

Foraging Ecology of Some Insectivorous and Nectarivorous Species of Birds in Forests and Woodlands of the Wet-Dry Tropics of Australia

M.G. BROOKER¹, R.W. BRAITHWAITE² & J.A. ESTBERGS²

¹ CSIRO Division of Wildlife and Ecology, LMB No 4, P.O. Midland W.A. 6056

² CSIRO Division of Wildlife and Ecology, Tropical Ecosystems Research Centre, Private Bag No 44, Winnellie, N.T. 0821

Received 9 May 1989, accepted 4 January 1990

Summary

Brooker, M.G., Braithwaite, R.W. & Estbergs, J.A. (1990). Foraging ecology of some insectivorous and nectarivorous species of birds in forests and woodlands of the wet-dry tropics of Australia. *Emu* **90**, 215-230.

The foraging ecology of 40 species of insectivorous and nectarivorous birds was studied in the monsoon forests, woodlands and open forests of the Kakadu National Park, Northern Territory. Most used a broad range of foraging heights, sites and behaviours. The more specialised species were usually terrestrial or aerial feeders. When taking invertebrates, honeyeaters used a narrower range of foraging strategies than did obligate insectivores. The degree of potential overlap in foraging ecology between species pairs was not related to abundances or morphological similarities. Food-related morphological characters of a species were not strongly related to its foraging ecology. The generalised foraging mode of most species and the apparent lack of interspecific competition are probably attributable to the climatic variability found in this region.

Introduction

An understanding of the ways in which birds exploit the resources available to them in their search for food and shelter is important in predicting the consequences of man-made changes to the environment. The introduction of exotic species, increased tourist activity, controlled burning and the prevention of previously frequent wildfires are but a few examples of disturbances which may change the botanical diversity and structure of our plant communities and thus influence the abundance and diversity of the birds which live in them. The Kakadu National Park is an area in which many recent changes (e.g. the introduction of feral buffaloes *Bubalus bubalis* and their subsequent eradication program; alteration to the traditional burning regime) have highlighted the need for basic biological research in this region so that biological aspects of park management may be improved.

There have been few studies of the foraging ecology of bird communities in the wet-dry tropics of Australia, although Keast (1985) has documented some feeding behaviours of 49 species in the South Alligator region of the Northern Territory. During the period 1980-1983, an ecological survey of Stages I and II of the Kakadu National Park was conducted by the CSIRO Division of Wildlife and Ecology (formerly Division of Wildlife and Rangelands Research) for the Australian National Parks and Wildlife Service. The Kakadu Fauna Survey identified 127 species of birds which feed in woodland, open forest and coastal monsoon forest within the Park (Brooker & Parker 1985). Correspondence analysis of the abundances of these species on 26 survey sites showed a basic division of the

sites into those we classified as monsoon forest versus those as open forest-woodland. The latter showed further, minor gradational differences between the avifauna (Braithwaite *et al.* 1985). This paper describes the insectivorous and nectarivorous bird community in three major habitats within Kakadu National Park (lowland monsoon forest, *Eucalyptus* open forest and *Eucalyptus* woodland [Taylor & Dunlop 1985]). The results are examined for evidence of resource partitioning within the community and for possible morphological relationships between species and their foraging ecology and we discuss some implications of our findings for the conservation of birds in this region.

Methods

Most of our observations were made within the time constraints of field work for the Kakadu Fauna Survey. They were confined therefore to the late dry (August-November) and wet (January-April) seasons and were biased toward the more common and conspicuous species. The bulk of the data was obtained by MGB, who spent a total of 150 hours in monsoon forest, open forest and woodland on Kapalga (Fig. 1) during February and March 1982 and 1983 and in August and September 1983. The data for White-browed Robins *Poecilodryas superciliosa* were obtained by MGB from Riversleigh, Queensland in June 1986. Kapalga observations were made in each habitat at all times of the day. Every feeding bout was recorded, with the following restrictions: (i) if two or more birds of the same species were feeding at the same time, the foraging behaviour of the closest individual was recorded; (ii) if different species were feeding at the same time, the foraging of the rarer species was recorded; (iii) no more than two consecutive bouts were recorded for any individual; (iv) no bird was watched for more than three minutes; (v) foraging behaviour which could be attributed to the presence of the observer (e.g. if the observer put up prey) was excluded; and (vi) feeding attempts where the intended prey escaped capture were not recorded. Further foraging

