The Bird Community of a Sandstone Plateau Monsoon Forest at Kakadu National Park, Northern Territory

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Summary

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We describe the bird species composition of a closed forest on sandstone plateau at Kakadu National Park. This bird community is very distinct from that of adjacent vegetation types and has more similarity with that of northern lowland closed forests. However, its bird community differs from that of lowland closed forests in its much lower density and diversity, and in having a different composition of foraging types (notably, fewer arboreal omnivores, large foliage-gleaners, sally insectivores, granivores and frugivores). Density and species diversity is low. There is clear segregation in foraging behaviour between all bird species of the plateau closed forest, in contrast to the richer closed forests of tropical Queensland where foraging groups of bird species may be tightly-packed.

Introduction

Fragmented sandstone ranges occur across northern Australia from the Gulf of Carpentaria to the Kimberleys. More than 20 vertebrate species are restricted to these outcrops, including the White-lined Honeyeater *Meliphaga albilineata*, White-quilled Rock-Pigeon *Petrophassa albipennis* and Chestnut-quilled Rock-Pigeon *P. rufipennis*, and a group of three grass-wrens, the Black *Amytornis housei*, White-throated *A. woodwardi* and Carpentarian *A. dorotheae* (Blakers *et al.* 1984). Additionally, the Banded Fruit-dove *Ptilonopus cinctus* is confined in Australia to the sandstone escarpment of Arnhem Land but also occurs beyond Australia.

Three main vegetation types occur on these sandstone ranges: moderately tall *Eucalyptus* open forest, low woodland of *Eucalyptus* species above a dense spinifex (*Triodia* and *Plectrachne* species) understorey, and closed monsoon forest ('semi-evergreen notophyll' and 'semi-evergreen microphyll vine forests': Webb 1968, 1978). In the Arnhem Land-Kakadu area these closed forests are dominated by the myrtaceous species *Allosyncarpia ternata*. Such forests now occur mainly as small patches in sites topographically protected from fire and their current fragmentary distribution is considered to be relictual (Russell-Smith 1986). Although of similar structure, the escarpment closed forests differ appreciably in floristics from the closed forests of lowland coastal northern Australia, with the sandstone monsoon forests being composed of more autochthonous and fewer Indo-Malesian plant species.

Although there are now detailed inventories of species from escarpment areas, at least in Kakadu National Park (Braithwaite 1985), only one previous work (Kikkawa & Monteith 1980; reiterated in Kikkawa *et al.* 1981) has considered ecology of bird communities of escarpment habitats. Here, we examine the bird community of an unusually large closed forest on a sandstone plateau in Kakadu National Park. The species composition, density and foraging behaviour of this bird community is compared with those of the two other (adjacent) vegetation types of the sandstone plateau, and to those of two closed forests of coastal Northern Territory.

Methods

Study site and vegetation

The study site was a 150 ha monsoon forest patch surrounded by open forest and spinifex-woodland, located on sandstone plateau (13°18'S 132°38'E; altitude 310 m; 70 km SSW of Jabiru; Fig. 1). The climate of the area is monsoonal, with a wet season between about December and March (in which about 85% of an annual average 1500-1600 mm rainfall occurs).

Vegetation was sampled along transects of at least 200 m in all vegetation types. Trees (> 5 cm DBH) were counted along a continuous 10 m wide belt transect, with species, DBH and height recorded for all stems. Understorey and groundcover components were sampled systematically in 1 x 2 m quadrats located every 5 m along the transect. For all quadrats we recorded plant species present, height class of woody species, percentage cover for graminoids and rocks and canopy cover. Vegetation details are summarised in Table 1.

Bird census procedure

Twenty-five 0.1 ha quadrats (31.6 x 31.6 m) were marked and

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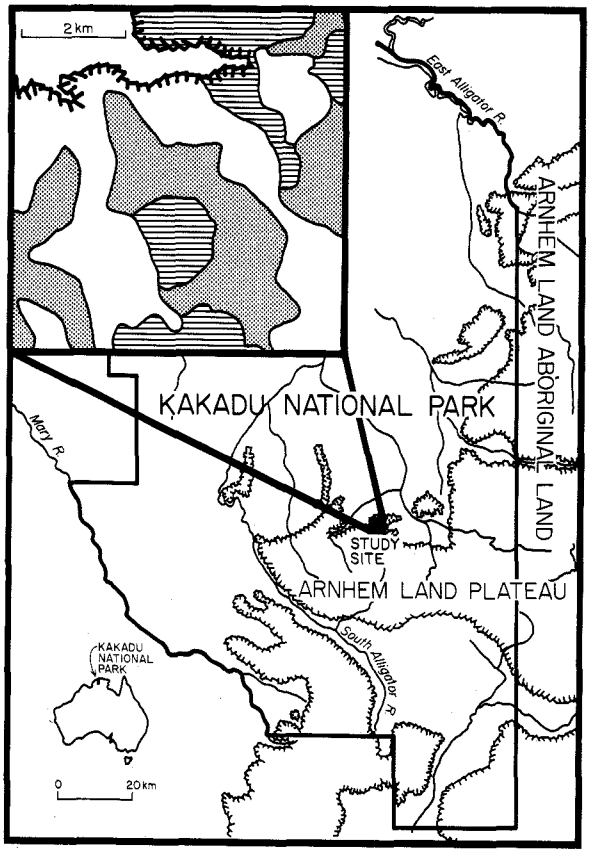

