F_{2,438} = 17.525$, 29.236, and 35.093 respectively, $P < 0.001$; Table 1).

Heterogeneity of foraging behaviour within the breeding cycle

The Grey-headed Bulbul showed significant plasticity in foraging behaviour during the different reproductive stages. Although the foraging behaviour varied between the reproductive stages, gleaning was the dominant method in all the stages (Fig. 3). There were significant differences in the mean height of trees used for foraging, and also in the mean foraging height (Table 2). During the incubation and brooding stages, bulbuls foraged on taller trees, however, the relative foraging height was less during these stages ($P < 0.001$, Table 2). Moreover, the birds foraged more in areas with high foliage cover during the incubation and

Table 1: Foraging height, height of the foraging tree, and relative foraging height during the breeding and non-breeding seasons of the Grey-headed Bulbul

Breeding Season					
Variable	2003	2004	2005	*F*	*P*
Foraging height (m)	5.39 ±2.86	4.90 ±2.77	4.99 ±2.20	2.783	0.062
Height of foraging tree (m)	7.36 ±3.95	6.63 ±3.68	5.69 ±2.42	21.004	0.001
Relative foraging height	0.76 ±0.18	0.76 ±0.18	0.89 ±0.17	86.900	0.001
Non-breeding Season					
Variable	2002	2003	2004	*F*	*P*
Foraging height (m)	2.62 ±0.97	3.49 ±1.62	2.77 ±1.24	17.525	0.001
Height of foraging tree (m)	3.66 ±1.61	4.96 ±2.63	3.18 ±1.46	29.236	0.001
Relative foraging height	0.76 ±0.18	0.74 ±0.18	0.90 ±1.70	35.093	0.001

Variable expressed as mean ±SE and *P* values after Bonferroni correction

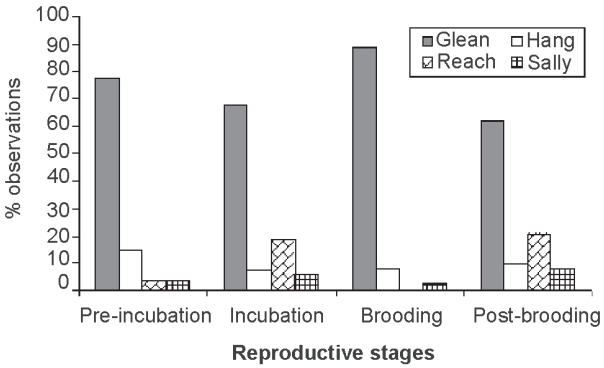

Fig. 3: Foraging methods of Grey-headed Bulbul during the different stages of reproduction (*n* = 324)

brooding stages than the other breeding stages (ANOVA: $F_{3,320} = 7.261$; $P < 0.001$).

Foraging in mixed-species flocks

The Grey-headed Bulbul was recorded foraging in 54 mixed-species flocks during the non-breeding season, associating with a total of 27 species (Table 3). The mean number of species per flock was 6.46 ±2.03 species (range: 3–11 species), and the mean number of individuals per flock was 21.94 ±8.90 birds (range: 8–53 birds). Table 4 gives the foraging niche breadth of ten common species involved in the mixed-hunting flocks, calculated from data on foraging manoeuvre, foraging height, height of the foraging tree, horizontal position in the canopy, and food items. The White-bellied Blue Flycatcher *Cyornis pallipes*, Asian Paradise-Flycatcher *Terpsiphone paradisi*, Common Iora *Aegithinia tiphia*, Grey-headed Canary-Flycatcher *Culicicapa ceylonensis*, and Yellow-browed Bulbul *Iole indica* had larger niche breadths than the Grey-headed Bulbul (Table 4). Even though the Grey-headed Bulbul was recorded to have generalized foraging manoeuvres, food, and use of canopy in mixed-foraging flocks, it is a specialist in terms of the selection of foraging trees and use of foraging heights (Table 4).

Although the foraging niche overlap with the Grey-headed Bulbul was high for some of the foraging attributes, most species exhibited a relatively low, overall foraging niche overlap with it (Table 5). Since most of the species (and the Grey-headed Bulbul) devoured insects during mixed-species foraging, a high overlap (ø >90) for food occurred. Although the Yellow-browed Bulbul and Common Iora showed high overlap in the foraging height with the Grey-headed Bulbul, canopy use varied significantly among them. The foraging intensity of Grey-headed Bulbul differed in the absence or presence of mixed-flocking species, showing a significantly higher feeding rate in mixed-flocks (8.29 ±0.16 pecks/min; $n = 171$) *vs* (4.70 ±0.10 pecks/min in their absence; $n = 240$; ANOVA: $F_{1,409} = 379.604$; $P < 0.001$).