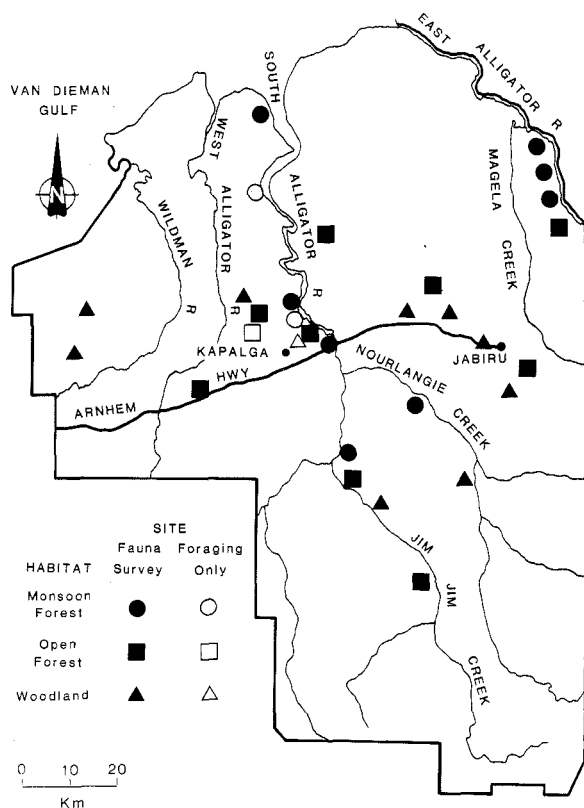


FIGURE 1 Stages I and II of Kakadu National Park, Northern Territory showing locations of study sites.

records were made opportunistically on 26 monsoon forest, open forest and woodland sites (Fig. 1) during the Kakadu Fauna Survey (September 1980–March 1983). Only data on foraging height and site for insectivorous and nectarivorous birds with at least ten records per habitat per season are analysed here (additional foraging information is available from the senior author). Observations from four Escarpment sites were too few to warrant inclusion. The methodology for all observations is described below.

Foraging height

The height at which a bird foraged was estimated to the nearest metre. The observer checked estimates from time to time against trees of known height. The height at which birds perched prior to sally or hawk was also recorded. The observations were assigned to six strata (0 (ground); <1; 1.1–3.9; 4.0–7.9; 8.0–14.0; >14.0 m). The last five are based on discontinuities in the frequency distribution of wet season foliage height classes (Whitbread & Braithwaite unpub. data).

Foraging site

Nine foraging sites were recognised: ground, tree trunk, shrub, inner foliage, outer foliage, air, dead branch, vine and dead leaf.

Foraging behaviour

Seven types of foraging behaviour were recognised. They follow closely those of Crome (1978). (1) *Flitting*: moving rapidly, often tumbling, over and through the substrate which appears to be only briefly examined. The bird usually pursues any arthropods disturbed or dislodged in this manner. The spiralling class of Crome (1978) is included by us in flitting as it was not possible to distinguish consistently between these two types of behaviour. (2) *Gleaning*: moving more slowly and deliberately than when flitting, searching the substrate more thoroughly. It is sometimes difficult to distinguish between gleaning and flitting — where doubt existed gleaning was recorded. (3) *Hovering*: hovering near the substrate. (4) *Sallying*: a direct flight toward prey sighted on a section of the substrate (other than air) remote from the bird. (5) *Hawking*: a flight which results in the capture of a flying insect. This includes cases where a bird disturbed an invertebrate from a substrate other than air and subsequently captured that prey in flight. (6) *Probing*: extracting prey from thick substrates such as dead branches and bunched dead leaves. (7) *Scratching*: is virtually restricted to terrestrial species foraging in litter.

Diet

Whenever possible, the food item was assigned to one of the following classes: seed, fruit, nectar, other vegetable matter, small insect (body length < 20 mm), large insect, vertebrate, carrion, leop. When a honeyeater was feeding at flowers, it was usually possible to distinguish food source (nectar or invertebrate) by the feeding action (see also Ford & Paton 1977). For nectar and fruit items, the species of tree or shrub was recorded.

Morphology, distribution and abundance

Body weights of northern Australian representatives of most species of birds were obtained from specimens housed in the Australian National Wildlife Collection, Canberra and the Western Australian Museum, Perth and from data held by the Australian Bird Banding Scheme, Canberra. Where possible, weights from at least five birds of each sex were used and means for each sex taken. Sufficient data were available for most birds weighing < 200 g. The weights of other species, especially raptors, were estimated from the literature. Other measurements used in this paper were provided by R. Schodde (pers. comm.). Measures of distribution and abundance are given in Appendices 5 and 6 of Braithwaite (1985) (see Brooker & Braithwaite [1988] for description of methodology).