FIGURE 1 Location of study site. Inset shows a vegetation map of the study area, with horizontal shading = monsoon forest; stippling = sandstone *Eucalyptus;* clear = sandstone spinifex.

censused for birds. Ten were in the monsoon forest, five in the *Eucalyptus* open forest, five in the spinifex woodland and five on the monsoon/open forest edge. Quadrats were separated by at least 50 m. Over the period 28 April to 1 May 1987 all quadrats were censused (by JCZW) on ten occasions. Censuses were spread throughout the daylight hours, although concentrated in the early mornings. A census consisted of 3 mins observation during which birds seen or heard in the quadrat were counted. Birds flying over the quadrat were excluded unless obviously hawking or hunting. For every quadrat, counts from all ten censuses were tallied and this tally used to estimate density (no. individuals/ha). Densities from quadrats of like vegetation type were compared with those from other vegetation types using one-way analysis of variance.

We used this quadrat size because vegetation density of monsoon vine forests made censuses of larger quadrats extremely difficult and because we preferred to census repeatedly many small quadrats, rather than making fewer visits to a small number of larger quadrats. We used 3 mins as the census time in a pragmatic compromise between the longer time required to search quadrats completely for birds and an instantaneous census (thereby excluding birds moving into the quadrat during the census

TABLE 1 Vegetation characteristics of the three plateau habitats considered.

	Closed forest	*Eucalyptus* open forest	Spinifex woodland
(a) Structural features			
Basal area (m^2/ha)	33.0	10.0	1.2
Canopy height (m)	24	20	17
Tree density (no./ha)	836	293	70
Canopy cover (%)	75	11	4
(b) Importance value for tree species[1]			
Allosyncarpia ternata	43.5	0	0
Callitris intratropica	16.5	9.2	0
Pouteria sericea	5.0	0	0
Carpentaria acuminata	4.4	0	0
Denhamia obscura	4.2	0	0
Notelaea microcarpa	3.7	0	0
Canarium australianum	2.0	0	0
Sterculia quadrifida	1.2	0	0
Eucalyptus miniata	0	35.1	0
Eucalyptus tetrodonta	0	33.4	19.3
Pandanus spiralis	0	3.8	0
Terminalia carpentariae	0	2.2	2.7
Owenia vernicosa	0	1.6	2.4
Buchanania obovata	0	1.0	0
Xanthostemon paradoxus	0	0	32.8
Eucalyptus arnhemensis	0	0	19.1
Grevillea pteridifolia	0	0.5	10.2
Regelia punicea	0	0	4.4
Eucalyptus kombolgiensis	0	0	3.9
Acacia torulosa	0.4	0	2.9
Verticordia cunninghamii	0	0	2.5
Dead stems	13.1	10.9	0
(c) Occurrence[2] of understorey species, with % > 20			
Scleria brownii	40		
Lomandra sp.	34		
Aristida superpendens	30		
Phyllanthus sp.	30		
Hibbertia sp.		39	
Lomandra tropica		33	
Pachynema junceum		29	
Aristida holathera		26	
Fimbristylis aphylla		23	
Gonocarpus leptothecus		21	
Triodia plectrachnoides			49
Micraira multinervia			40
Sorghum stipoideum			28

[1] Importance value is the sum of relative density and relative basal area, divided by two.

[2] Occurrence of understorey species based on 50 quadrats in closed forest and 80 in each of open forest and spinifex woodland.

period) which would more ideally be used to derive density. In practice, there was very little movement of birds into quadrats while these were being censused, and accordingly our density estimates suffer little bias.

The bird species composition of the three vegetation types were compared using the similarity index:

$$S.I.\ (x,y) = \Sigma \min (P_{xi}, P_{yi})$$

where P_{xi} is the density of species i in vegetation type x divided by the total density of birds in vegetation type x, and P_{yi} is the corresponding value of species i in vegetation type y (Hurlbert 1978).

Wide-ranging searches were also made in all three vegetation types.

Scientific names of birds recorded in this study are given in Tables 2 & 3.