DISCUSSION

Foraging behaviour and diet

The Grey-headed Bulbul uses a number of foraging manoeuvres and food handling techniques, of which gleaning was the most frequently used method to obtain both fruits and invertebrates. Gleaning is an energy conserving foraging technique as it involves only a simple pick of the food items from a nearby substrate without the full extension of legs, neck, or any acrobatic movements. Other manoeuvres such as reach, hang, and sally were used only when a fruit or an insect could not be obtained from a perch. The food handling techniques of the Grey-headed Bulbul were found to vary with the size of food items – handling small fruits and arthropods by engulfing or gulping, and larger fruits such as *Persea macrantha*, *Litsea* spp. and *Syzygium* spp. by biting.

Bulbuls are reported to use a variety of foraging behaviour based on food resources. Ali (1932) reported that the Red-vented Bulbul *Pycnonotus cafer* nipped open mature buds of mistletoe (Loranthaceae) and probed into the exposed corolla tubes for nectar. In Africa, species such as *Criniger barbatus* and *Andropadus tephrolaemus* took all their fruits from a perch, while another species *Andropadus latirostris* frequently used its wings to pick a fruit while fluttering or flying (Moermond 1990). Gleaning of fruits while airborne has also been recorded in the Square-tailed Black Bulbul *Hypsipetes ganeesa* in southern India (P. Balakrishnan, *unpubl*.). The Grey-headed Bulbul used aerial manoeuvres

Table 2: Foraging height, height of the foraging tree, and relative foraging height of Grey-headed Bulbul during the different stages of reproduction

Variable	Pre-incubation	Incubation	Brooding	Post-brooding	*F*	*P*
Foraging height (m)	4.79 ±2.29	6.73 ±2.03	6.08 ±1.84	5.40 ±2.14	14.811	0.001
Height of foraging tree (m)	6.55 ±3.40	9.31 ±2.99	9.31 ±3.16	6.40 ±2.54	22.404	0.001
Relative foraging height	0.76 ±0.16	0.74 ±0.17	0.68 ±0.13	0.86 ±0.17	11.447	0.001

Variables expressed as mean ±SE and *P* values after Bonferroni correction

Table 3: Frequency of occurrence and flock characteristics of mixed-species flocks associated with Grey-headed Bulbul in Muthikkulam Reserve Forest

Sl. No.	Bird species	No. of flocks	Frequency of occurrence	Mean flock size	SE	Min. & Max. no./flock
1	Grey-headed Bulbul *Pycnonotus priocephalus*	54	100.00	1.87	0.39	1-3
2	Indian Scimitar-Babbler *Pomatorhinus horsfieldii*	27	50.00	4.81	1.39	2-7
3	Grey-headed Canary-Flycatcher *Culicicapa ceylonensis*	24	44.44	10.17	5.80	4-24
4	Yellow-browed Bulbul *Iole indica*	19	35.19	2.21	0.92	1-4
5	White-bellied Blue Flycatcher *Cyornis pallipes*	18	33.33	1.78	0.43	1-2
6	White-bellied Treepie *Dendrocitta leucogastra*	17	31.48	5.53	1.55	2-9
7	Asian Paradise-Flycatcher *Terpsiphone paradisi*	17	31.48	1.94	0.43	1-3
8	Common Iora *Aegithinia tiphia*	14	25.93	1.86	0.36	1-2
9	Dark-fronted Babbler *Rhopocichla atriceps*	13	24.07	8.08	2.56	5-12
10	Oriental White-eye *Zosterops palpebrosa*	13	24.07	7.00	2.83	3-13
11	Black-lored Yellow Tit *Parus xanthogenys*	12	22.22	1.83	0.58	1-3
12	Black Drongo *Dicrurus macrocercus*	12	22.22	1.83	0.39	1-2
13	Scarlet Minivet *Pericrocotus flammeus*	11	20.37	2.00	0.00	2-2
14	Greater Racket-tailed Drongo *Dicrurus paradiseus*	11	20.37	1.91	0.30	1-2
15	Common Flameback *Dinopium javanense*	11	20.37	1.82	0.40	1-2
16	Red-whiskered Bulbul *Pycnonotus jocosus*	9	16.67	3.22	3.03	1-11
17	Square-tailed Black Bulbul *Hypsipetes ganeesa*	8	14.81	5.88	3.04	2-12
18	Brown-cheeked Fulvetta *Alcippe poioicephala*	8	14.81	2.13	0.35	2-3
19	Rufous Treepie *Dendrocitta vagabunda*	7	12.96	1.71	0.49	1-2
20	White-cheeked Barbet *Megalaima viridis*	8	14.81	1.75	0.46	1-2
21	Velvet-fronted Nuthatch *Sitta frontalis*	7	12.96	1.86	0.38	1-2
22	Heart-spotted Woodpecker *Hemicircus canente*	7	12.96	1.57	0.53	1-2
23	Black-headed Oriole *Oriolus xanthornus*	6	11.11	1.67	0.52	1-2
24	Asian Fairy-Bluebird *Irena puella*	5	9.26	2.00	0.00	2-2
25	Small Minivet *Pericrocotus cinnamomeus*	5	9.26	1.80	0.45	1-2
26	Black-naped Blue Monarch *Hypothymis azurea*	4	7.41	1.25	0.50	1-2
27	Malabar Barbet *Megalaima malabarica*	2	3.70	1.50	0.71	1-2