Diversities, overlaps and ratios

We used methods described in detail by Crome (1978) to calculate foraging diversity and foraging overlap of height, site and behaviour for species with ten or more records. Structural overlaps were obtained by averaging site and height overlaps. Simple correlations were calculated between selected physical attributes (bodyweight and bill, wing, tail and tarsus lengths) and our observed foraging diversities and, for each species pair, between the ratios (larger/smaller) and the differences (larger minus smaller) for each of these attributes with their corresponding foraging overlaps. There is evidence (e.g. Hespeneide [1971] for bodyweight) that these measures of morphology are related to the size of the prey eaten.

Results and discussion

Foraging height

A summary of foraging observations in monsoon forest are shown in Table 1. The insectivorous species here were height generalists, except for the Rainbow Pitta *Pitta iris*. Of the rarer diurnal species for which we have no data, only the Bush Thick-knee *Burhinus magnirostris*, Australian Magpie-lark *Grallina cyanoleuca* (ground-feeders) and Pacific Baza *Aviceda subcristata* (canopy-feeder) are likely to be height specialists. Two nocturnal species (Tawny Frogmouth *Podargus strigoides* and Australian Owlet-nightjar *Aegotheles cristatus*) feed mainly on or near the ground. The honeyeaters rarely foraged for insects in the two lowest strata of the monsoon forest, with the White-throated Honeyeater *Melithreptus albobularis* using the canopy more than the other species.

The honeyeaters took invertebrates at higher strata than did the insectivores in monsoon forest (Table 1). This height difference is accentuated if nectar-feeding records

for these species (Table 2) are taken into account. Almost half the nectar-feeding records were in the highest (> 14 m) stratum, as were those of the two other major avian nectarivores, Red-collared Lorikeet *Trichoglossus rubritorquus* and Varied Lorikeet *Psitteuteles versicolor*.

In open forest and woodland (Table 3) the White-bellied Cuckoo-shrike *Coracina papuensis* and Little Friarbird *Philemon citreogularis* foraged for invertebrates in lower strata in the wet than in the dry season. As in monsoon forest, most of the common insectivores in open forest and woodland, apart from the ground-feeding Australian Magpie-lark, were height generalists. The remaining insectivorous species in these habitats are probably also height generalists (Blakers *et al.* 1984) except for seven ground-feeders: Cattle Egret *Ardeola ibis*, Straw-necked Ibis *Threskiornis spinicollis*, Bush Thick-knee, Tawny Frogmouth, Hooded Robin *Melanodryas cucullata*, Golden-

TABLE 1 Observations of birds feeding on invertebrates in monsoon forest during the dry season showing the percentage of records in six height categories and the foraging height diversity (H^1).

Species	n	Foraging Height (m)						H^1
		0	1	2-3	4-7	8-14	> 14	
Rainbow Pitta <i>Pitta iris</i>	10	100						0
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	14			14	21	43	21	1.30
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	17	6	18	18	18	6	35	1.62
White-browed Robin <i>Poecilodryas superciliosa</i>	20	30	15	40	10	5		1.39
Grey Whistler <i>Pachycephala simplex</i>	11			18	82			0.47
Rufous Whistler <i>Pachycephala rufiventris</i>	10			20	70	10		0.80
Little Shrike-thrush <i>Colluricincla megarrhyncha</i>	18	6	11	22	33	17	11	1.65
Leaden Flycatcher <i>Myiagra rubecula</i>	18			28	50	17	6	1.16
Shining Flycatcher <i>Myiagra alecto</i>	23	13	9	30	39	9		1.42
Rufous Fantail <i>Rhipidura rufifrons</i>	20	5	10	35	30	20		1.43
Northern Fantail <i>Rhipidura rufiventris</i>	24	8	21	21	25	17	8	1.71
Willie Wagtail <i>Rhipidura leucophrys</i>	15	33	53	7	7			1.06
White-gaped Honeyeater <i>Lichenostomus unicolor</i>	11				55	45		0.69
White-throated Honeyeater <i>Melithreptus albobularis</i>	12			25		42	33	1.08
Bar-breasted Honeyeater <i>Ramsayornis fasciatus</i>	10			40	20	10	30	1.28
Dusky Honeyeater <i>Myzomela obscura</i>	16				25	69	6	0.78
Spangled Drongo <i>Dicrurus hottentottus</i>	14	14	7	21	21	7	29	1.67

headed *Cisticola exilis* and Rufous Songlark *Cinchorhamphus mathewsi*. The foraging heights of honeyeaters were much the same as those of the insectivores (Table 2), except that honeyeaters did not forage on the ground.

Foraging site

In both monsoon forest and open forest-woodland, only three species (Rainbow Bee-eater *Merops ornatus*, Rainbow Pitta and Australian Magpie-lark) showed marked specialisation for site (Tables 4 & 5). Two species in open forest-woodland (White-bellied Cuckoo-shrike and Little Friarbird) showed differences in site selection between seasons. For both species, ground and shrub sites were used more often in the wet than in the dry (χ^2 tests, $P < 0.01$). In open forest-woodland, there were no significant differences between dry and wet season estimates of foraging site diversity index (H^1), nor between the indices for insectivores and honeyeaters (t -tests, $P > 0.05$). Honeyeaters did not often forage for invertebrates on the ground but, as a group, made use of the other eight sites.