Comparison with lowland sites

In two lowland monsoon forest types (semi-deciduous vine thicket and semi-evergreen monsoon vine forest: Webb 1968), at a site 220 km WNW of the study area, Woinarski *et al.* (1988) censused five 0.25 ha quadrats ten times at a comparable period (8 April to 16 May) of the previous year. The vegetation of these sites is given in Wilson & Bowman (1987). In summary, unit 1 was dominated by *Acacia auriculiformis* (basal area of 4.1 m^2/ha), *Mallotus nesophilus* (0.9 m^2/ha), *Polyalthia holtzeana* (0.7 m^2/ha) and *Syzygium armstrongii* (0.5 m^2/ha), had a canopy cover of 79% and canopy height of 15 m. Unit 4 was dominated by *Nauclea orientalis* (2.0 m^2/ha), *Livistona benthamii* (1.7 m^2/ha), *Acacia auriculiformis* (1.4 m^2/ha), *Barringtonia acutangula* (0.8 m^2/ha) and *Ficus virens* (0.7 m^2/ha), had a canopy cover of 77% and canopy height of 17 m.

The bird community of the sandstone closed forest was compared with these two lowland closed forests, using similarity indices (for overall bird species composition) and *t*-tests (for densities of individual species and all species combined). Similarly, the bird species composition of the plateau *Eucalyptus* open forest was compared with that of two lowland *Eucalyptus* forests of similar structure and floristics (units 8 and 9) surveyed by Woinarski *et al.* (1988). The matrix of similarity indices was illustrated using the dendrogram method of Cody (1974).

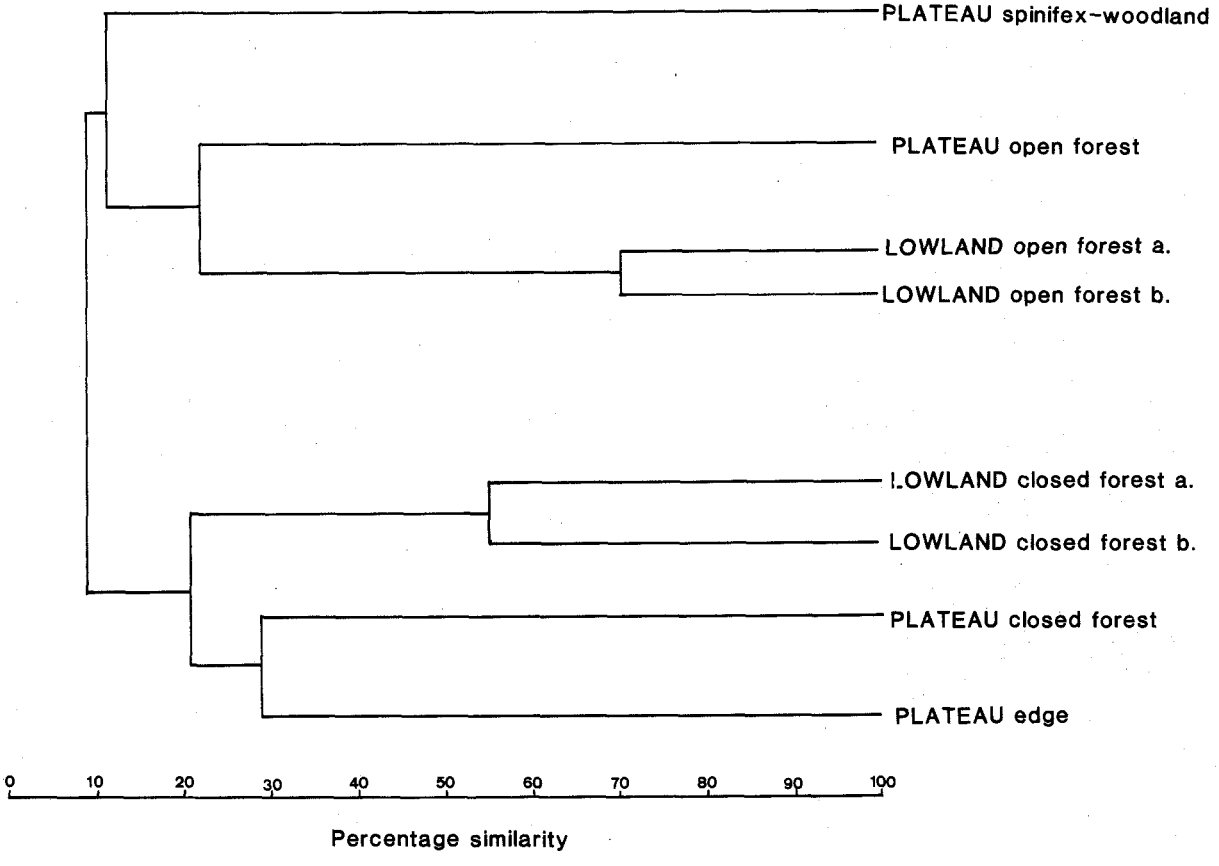

FIGURE 2 Dendrogram of similarity in bird species composition between the three plateau habitats, the plateau closed forest/open forest edge, and four lowland sites censused by Woinarski *et al.* (1988).