Table 4: Foraging niche-breadths of the common bird species recorded in the mixed-species flocks (*n*=10) with Grey-headed Bulbul

Species	Niche breadth					
	Foraging manoeuvre	Foraging height	Foraging tree height	Horizontal position in canopy	Food	Overall
Grey-headed Bulbul	4.25	2.87	2.91	3.65	1.56	3.05
Indian Scimitar-Babbler	2.08	2.11	2.08	1.95	1.42	1.93
Grey-headed Canary-Flycatcher	4.38	4.33	4.92	2.40	1.12	3.43
Yellow-browed Bulbul	2.53	4.74	4.61	3.57	1.69	3.43
White-bellied Blue Flycatcher	3.76	4.38	4.59	5.83	1.10	3.93
White-bellied Treepie	2.87	2.17	3.66	3.90	1.41	2.80
Asian Paradise-Flycatcher	4.15	5.38	4.46	3.85	1.06	3.78
Common Iora	4.03	3.74	2.60	5.33	1.53	3.45
Dark-fronted Babbler	2.34	3.06	2.99	3.84	1.05	2.66
Oriental White-eye	1.34	4.26	3.31	4.27	1.87	3.01

Table 5: Foraging niche overlap of Grey-headed Bulbul with common species in mixed-species flocks (*n*=9)

Species	Niche overlap					
	Foraging manoeuvre	Foraging height	Foraging tree height	Horizontal position in canopy	Food	Overall
Indian Scimitar-Babbler	0.60	0.04	0.15	0.03	0.99	0.36
Grey-headed Canary-Flycatcher	0.88	0.74	0.79	0.02	0.96	0.68
Yellow-browed Bulbul	0.88	0.89	0.78	0.02	0.54	0.62
White-bellied Blue Flycatcher	0.80	0.37	0.49	0.06	0.96	0.54
White-bellied Treepie	0.69	0.02	0.15	0.03	0.97	0.37
Asian Paradise-Flycatcher	0.79	0.49	0.73	0.20	0.96	0.63
Common Iora	0.89	0.86	0.91	0.03	0.99	0.74
Dark-fronted Babbler	0.86	0.52	0.99	0.28	0.96	0.72
Oriental White-eye	0.74	0.74	0.94	0.03	0.32	0.55

while hunting insects among the foliage. The differential strategies used by the Grey-headed Bulbul for obtaining fruits and insects indicate its flexibility in the use of foraging techniques based on the type and size of resources.

Fruits were the most preferred food of Grey-headed Bulbul, followed by insects and nectar. This is similar to patterns reported for the majority of pycnonotids, which are essentially frugivores that augment their diet with a certain amount of arthropod food (Ali and Ripley 1987; Bhatt and Kumar 2001; Fishpool and Tobias 2005; Vijayan 1975). However, a significant number of species, mostly in Africa and Madagascar, are insectivorous, some with quite specialized niches (Fishpool and Tobias 2005). Many open country species are skilled opportunists and extreme generalists. The Yellow-vented Bulbul *Pycnonotus goiavier* of Southeast Asia, for example, has one of the broadest foraging niches yet measured among non-forest passerines studied globally (Fishpool and Tobias 2005). In this study, I did not record any significant variation in the proportionate use of fruits and arthropods by the Grey-headed Bulbul between the breeding and non-breeding seasons.