Behaviour

The foraging behaviours of insectivores (Table 6) and nectarivores taking invertebrates (Table 7) have been pooled for seasons and habitats, as differences between these categories were not numerous or large, except for the White-bellied Cuckoo-shrike, which was not recorded flitting in the wet ($n = 20$) whereas flitting comprised 30% of records in the dry season ($n = 37$). Habitat differences were found for the Leaden Flycatcher *Myiagra rubecula* that hawked more ($\chi^2 = 4.0$, $P < 0.05$) and flitted less ($\chi^2 = 4.1$, $P < 0.05$) in monsoon forest than open forest-woodland and the White-throated Honeyeater which used gleanings more often ($\chi^2 = 4.9$, $P < 0.05$) in monsoon forest than in other habitats.

Few species showed specialised foraging behaviours. In spite of the small sample sizes for some species, none used only one technique and only four species (10.5%) used two, whereas 22 species (57.9%) used four or more methods. This applied to nectarivores as well as insectivores. However, as a group, the honeyeaters more often used the less

TABLE 2 Percentage of nectar-foraging observations in six height categories and the foraging height diversity (H^1) for bird species in forest and woodland.

Species	Habitat ¹	Season ²	n	Foraging Height (m)						H^1
				0	1	2-3	4-7	8-14	> 14	
Red-collared Lorikeet <i>Trichoglossus rubritorquis</i>	MF	DW	20			5	5	15	75	0.80
		D	21			10	43	38	10	1.18
		W	14				21	36	43	1.06
Varied Lorikeet <i>Psitteuteles versicolor</i>	OFW	D	16				31	31	38	1.09
		W	20				20	45	35	1.05
Silver-crowned Friarbird <i>Philemon argenticeps</i>	OFW	D	15		7	7	47	20	20	1.36
		W	7				43	29	29	-
Little Friarbird <i>Philemon citreogularis</i>	OFW	D	15			13	53	33		0.97
		W	12			8	25	25	42	1.26
White-throated Honeyeater <i>Meliphreptus albogularis</i>	MF	DW	8		25	25	12	12	25	-
		D	11			9	45	36	9	1.16
		W	29			21	38	38	3	1.18
Brown Honeyeater <i>Lichmera indistincta</i>	MF	DW	7				43	14	43	-
		D	20		5	10	50	30	5	1.24
		W	21		9	24	29	29	9	1.50
Rufous-banded Honeyeater <i>Conopophila albogularis</i>	MF	D	10				10	20	70	0.80
Dusky Honeyeater <i>Myzomela obscura</i>	MF	D	15			7	47	20	27	1.21
		W	8		12	25	25	38		-

¹ MF = monsoon forest; OFW = open forest and woodland

² D = dry season; W = wet season

mobile behaviours of gleaning and probing than did the insectivore group (Tables 6 & 7), although both groups employed flitting. The honeyeaters took more 'falling arthropods' (i.e. arthropods which fell or flew to substrates

below the site when disturbed by the foraging bird Fig. 2) than did the three fantails and the three *Myiagra* spp. that usually took prey attempting to escape horizontally from the point of disturbance ($\chi^2 = 3.98$, $P < 0.05$). The

TABLE 3 Observations of birds feeding on invertebrates in open forest and woodland showing the percentage of records in each of six height categories and the foraging height diversity (H').