TABLE 2 Mean density (No./ha) of bird species recorded in quadrats in the three plateau vegetation types, and monsoon forest/open forest edge. Standard deviations are given in brackets. '+' denotes species recorded in the vegetation type but not in quadrats being censused.

	Monsoon forest	Open forest	Spinifex-woodland	Edge	F[1]
Emu *Dromaius novae-hollandiae*	+	+		+	
Brown Goshawk *Accipiter fasciatus*	+			0.4 (0.6)	
Brown Falcon *Falco berigora*		+			
Chestnut-backed Button-quail *Turnix castanota*			+		
Banded Fruit-Dove *Ptilonopus cinctus*	0.3 (0.5)			0.2 (0.5)	
Peaceful Dove *Geopelia placida*			0.4 (0.9)		
Bar-shouldered Dove *G. humeralis*	+	0.4 (0.9)	0.8 (1.8)	0.8 (0.8)	
Emerald Dove *Chalcophaps indica*	0.5 (0.7)			+	
Common Bronzewing *Phaps chalcoptera*			+		
Chestnut-quilled Rock-Pigeon *Petrophassa rufipennis*		+			
Red-tailed Black-Cockatoo *Calyptorhynchus magnificus*		+			
Sulphur-crested Cockatoo *Cacatua galerita*	+	+		+	
Red-collared Lorikeet *Trichoglossus rubritorquis*	+	0.6 (1.3)	+	1.4 (3.1)	
Varied Lorikeet *Psitteuteles versicolor*	+	0.8 (1.1)	+	+	3.7*
Red-winged Parrot *Aprosmictus erythropterus*		+		+0.4 (0.9)	
Northern Rosella *Platycercus venustus*		0.8 (0.8)	0.2 (0.5)	0.4 (0.9)	
Pheasant Coucal *Centropus phasianinus*		0.4 (0.6)			
Southern Boobook *Ninox novaeseelandiae*	+	+	+	+	
Tawny Frogmouth *Podargus strigoides*	+	+	+	+	
Australian Owlet-nightjar *Aegotheles cristatus*		+	+	+	
Spotted Nightjar *Caprimulgus guttatus*		+	+	+	
Blue-winged Kookaburra *Dacelo leachii*	+	0.2 (0.5)		0.2 (0.5)	
Forest Kingfisher *Halcyon macleayii*	+	+		0.4 (0.9)	
Sacred Kingfisher *H. sancta*		+			
Rainbow Bee-eater *Merops ornatus*		+	+	+	
Rainbow Pitta *Pitta iris*	1.0 (1.5)			+	
White-bellied Cuckoo-shrike *Coracina papuensis*	+	+		+	
White-winged Triller *Lalage sueurii*		+	1.0 (1.7)		
Varied Triller *L. leucomela*	0.4 (0.7)			0.2 (0.5)	
Rufous Whistler *Pachycephala rufiventris*	+	+		0.2 (0.5)	
Little Shrike-Thrush *Colluricincla megarhyncha*	1.2 (1.3)				5.2***
Leaden Flycatcher *Myiagra rubecula*	+	+		+	
Northern Fantail *Rhipidura rufiventris*	0.3 (0.5)			0.4 (0.9)	
Willie Wagtail *R. leucophrys*		+	0.4 (0.6)		
Grey-crowned Babbler *Pomatostomus temporalis*		+	0.6 (1.3)		
Variegated Fairy-wren *Malurus lamberti*			+		
Green-backed Gerygone *Gerygone chloronota*	2.1 (1.4)			0.4 (0.6)	20.9***
Helmeted Friarbird *Philemon buceroides*	0.8 (1.1)	+	0.2 (0.5)	5.8 (8.0)	7.6**
Silver-crowned Friarbird *P. argenticeps*		+	+	0.2 (0.5)	
Blue-faced Honeyeater *Entomyzon cyanotis*		0.2 (0.5)	+	+	
Yellow-throated Miner *Manorina flavigula*		1.4 (1.1)		+	10.7***
Brown Honeyeater *Lichmera indistincta*	0.2 (0.4)	+	+	0.4 (0.6)	
Banded Honeyeater *Certhionyx pectoralis*		+	1.6 (2.5)	0.2 (0.5)	4.0*
Dusky Honeyeater *Myzomela obscura*	+	+	+	0.2 (0.5)	
Mistletoebird *Dicaeum hirundinaceum*	0.2 (0.4)	+	0.4 (0.9)	2.0 (1.6)	6.1**
Striated Pardalote *Pardalotus striatus*		1.0 (0.7)	0.6 (0.6)	0.2 (0.5)	6.9**
Spangled Drongo *Dicrurus hottentottus*	0.7 (1.0)	+		0.8 (0.8)	
Great Bowerbird *Chlamydera nuchalis*	+	+		+	
Australian Magpie-lark *Grallina cyanoleuca*		+	+		
Little Woodswallow *Artamus minor*		+	+		
Grey Butcherbird *Cracticus torquatus*	0.1 (0.3)	1.8 (1.3)	+	+	22.1***
Pied Butcherbird *C. nigrogularis*		0.2 (0.5)			
Torresian Crow *Corvus orru*	+	+	+	+	
No. spp./quadrat	4.7 (1.4)	5.0 (1.8)	3.2 (2.2)	6.8 (1.8)	3.8*
Total density	8.0 (3.2)	7.8 (2.9)	5.6 (5.2)	15.2 (9.0)	3.5*
Diversity index	2.15	2.16	2.23	2.28	