Although the Grey-headed Bulbul uses similar general foraging strategies for the breeding and non-breeding seasons, there were differences in the foraging height and foraging tree use. During the breeding season, birds foraged at an average height of 5 m, while it was below 3 m during the non-breeding season. Similarly, the height of the trees selected for foraging was also considerably lower during the non-breeding season (3.81 m) than in the breeding season (6.41 m). These variations could be mainly due to the differences in the vegetation structure of the breeding and non-breeding habitats, as they were restricted to the evergreen forests during the breeding season, and in the lowland evergreen forests, moist deciduous forests, and thorny scrub during the non-breeding season. However, the relative foraging height (relative to the height of the foraging tree) was the same during both the seasons, since the species preferred the inner canopy zone, probably to avoid predators and/or to avoid dominant competitors. Although fruits in the majority of the plants were congregated at the periphery, the Grey-headed Bulbul tended to forage inside the canopy, while the other dominant and larger species such as Square-tailed Black Bulbul, Yellow-browed Bulbul, and pigeons foraged at the extreme periphery of the canopy. This indicates that the Grey-headed Bulbul has a specialized foraging niche, presumably due to competition with congeners, and species with similar food resources. The intra-species variation in the heights of the fruit bearing trees could be a plausible reason for the annual variations in the foraging heights.

Behavioural plasticity within the breeding seasons

Birds have to resolve many constraints during incubation and brooding compared to other stages of their life cycle. Changes in foraging behaviour during the different nesting stages have received limited attention, but energy expenditure and acquisition during differing stages of breeding are critical elements in understanding life history strategies (Martin 1987). The Grey-headed Bulbul showed significant variations in foraging behaviour during the different breeding stages. These variations could be considered as the responses of birds to time or energy constraints, or changing prey availability and distribution (Root 1967). During all the stages, breeding bulbuls foraged away from the nest sites, probably to reduce parental activity at the nest sites to help reduce nest predation (Balakrishnan 2007). Similar observations were reported by several authors (e.g., Martin *et al.* 2000; Fontaine and Martin 2006). Foraging in areas with high foliage density during the incubation and brooding stages could reduce

predation risks. Although gleaning was, overall, the most frequently used foraging manoeuvre during the breeding season, energetically expensive manoeuvres such as sallying were higher towards the end of the nestling stage. Feeding rates were significantly higher during the incubation and brooding periods, as reported in many previous studies (Lovette and Holmes 1995; Martin and Karr 1990). The rapid foraging rates during the incubation and nestling stages compared to the egg-laying stage suggests that incubation may also place time constraints on females, requiring them to forage speedily and return to the nest quickly (Dobbs and Martin 1998; Sakai and Noon 1990). The tradeoff between the thermal needs of the eggs and the energy needs of the adult could be overcome by this increased feeding rate. Therefore, it is clear that breeding birds use different behavioural mechanisms to cope with energetic constraints and predation risks.

Mixed-hunting, and its significance in the non-breeding season

Many species of insectivorous birds in both the temperate and tropical latitudes are known to gather in mixed-hunting flocks during the non-breeding season (Chen and Hsieh 2002; Jullien and Thiollay 1998). There could be several advantages for a species to be associated with mixed-hunting flocks. An individual may increase its rate of food capture by associating with other individuals. For example, among the insect-eating birds, flocking may be advantageous because prey may be flushed by the activities of other individuals. Another advantage of flocking behaviour is the reduction in predation rates. Moreover, grouping may have an anti-predator function by the mobbing responses of several species (see Chen and Hsieh 2002; Jullien and Thiollay 1998).

The Grey-headed Bulbul was recorded to participate in mixed-hunting flocks led by different nucleus species during the non-breeding season. The most numerous participants in mixed-species flocks were resident species of the area, most being insectivores. On an average, the flocks consisted of around six species comprising totally *c.* 21 individuals. Although identification of the nucleus species in many of these mixed-species flocks was difficult, the White-bellied Treepie *Dendrocitta leucogastra* and Common Flameback *Dinopium javanense* appeared to be the 'leaders' in several flocks. The alertness of the nucleus species and its propensity to give alarm calls could be the greatest incentive for attendant species to join the flock and exploit them further (Sullivan 1984). Several species appeared as sentinel species, and were recorded giving alarm calls at the approach of predators. The Common Flameback, Indian Scimitar-Babbler *Pomatorhinus horsfieldii*, Dark-fronted Babbler *Rhopocichla atriceps*, and Brown-cheeked Fulvetta *Alcippe poioicephala* gave repeated alarm calls when predators approached. In Peru, Munn (1986) reported that the flock members rely mainly on the alarm calls of the sentinel species in the understorey and canopy flocks. A similar alertness of both nucleus and sentinel species on the approach of predators was common in the flocks observed, which lends support to this foraging efficiency and anti-predator hypothesis, and justifies the participation of the Grey-headed Bulbul during non-breeding season in mixed-hunting flocks.