Species	Season ¹	n	Foraging Height (m)						H'
			0	1	2-3	4-7	8-14	> 14	
Rainbow bee-eater <i>Merops ornatus</i>	D	20	5	15		40	20	20	1.44
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	D	19	16	5	16	42	16	5	1.55
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	D	28			7	21	50	21	1.20
White-winged Triller <i>Lalage sueurii</i>	W	16	19	12	25	25	19		1.58
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	D	37	8	3	3	19	46	22	1.40
Rufous Whistler <i>Pachycephala rufiventris</i>	D	18	6		11	17	56	11	1.27
Grey Shrike-thrush <i>Colluricincla harmonica</i>	W	6		17		67	17		-
Leadon Flycatcher <i>Myiagra rubecula</i>	D	63	6	5	11	32	36	10	1.52
Northern Fantail <i>Rhipidura rufiventris</i>	W	18		17	17	33	28	6	1.48
Willie Wagtail <i>Rhipidura leucophrys</i>	D	14	43	7		36	14		1.20
Red-backed Fairy-wren <i>Malurus melanocephalus</i>	W	8	25	25	12	12	25		-
Weebill <i>Smicromis brevirostris</i>	D	17				12	82	6	0.58
Varied Sittella <i>Daphoenositta chrysoptera</i>	W	6			17	17	50	17	-
Black-tailed Treecreeper <i>Climacteris melanura</i>	D	29		7	21	38	24	10	1.46
Silver-crowned Friarbird <i>Philemon argenteiceps</i>	W	13		8	15	54	15	8	1.30
Little Friarbird <i>Philemon citreogularis</i>	D	50	24	26	16	16	12	6	1.70
Blue-faced Honeyeater <i>Entomyzon cyanotis</i>	W	25	28	8	32	24	4	4	1.52
White-throated Honeyeater <i>Melithreptus albogularis</i>	D	26	23	4	19	27	23	4	1.60
Brown Honeyeater <i>Lichmera indistincta</i>	W	17	29	12	12	41	6		1.40
Rufous-throated Honeyeater <i>Conopophila rufogularis</i>	D	22	36	23	23	18			1.35
Striated Pardalote <i>Pardalotus striatus</i>	W	7	14	43	14	29			-
Australian Magpie-lark <i>Grallina cyanoleuca</i>	D	58		3	3	17	62	14	1.10
Black-faced Woodswallow <i>Artamus cinereus</i>	W	43		2	12	42	42	2	1.15
	D	11		9		27	36	27	1.29
	W	9			11	11	33	44	-
	D	52	4	8	12	29	42	6	1.46
	W	21	5		10	48	33	5	1.23
	D	21		29	5	29	33	5	1.37
	W	10			30	10	20	40	1.28
	D	26		4	12	27	50	8	1.27
	W	25	8	32	20	24	16		1.52
	D	6			17	67		17	-
	W	8	12	12	50		25		-
	D	56		2	9	36	36	18	1.33
	W	27				44	44	11	0.96
	D	30		3	20	40	37		1.17
	W	11		27	9	18	45		1.24
	D	11		27		18	55		0.99
	W	14		36	14	36		14	1.29
	D	22			14	18	50	18	1.24
	W	11		9		9	73	9	0.89
	D	16	100						0
	D	12	33		8		8	50	1.13
	W	8	12	12		12		63	-

¹ D = dry season; W = wet season

distances travelled (Fig. 2) did not differ between species and most distances were of 3 m or less. The honeyeaters usually took nectar by gleaning or probing flowers, although most species also used hovering.

There were subtle variations within the foraging behaviours of the honeyeaters which probably result in differences in the type of prey taken. When flitting, the friarbirds, especially the Little, scrambled roughly through the foliage — a technique for dislodging arthropods that are then captured as they fall or land below. The White-gaped Honeyeater *Lichenostomus unicolor* and Bar-breasted Honeyeater *Ramsayornis fasciatus* also moved roughly and quickly through foliage but, in addition, fidgeted constant-

ly with their heads, wings and tails. Presumably, this technique uncovered a suite of potential prey not available to the friarbirds. Brown Honeyeaters *Lichmera indistincta*, Dusky Honeyeaters *Myzomela obscura*, Rufous-throated Honeyeaters *Conopophila rufogularis*, Rufous-banded Honeyeaters *C. albogularis* and Banded Honeyeaters *Certhionyx pectoralis* moved actively when foraging but did not fidget or disturb foliage to put up prey. Rather, they moved from site to site in a series of short jumps or flights. The foraging movements of the White-throated Honeyeater were slower than those of the preceding species, with leaf-by-leaf inspections, suggesting that it took cryptic prey. Blue-faced Honeyeaters *Entomyzon cyanotis* often hovered and probed to take arthropods. They were ob-

TABLE 4 Observations of birds feeding in monsoon forest during the dry season showing the percentage use of sites and the foraging site diversity (H^1).

Species	n	Foraging site ¹									H^1
		G	Sh	Tr	DB	V	IF	OF	DL	A	
Rainbow Pitta <i>Pitta iris</i>	10	100									0
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	14			7		14	36	43			1.20
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	17	6			18		6	41		29	1.36
White-browed Robin <i>Poecilodryas superciliosa</i>	20	25	10			10		50		5	1.30
Grey Whistler <i>Pachycephala simplex</i>	11					27	54	18			0.99
Rufous Whistler <i>Pachycephala rufiventris</i>	10	10					40	50			0.94
Little Shrike-thrush <i>Colluricincla megarrhyncha</i>	18	6	17		11	22	33	11			1.65
Leaden Flycatcher <i>Myiagra rubecula</i>	18					6	33	22		39	1.23
Shining Flycatcher <i>Myiagra alecto</i>	23	17	4	13		22	17	17	4	4	1.92
Rufous Fantail <i>Rhipidura rufifrons</i>	20					20	10	5		65	0.98
Northern Fantail <i>Rhipidura rufiventris</i>	24	8		4	4	4	12	8		58	1.39
Willie Wagtail <i>Rhipidura leucophrys</i>	15	33	7	7	7	7				40	1.45
White-gaped Honeyeater <i>Lichenostomus unicolor</i>	11					36	9	45	9		1.16
White-throated Honeyeater <i>Melithreptus albogularis</i>	12						8	67	25		0.82
Bar-breasted Honeyeater <i>Ramsayornis fasciatus</i>	10		10			10	20	50	10		1.36
Dusky Honeyeater <i>Myzomela obscura</i>	16					12	12	56	19		1.16
Spangled Drongo <i>Dicrurus hottentottus</i>	14	14			7		21	28		28	1.51