[1] F-ratios are only given where densities differ significantly (based on ANOVA) between habitats. Probability levels: $*P < 0.05$, $** P < 0.01$, $*** P < 0.001$.

Foraging behaviour

Records were made of all birds seen foraging in the escarpment monsoon forest. The behavioural categories of Crome (1978) and Frith (1984) were used in order to allow comparison with their lowland and mountain (respectively) Queensland rainforest bird communities. Up to five foraging records were made per individual bird observed. Heights of foraging birds were recorded using the divisions given by Frith (1984). We also noted the plant species being used by foraging birds. For every bird species we compared use of plant species with the relative abundance of those plant species, using the same formula for Similarity Index given above (such that species which forage unselectively would have a similarity index of 100, while those which select rare plant species have a similarity index close to 0).

Results

Comparisons between plateau habitats

Densities of birds in quadrats of the three plateau vegetation types and the monsoon forest/open forest edge are presented in Table 2. The edge quadrats were richest in number of species and total density and the spinifex-woodland quadrats were poorest. Quadrats in the monsoon forest and *Eucalyptus* open forest had similar bird densities and diversities, although more bird species were recorded in the open forest in general observations.

The bird species composition of the monsoon forest showed little similarity with those of the adjacent vegetation types (Fig. 2). The three most common species in monsoon forest were Green-backed Gerygone, Little Shrike-thrush and Rainbow Pitta; in the open forest, Grey Butcherbird, Yellow-throated Miner and Striated Pardalote; in the spinifex-woodland, Banded Honeyeater, White-winged Triller and Bar-shouldered Dove; and in the forest edge, Helmeted Friarbird, Mistletoebird and Red-collared Lorikeet.

The density of birds in edge habitat was inflated by one quadrat (with density of 31 birds/ha) where a large *Eucalyptus miniata* was flowering; this attracted many friarbirds and lorikeets. If this quadrat is excluded the average density of birds in edge habitat falls to 11.3 birds/ha; however, this is still significantly greater than for monsoon forest ($t = 2.2$, $P < 0.05$) and spinifex-woodland ($t = 4.4$, $P < 0.01$) quadrats.

Bird species diversity was similar for the three plateau habitats and the plateau forest edge (Table 2).

Comparison between lowland and plateau habitats

The plateau monsoon forest had a total bird density of less than one-third that of the two lowland monsoon forests considered (Table 3). The bird species diversity of the plateau monsoon forest was also appreciably less (2.15) than that of the two lowland monsoon forests (3.01 for unit 1 and 3.49 for unit 4). In contrast, there was no significant difference between the plateau and lowland *Eucalyptus* open forests, in bird density (7.8 birds/ha for plateau compared with 10.2 and 7.4 birds/ha for lowland units 8 and 9) or diversity (2.16 compared with 1.89 and 2.22 respectively).

TABLE 3 Species which differed significantly in density between lowland and plateau monsoon forests.