Preference of arthropod food by the Grey-headed Bulbul during mixed-species flocking resulted in a high food niche overlap with most of the flock members. It hunted for arthropods in the middle or outer canopy, using several foraging manoeuvres, and avoided the upper canopy where the highly niche-overlapping, generalist species such as Yellow-browed Bulbul *Iole indica* and Common Iora *Aegithinia tiphia* were abundant. Although it is restricted to certain heights, apparently due to the presence of other species with similar niches, it showed much generalized foraging manoeuvres and use of horizontal positions in the canopy during flock participation. The Grey-headed Bulbul was seen to associate with flocks having the Square-tailed Black and Red-whiskered Bulbuls at Muthikkulam, but the number of observations was not sufficient to work on niche overlaps. In the lower altitude, non-breeding habitats (scrub forest), it also associated with other bulbuls, namely, Red-vented Bulbul *Pycnonotus cafer* and White-browed Bulbul *Pycnonotus luteolus*. The foraging rate was significantly higher while foraging in mixed-species flocks than those of singletons.

ACKNOWLEDGEMENTS

I thank the Ministry of Environment and Forests, and Science and Engineering Research Board (SERB), Department of Science and Technology, Government of India for funding. For helpful discussions, encouragement, and support during the field work, I would like to thank V.S. Vijayan, L. Vijayan, the late R. Sankaran, P.A. Azeez, L.D.C. Fishpool, K.S.A. Das, S. Suresh, Divin Murukesh, and M. Vimal. I am grateful to the Forest and Wildlife Department of Kerala for permissions, generous support and cooperation, and SACON, JNTBGRI, and WRCT for infrastructure facilities. I thank Karuppusamy, Jose, Mohandas, Mahesh, Sainudheen, Kaliappan, and Mari for field assistance. V.S. Vijayan, K.S.A. Das, A.P. Zaibin, T.N. Bindu and anonymous reviewers provided helpful comments on earlier versions of the manuscript.

REFERENCES

Ali, S. & S.D. Ripley (1987): Handbook of the Birds of India and Pakistan. Compact edn. Oxford University Press, New Delhi.

Ali, S. (1932): Flower-birds and bird-flowers in India. *J. Bombay Nat. Hist. Soc. 35(3)*: 573–605.

Balakrishnan, P. (2007): Status, distribution and ecology of the Grey-headed Bulbul *Pycnonotus priocephalus* in the Western Ghats, India. Ph.D. thesis, Bharathiar University, Coimbatore.

Balakrishnan, P. (2011): Breeding biology of the Grey-headed Bulbul *Pycnonotus priocephalus* (Aves: Pycnonotidae) in the Western Ghats. India. *Journal of Threatened Taxa 3*: 1415–1424.

Basha, S.C. (1999): Forest types of Silent Valley. Pp. 109–116. *In*: Manoharan, T.M., S.D. Biju, T.S. Nayar & P.S. Easa (Eds): Silent Valley Whispers of Reason. Kerala Forest Department, Thiruvananthapuram.

Bhatt, D. & A. Kumar (2001): Foraging ecology of Red-vented Bulbul *Pycnonotus cafer* in Haridwar, India. *Forktail 17*: 109–110.

BirdLife International (2014): Species factsheet: *Pycnonotus priocephalus*. Downloaded from http://www.birdlife.org on 30/10/2014.

Brennan, L.A. & M.A. Morrison (1990): Influence of sample size on interpretations of foraging patterns by Chestnut-backed Chickadees. *Studies in Avian Biology 13*: 187–192.

Chen, C. & F. Hsieh (2002): Composition and foraging behaviour of mixed-species flocks led by the Grey-cheeked Fulvetta in Fushan Experimental Forest, Taiwan. *Ibis 144*: 317–330.

Collar, N.J., M.J. Crosby & A.J. Stattersfield (1994): Birds to watch 2. The world list of threatened birds. BirdLife International, Cambridge.