¹ G = ground; Sh = shrub; Tr = trunk and large branches; DB = dead branches; V = vines; IF = inner foliage; OF = outer foliage; DL = dead leaves; A = air.

TABLE 5 Observations of birds feeding on invertebrates in open forest and woodland, showing the percentage use of sites and foraging site diversity (H¹).

Species	Season ¹	n	Foraging site ²								H ¹
			G	Sh	Tr	DB	IF	OF	DL	A	
Rainbow Bee-eater <i>Merops ornatus</i>	D	20	5					5		90	0.39
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	D	19	21	5			10	53		10	1.29
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	D	28					7	89		4	0.41
	W	16	19	38		6		38			1.22
White-winged Triller <i>Lalage sueurii</i>	D	37	8				30	54	5	3	1.15
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	D	18	6	6	11		17	39		22	1.56
	W	6					17	66		17	-
Rufous Whistler <i>Pachycephala rufiventris</i>	D	63	6	3	2	6	32	51			1.23
	W	18				6	50	39		6	1.04
Grey Shrike-thrush <i>Colluricincla harmonica</i>	D	14	36	7	7		43		7		1.30
	W	8	25	25	12		25	12			-
Leaden Flycatcher <i>Myiagra rubecula</i>	D	17			6		12	65	6	12	1.12
	W	6				17	33	50			-
Northern Fantail <i>Rhipidura rufiventris</i>	D	29			3	3	3	21		69	0.93
	W	13					15	8		77	0.69
Willie Wagtail <i>Rhipidura leucophrys</i>	D	50	22		10	2	12	6		48	1.42
	W	25	24		8		8	8		52	1.29
Grey-crowned Babbler <i>Pomatostomus temporalis</i>	D	26	31		27	15	19	4	4		1.57
	W	17	24	6	24	35	6	6			1.55
Red-backed Fairy-wren <i>Malurus melanocephalus</i>	D	22	27	50		4	14	4			1.25
	W	7	14	43			29	14			-
Weebill <i>Smicromis brevirostris</i>	D	58		3	2	2	17	76			0.77
	W	43					5	95			0.19
Varied Sittella <i>Daphoenositta chrysoptera</i>	D	11			54	18	27				0.99
	W	9			56	22	22				
Black-tailed Treecreeper <i>Climacteris melanura</i>	D	52	6	4	77	4	10				0.88
	W	21	5		71	10	10	5			0.98
Silver-crowned Friarbird <i>Philemon argenteiceps</i>	D	21		10	5	5	24	43	5	10	1.59
	W	10		10				50		40	0.94
Little Friarbird <i>Philemon citreogularis</i>	D	26			8		42	46	4		1.04
	W	25	4	32		4	8	44		8	1.39
Blue-faced Honeyeater <i>Entomyzon cyanotis</i>	D	6			33		33	17	17		-
	W	8	12	12	12		50	12			-
White-throated Honeyeater <i>Melithreptus albogularis</i>	D	56		2	7		21	61	5	4	1.17
	W	27				7	18	70		4	0.86
Brown Honeyeater <i>Lichmera indistincta</i>	D	30		10	7		23	43	7	10	1.52
	W	11		9	9		9	64		9	1.16
Rufous-throated Honeyeater <i>Conopophila rufogularis</i>	D	11		27			27	45			1.07
	W	14		29			36	21		14	1.33
Striated Pardalote <i>Pardalotus striatus</i>	D	22					14	86			0.40
	W	11		9			18	73			0.76
Australian Magpie-lark <i>Grallina cyanoleuca</i>	D	16	100								0
Black-faced Woodswallow <i>Artamus cinereus</i>	D	12	33							67	0.64
	W	8	12			12				75	-

¹ G = ground; Sh = shrub; Tr = trunks and large branches; DB = dead branches; IF = inner foliage; OF = outer foliage; DL = dead leaves; A = air² D = dry season; W = wet season

TABLE 6 Percentages of foraging observations of insectivorous species according to behaviour and the foraging behaviour diversity (H¹).