Species	Density[1]		
	Plateau	Unit 1	Unit 4
Rose-crowned Fruit-Dove *Ptilinopus regina*	0	0.5 (0.4)*	
Bar-shouldered Dove *Geopelia humeralis*	0	1.5 (1.0)**	1.4 (0.6)***
Emerald Dove	0.5 (0.7)*	0	
Little Bronze-Cuckoo *Chrysococcyx minutillus*	0	0.7 (0.3)***	
Rainbow Bee-eater *Merops ornatus*	0		0.9 (0.6)**
Varied Triller	0.4 (0.7)	2.8 (1.2)**	2.1 (1.3)*
Grey Whistler *Pachycephala simplex*	0	3.9 (1.7)***	1.2 (0.8)**
Little Shrike-thrush	1.2 (1.3)*	0	
Shining Flycatcher *Myiagra alecto*	0		2.1 (1.0)***
Large-billed Gerygone *Gerygone magnirostris*	0		1.7 (1.0)**
Helmeted Friarbird	0.8 (1.1)*		0
White-gaped Honeyeater *Lichenostomus unicolor*	0		1.0 (0.6)**
Red-headed Honeyeater *Myzomela erythrocephala*	0	1.8 (1.0)**	
Yellow Oriole *Oriolus flavocinctus*	0	3.4 (2.5)**	2.0 (0.8)***
Total density	8.0 (3.2)	27.3 (12.0)**	24.2 (3.3)***

[1] Values shown are means with standard deviations in brackets. Only densities which differ significantly (*t*-test) are shown. Significance levels as for Table 2.

The similarity in bird species composition between plateau and lowland monsoon forests was moderately low, albeit appreciably higher than that between the three escarpment vegetation types. Only three species (Banded Fruit-dove, Grey Butcherbird and Mistletoebird) that were recorded in plateau monsoon forest quadrats were not also recorded in lowland monsoon forests. In contrast, 32 and 37 bird species recorded in lowland monsoon forest quadrats (units 1 and 4 respectively) were not recorded in the plateau monsoon forest quadrats. Species whose density differed significantly between the plateau and lowland monsoon forests are listed in Table 3. The 11 species that had significantly higher densities in lowland forests cover a broad ecological range; two are frugivores, two are nectarivores and the remainder insectivores of varied foraging behaviour. Notably, five species (Grey Whistler, Little Bronze-cuckoo, Large-billed Gerygone, Shining Flycatcher and Red-headed Honeyeater) are typically found at least as commonly in mangrove vegetation (Ford 1982) that occurred near the lowland monsoon forest quadrats.

Foraging behaviour

Because of limited observing time and the low density of birds, the number of foraging records gathered was small (Table 4). We recorded at least ten foraging observations for only 12 species (*cf.* Crome [1978], who had 36 species

TABLE 4 Foraging sites, behaviour and height for birds of the plateau monsoon forest.

Foraging Site	Bird species											
	VT	NF	LST	GBG	HFB	DHE	BHE	RP	MB	ED	LF	SD
(a) Foraging site												
Air	13.5	54.1	6.6	16.7	0	12.0	15.0	0	0	0	33.3	63.6
Leaves	75.0	37.8	49.2	81.3	13.0	32.0	0	0	0	0	66.7	36.4
Trunk	0	0	8.2	0	0	0	0	0	0	0	0	0
Branches	7.7	2.7	21.3	2.1	0	0	0	0	0	0	0	0
Litter	3.8	0	3.3	0	0	0	0	100	0	100	0	0
Flowers	0	0	0	0	87.0	56.0	75.0	0	0	0	0	0
Fruit	0	0	1.6	0	0	0	0	0	95.0	0	0	0
Palm Leaves	0	2.7	1.6	0	0	0	10.0	0	0	0	0	0
Dead Leaves	0	0	4.9	0	0	0	0	0	0	0	0	0
Dead Branches	0	0	3.3	0	0	0	0	0	0	0	0	0
Mistletoe	0	0	0	0	0	0	0	0	5.0	0	0	0
Diversity Index	0.81	0.90	1.50	0.55	0.39	0.94	0.73	0	0.20	0	0.64	0.66
(b) Behaviour												
Flitting	7.7	13.5	3.3	8.3	0	0	0	0	0	0	0	0
Searching	48.1	8.1	70.5	52.1	100	88.0	80.0	100	100	95.5	50.0	18.2
Hovering	1.9	16.2	1.6	10.4	0	0	0	0	0	0	0	0
Sallying	42.3	35.1	21.3	20.8	0	8.0	20.0	0	0	0	41.7	72.7
Hawking	0	21.6	0	4.2	0	4.0	0	0	0	0	8.3	9.0
Spiralling	0	5.4	1.6	4.2	0	0	0	0	0	0	0	0
Scratching	0	0	0	0	0	0	0	0	0	4.5	0	0
Diversity Index	0.99	1.62	0.82	1.37	0	0.44	0.50	0	0	0.18	0.92	0.76
(c) Foraging height (m)												
17.5-25	13.5	5.4	4.9	6.3	8.7	12.0	25.0	0	35.0	0	8.3	63.6
10-17.5	26.9	21.6	13.1	50.0	73.9	64.0	50.0	0	60.0	0	75.0	36.4
5-10	19.2	37.8	32.9	25.0	17.4	16.0	25.0	0	5.0	0	16.7	0
1-5	32.7	35.1	45.9	18.8	0	8.0	0	0	0	0	0	0
< 1	3.8	0	0	0	0	0	0	0	0	0	0	0
Ground	3.8	0	3.3	0	0	0	0	100	0	100	0	0