Dobbs, R.T. & T.E. Martin (1998): Variation in foraging behavior among nesting stages of female red-faced warblers. *Condor 100*: 741–745.

Fishpool, L.D.C. & J.A. Tobias (2005): Family Pycnonotidae (Bulbuls). Pp. 124–253. *In*: del Hoyo, J., A. Eliott & D.A. Christie (Eds): Handbook of the Birds of the World. Vol. 10. Lynx Edicions, Barcelona.

Fontaine, J.J. & T.E. Martin (2006): Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters 9*: 428–434.

Goodale, E., B.Z. Nizam, V.V. Robin, H. Sridhar, P. Trivedi, S.W. Kotagama, U.K.G.K. Padmalal, R. Perera, P. Pramod & L. Vijayan (2009): Regional variation in the composition and structure of mixed-species bird flocks in the Western Ghats and Sri Lanka. *Current Science 97*: 648–663.

Hutto, R.L. (1990): Measuring the availability of food resources. *Studies in Avian Biology 13*: 20–28.

Jullien, M. & J.M. Thiollay (1998): Multi-species territoriality and dynamic of neotropical forest understorey bird flocks. *Journal of Animal Ecology 67*: 227–252.

Krebs, J.R. & A. Kacelnik (1991): Decision making. Pp. 105–136. *In*: Krebs, J.R. & N.B. Davies (Eds): Behavioural Ecology: An Evolutionary Approach. Blackwell Scientific, Oxford.

Lack, D. (1971): Ecological isolation in birds. Blackwell Scientific Publications, Oxford and Edinburgh.

Levins, R. (1968): Evolution in Changing Environments. Princeton University Press, Princeton.

Lovette, I.J. & R.T. Holmes (1995): Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. *Condor 97*: 782–791.

Martin, T.E. (1987): Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics 18*: 453–487.

Martin, T.E. & J.R. Karr (1990): Behavioral plasticity of foraging manoeuvres of migratory warblers: multiple selection periods for niches? *Studies in Avian Biology 13*: 353–359.

Martin, T.E, J. Scott & C. Menge (2000): Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London Series B, Biological Sciences 267*: 2287–2294.

Milinski, M. & G.A. Parker (1991): Competition for resources. Pp. 137–168. *In*: Krebs, J.R. & N.B. Davies (Eds): Behavioural Ecology. An Evolutionary Approach. Blackwell Scientific, Oxford.

Moermond, T.C. (1990): A functional approach to foraging: morphology, behaviour, and the capacity to exploit. *Studies in Avian Biology 13*: 427–430.

Morrison, M.L., C.J. Ralph, J. Verner & J.R. Jehl Jr. (Eds) (1990): *Avian foraging: theory, methodology, and applications.* Studies in Avian Biology No. 13. Cooper Ornithological Society, California.

Munn, C.A. (1986): Birds that 'cry wolf'. *Nature 319*: 143–145.

Nair, P.V. & K. Balasubramanyan (1985): Long-term environmental and ecological impact of multipurpose river valley projects. KFRI Research Report 26. Kerala Forest Research Institute, Peechi.

Pianka, E.R. (1973): The structure of lizard communities. *Annual Review of Ecology and Systematics 4*: 53–74.

Remsen Jr., J.V. & S.K. Robinson (1990): A classification scheme for foraging behaviour of birds in terrestrial habitats. *Studies in Avian Biology 13*: 144–160.

Root, R.B. (1967): The niche-exploitation pattern of the Blue-gray Gnatcatcher. *Ecological Monographs 37*: 317–350.

Sakai, H.F. & B.R. Noon (1990): Variation in the foraging behaviours of two flycatchers: associations with the stage of the breeding cycle. *Studies in Avian Biology 13*: 237–244.

Sridhar, H., G. Beauchamp & K. Shanker (2009): Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Animal Behaviour 78*: 337–347.

Stotz, D.F. (1993): Geographic variation in species composition of mixed species flocks in lowland humid forests in Brazil. *Papéis Avulsos Zoologia 38*: 61–75.

Sullivan, K.A. (1984): Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour 91*: 294–311.

Vijayan, V.S. (1975): Ecological isolation of Bulbuls with special reference to *Pycnonotus cafer cafer* and *P. luteolus luteolus* at Point Calimere, Tamil Nadu. Ph.D. thesis, University of Bombay, Bombay.

Zar, J.H. (1999): Biostatistical Analysis. 4th edn. Prentice-Hall, New Jersey.

■ ■ ■