Species	n	Foraging behaviour ¹						H ¹
		Fl	Gl	Ho	Sa	Ha	Pr	
Rainbow Bee-eater <i>Merops ornatus</i>	34				9	91		0.30
Rainbow Pitta <i>Pitta iris</i>	10		80					0.50
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i>	19	5	21		63	11		1.01
White-bellied Cuckoo-shrike <i>Coracina papuensis</i>	57	19	16	3	58	3		1.16
White-winged Triller <i>Lalage sueurii</i>	36	39	55		3	3		0.89
Lemon-bellied Flycatcher <i>Microeca flavigaster</i>	42	12	2	2	62	21		1.06
White-browed Robin <i>Poecilodryas superciliosa</i>	20				95	5		0.20
Grey Whistler <i>Pachycephala simplex</i>	11	45	55					0.69
Rufous Whistler <i>Pachycephala rufiventris</i>	82	26	44	4	24	1	1	1.28
Little Shrike-thrush <i>Colluricincla megarrhyncha</i>	18	17	72		11			0.78
Grey Shrike-thrush <i>Colluricincla harmonica</i>	15	13	80		7			0.63
Leaden Flycatcher <i>Myiagra rubecula</i>	38	47	5	13	13	21		1.37
Shining Flycatcher <i>Myiagra alecto</i>	29	38	24	7	28	3		1.37
Restless Flycatcher <i>Myiagra inquieta</i>	13	8	8	8	38	31	8	1.52
Rufous Fantail <i>Rhipidura rufifrons</i>	25	20	4	8	4	64		1.07
Northern Fantail <i>Rhipidura rufiventris</i>	68	12	1		13	74		0.81
Willie Wagtail <i>Rhipidura leucophrys</i>	89	34	2	3	22	37	1	1.32
Grey-crowned Babbler <i>Pomatostomus temporalis</i>	39		62				33	0.82
Red-backed Fairy-wren <i>Malurus melanocephalus</i>	30	30	60		10			0.90
Weebill <i>Smicrornis brevirostris</i>	79	18	62	19		1		0.97
Green-backed Gerygone <i>Gerygone chloronata</i>	11	18	73	9				0.76
Varied Sittella <i>Daphoenositta chrysoptera</i>	17	12	76				12	0.71
Black-tailed Treecreeper <i>Climacteris melanura</i>	70	6	73				21	0.72
Striated Pardalote <i>Pardalotus striatus</i>	35		97	3				0.13
Spangled Drongo <i>Dicrurus hottentottus</i>	10		20	10	30	40		1.28
Australian Magpie-lark <i>Grallina cyanoleuca</i>	14	7	86					0.51
Black-faced Woodswallow <i>Artamus cinereus</i>	19		5	21	74			0.71

¹ Fl = flit; Gl = glean; Ho = hover; Sa = sally; Ha = hawk; Pr = probe; Sc = scratch.

served probing under the eaves on buildings and down roadside pipes and hovering to take prey from the top of grass — all sites favoured by Red-backed Spiders *Latrodectus* sp. in this region.

We recorded 18 instances where one species appeared to exploit the foraging behaviour of another in order to capture prey. These involved Shining Flycatcher *Myiagra alecto* ($n = 1$) exploiting Grey Whistler *Pachycephala simplex*; Restless Flycatcher *Myiagra inquieta* ($n = 1$) with Black Butcherbird *Cracticus quoyi*; Rufous Fantail *Rhipidura rufifrons* ($n = 2$) with Grey Whistler and Little Shrike-thrush *Colluricincla megarhyncha*; Northern Fantail *Rhipidura rufiventris* ($n = 3$) with Rufous Whistler *Pachycephala rufiventris*, Green-backed Gerygone *Gerygone chloronata* and Varied Sittella *Daphoenositta chrysoptera*; and Willie Wagtail *Rhipidura leucophrys* ($n = 11$) with Partridge Pigeon *Petrophassa smithii* ($n = 1$), White-winged Triller *Lalage sueurii* ($n = 1$), Rufous Whistler ($n = 5$), Varied Sittella ($n = 1$) and Black-tailed Treecreeper *Climacteris melanura* ($n = 3$). The activity of the exploiter species was characterised by its close proximity to the exploited species (usually within 2 m) and by the way in which it followed and usually faced the bird being exploited. This behaviour, which is rare among passerines according to Robbins (1981), was found in both wet and dry seasons and may be an important feeding tactic for *Rhipidura* spp.