Abbreviations for bird species and no. of foraging records: VT Varied Triller (52), NF Northern Fantail (37), LST Little Shrike-thrush (61), GBG Green-backed Gerygone (48), HFB Helmeted Friarbird (23), DHE Dusky Honeyeater (25), BHE Brown Honeyeater (20), RP Rainbow Pitta (22), MB Mistletoe bird (20), ED Emerald Dove (22), LF Leaden Flycatcher (12), SD Spangled Drongo (11).

with at least 20 observations, and Frith [1984] 24 species with at least ten observations).

Three species (Helmeted Friarbird, Dusky Honeyeater and Brown Honeyeater) were predominantly nectarivorous (although all probably also took some invertebrates) and foraged mainly on the flowers of a mistletoe *Decaisnina* sp. that grew high in the canopy (Tables 4 & 5). The only other plant flowering in the monsoon forest was *Xanthostemon paradoxus*, whose few individuals also attracted these honeyeaters. The Mistletoebird was a frugivore whose foraging was also restricted to *Decaisnina* sp. The Emerald Dove foraged on the ground for fallen seeds and fruit. All other species considered were insectivorous, of which one (Rainbow Pitta) foraged only from the forest floor.

The remaining six species graded from those that foraged mainly by flitting, sallying and hawking for flying insects (Northern Fantail, Spangled Drongo) to those whose movements were more deliberate and which fed on invertebrates occurring in foliage or on branches (notably Little Shrike-thrush). These species also varied in foraging height. Spangled Drongo, Leaden Flycatcher and Green-backed Gerygone foraged mainly above 10 m; Varied Triller, Northern Fantail and Little Shrike-thrush foraged progressively lower in the understorey. Foraging site and plant species use also separated these species (Tables 4 & 5). Compared with the nectarivorous species, the insectivores were unselective in-their use of plant species (Table 5).

The combined density of all species categorised into foraging groups is given in Table 6 and compared with that for the two lowland sites of Woinarski *et al.* (1988). The plateau monsoon forest had lower densities for all foraging groups. This was especially pronounced for arboreal omnivores (e.g. orioles), large foliage-gleaners (e.g. cuckoos, whistlers), sally insectivores (e.g. fantails), gramnivores and frugivores.

Discussion

The bird community of the plateau monsoon forest was extremely dissimilar to that of adjacent vegetation types and showed more similarity with that of lowland monsoon forests more than 200 km distant. The few species which occurred across all plateau habitats (e.g. Helmeted Friarbird, Mistletoebird, Brown Honeyeater) were observed to forage in only a very limited number of plant species and the distribution of these plant species was not related closely to the identified plant communities. In contrast, the bird species whose local distribution was restricted to plateau monsoon forest used a wide range of the plant species occurring there. This observation, and the occurrence of most of these bird species also in the floristically distinct lowland monsoon forests, suggests that the distribution of these bird species may be related mainly to vegetation structural features.

Frugivorous species may be a notable exception, as their relative restriction to monsoon forests matches the high density and diversity of plant species bearing fleshy fruits in these vegetation types relative to the *Eucalyptus* open forests and woodlands (Taylor & Dunlop 1985; Russell-Smith 1986). The somewhat low density and diversity of frugivores found here in the plateau monsoon forest may

TABLE 5 Plant species used by birds foraging in the plateau monsoon forest. Abbreviations for bird species and sample sizes as in Table 4.

Plant species	Bird species									
	VT	NF	LST	GBG	HFB	DHE	BHE	MB	LF	SD
Allosyncarpia ternata	40.4	45.9	46.4	50.0	13.0	36.0	0	0	33.3	100
Callitris intratropica	23.1	27.0	0	22.9	0	0	15.0	0	41.7	0
Decaisnina sp.	0	0	0	0	73.9	40.0	75.0	100	0	0
Denhamia obscura	5.8	0	0	16.7	0	0	0	0	0	0
Distichostemon arnhemicus	7.7	0	0	0	0	8.0	0	0	0	0
Drypetes lasiogyna	0	10.8	8.9	0	0	0	0	0	0	0
Carpentaria acuminata	0	2.7	3.6	0	0	0	10.0	0	0	0
Notelaea microcarpa	17.3	0	16.1	10.4	0	0	0	0	0	0
Pouteria sericea	5.8	10.8	14.3	0	0	0	0	0	25.0	0
Xanthostemon paradoxus	0	0	0	0	13.0	16.0	0	0	0	0
Other	0	2.7	10.7	0	0	0	0	0	0	0
Similarity Index	69.8	69.3	60.4	67.9	13.0	36.0	19.4	0	54.8	43.5
Diversity Index	1.54	1.39	1.50	1.22	0.75	1.23	0.73	0	1.08	0

TABLE 6 Foraging group composition of plateau and two lowland closed-forest sites.

Foraging group	Plateau		Lowland			
			Unit 1		Unit 4	
	Density (No./ha)	%	Density	%	Density	%
Raptores	0	(0)	0.1	(0.4)	0.2	(0.8)
Terrestrial omnivores	1.0	(12.8)	1.3	(4.8)	1.0	(4.2)
Arboreal omnivores	0.1	(1.3)	0.6	(2.2)	0.7	(2.9)
Large foliage-gleaners	1.6	(20.5)	7.6	(27.9)	5.0	(21.0)
Small foliage-gleaners	2.1	(26.9)	4.0	(14.7)	3.8	(16.0)
Sally insectivores	1.0	(12.8)	2.6	(9.6)	6.2	(26.1)
Aerial hawkers	0	(0)	1.6	(5.9)	0.3	(1.3)
Gramnivores	0	(0)	2.1	(7.7)	2.7	(11.3)
Frugivores	1.0	(12.8)	4.7	(17.3)	2.3	(9.7)
Nectarivores	1.0	(12.8)	2.6	(9.6)	1.6	(6.7)

be due to the very limited period of our survey, which occurred at a time when no major plant species of the monsoon forest was flowering or fruiting. Nonetheless, it is notable that the dominant plant species of the plateau monsoon forests, *Allosyncarpia ternata*, has fruits which are not used by birds (Russell-Smith 1986).

The closed forest structure may determine suitability indirectly for the ground-feeding insectivorous Rainbow Pitta through a high rate of leaf fall and little penetration of light to the forest floor. This results in a relatively dense and moist cover of litter and inhibits grasses whose dense growth is characteristic of other habitats. In turn, these factors may reduce fire frequency, thereby further emphasising differences in litter cover between adjacent closed and open forest formations.

In contrast to lowland monsoon forests, the plateau monsoon forest had low bird species diversity and density. The low diversity may be due to biogeographical factors: the plateau monsoon forests are isolated and typically occur in very small patches. Additionally, they are surrounded by vegetation types that have very dissimilar bird communities. The lack of surface water in the plateau monsoon forest patch that we studied may also have excluded some species characteristically associated with pools or streams (e.g. Shining Flycatcher, Azure Kingfisher *Ceyx azurea*, White-browed Robin *Poecilodryas superciliosa*).

The very different evolutionary history of plateau and lowland monsoon forests, and their consequent differences in plant species composition and origins, may account for the (relatively few) remaining differences between the bird species compositions of these areas. Anomalous is the apparent restriction of the frugivorous Banded Fruit-dove to the plateau monsoon forests (Frith 1972; Kikkawa *et al.* 1981), given the comparatively high fruit availability in lowland monsoon forests and the presumed derivation of this endemic subspecies from a parent taxon in the Lesser Sunda Islands (Frith 1972).

Related to the very low bird species diversity in the plateau monsoon forest is its very simple bird community structure. There were distinct foraging differences between all bird species recorded, with the possible exception of the three nectarivorous species which were not common and had a distinct size and dominance hierarchy. This ecological segregation between species is in marked contrast to the dense packing of species along the foraging dimensions considered by Crome (1978) and Frith (1984) in the species-rich Queensland rainforests.

Elsewhere (e.g. MacArthur *et al.* 1972) island birds have been found to 'compensate' for this simple structure and low diversity by increasing the average population density of individual species such that total density may be similar to that of the more diverse 'continental' patches. Such is not the case for the plateau monsoon forest patch, where no species had unusually high density, and the total density was low relative to that of other rainforests (about 8 birds/ha, *cf.* 24 to 27 birds/ha in lowland Northern Territory monsoon forests [Woinarski *et al.* 1988] and 69 birds/ha in lowland New Guinea rainforests [Bell 1982]). The observed low density may be attributable to seasonal fluctuations in resources, notably the near absence of flowering or fruiting plant species in the escarpment monsoon forest during our study. Conversely, the dry season is characterised by aggregations and high densities of invertebrates (Kikkawa *et al.* 1981) and amphibians (Martin & Freeland in press) inside monsoon forests.

The edge of the escarpment monsoon forest had a higher diversity and density of birds than did the two habitats forming it. This was partly an effect of one particularly rich nectar source in one edge quadrat. No species was confined

to this ecotone, and those species which occurred most commonly in the edge quadrats shared no other obvious ecological characteristics.

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