With the exception of the aerial feeding Rainbow Bee-eater and the ground-feeding Rainbow Pitta and Australian Magpie-lark, most of the 38 species studied used a variety of foraging behaviours. A classification by feeding behaviour of all species whose diet includes invertebrates (Table 8) shows that the majority of insectivores and nectarivores were gleaners. Species which take fruit, seed and/or vertebrates, as well as invertebrates, were mainly gleaners or salliers.

Foraging overlap

All species-pairs were examined for structural (height and site) and behavioural overlaps within monsoon forest and open forest-woodland. These comparisons included some pairs comprising obligate insectivores and honeyeaters taking invertebrates.

In monsoon forest, five species-pairs (Grey Whistler and Rufous Whistler; Leaden Flycatcher and Rufous Fantail; Leaden Flycatcher and Northern Fantail; Rufous Fantail and Northern Fantail; Bar-breasted Honeyeater and Dusky Honeyeater) showed high structural and behavioural overlaps (> 0.6) and were similar in bodyweight and bill length (ratios < 1.5). Rufous Whistlers were common in this habitat only in the dry season (Brooker & Parker 1985). Leaden Flycatchers and Northern and Rufous Fantails

TABLE 7 The percentages of observations on foraging behaviour for honeyeaters feeding on invertebrates and their foraging behaviour diversity (H^1).

Species	n	Foraging behaviour ¹						H^1
		Fl	Gl	Ho	Sa	Ha	Pr	
Silver-crowned Friarbird <i>Philemon argenticeps</i>	23	30	30	4	9	22	4	1.54
Little Friarbird <i>Philemon citreogularis</i>	52	33	44	2	10	6	6	1.36
Blue-faced Honeyeater <i>Entomyzon cyanotis</i>	13	8	15	31		8	38	1.41
White-gaped Honeyeater <i>Lichenostomus unicolor</i>	25	8	68		8		16	0.96
White-throated Honeyeater <i>Melithreptus albogularis</i>	90	12	71	3	3	2	8	1.01
Brown Honeyeater <i>Lichmera indistincta</i>	43	35	37	14	2	5	7	1.43
Bar-breasted Honeyeater <i>Ramsayornis fasciatus</i>	17	12	47	24		18		1.25
Rufous-banded Honeyeater <i>Conopophila albogularis</i>	11	9	82				9	0.60
Rufous-throated Honeyeater <i>Conopophila rufogularis</i>	24	17	50	12	8	8	4	1.45
Banded Honeyeater <i>Certhionyx pectoralis</i>	10	10	60	30				0.90
Dusky Honeyeater <i>Myzomela obscura</i>	24	12	58	8	8		12	1.25

¹ Fl = flit; Gl = glean; Ho = hover; Sa = sally; Ha = hawk; Pr = probe; Sc = scratch.

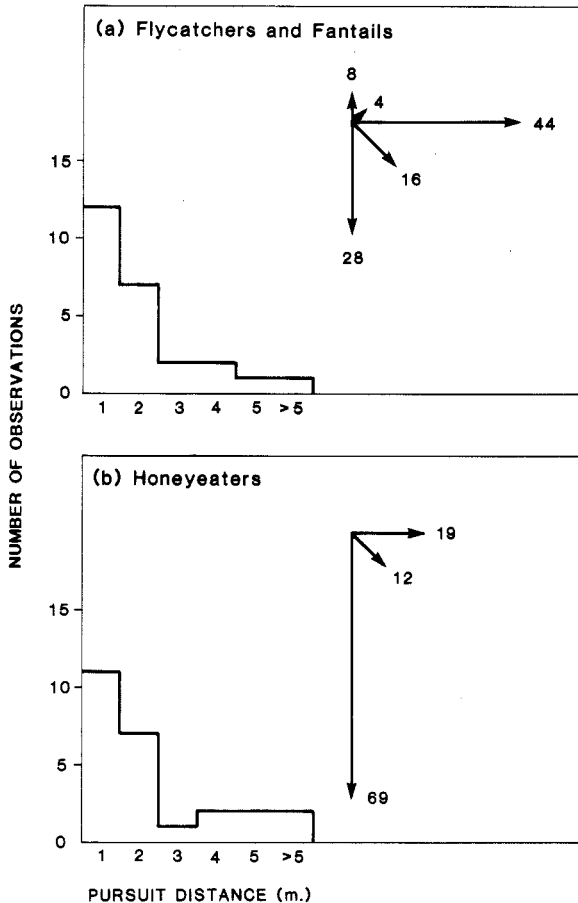


FIGURE 2 Length and angle of pursuit flights of birds capturing invertebrates which were disturbed or dislodged from foraging substrate. Numbers indicate the percentage of flights in the direction indicated.

appear to have similar feeding ecologies and all three species are present in monsoon forest in the late dry season (Brooker & Parker 1985). The Bar-breasted Honeyeater appears to have a similar foraging ecology to the Dusky Honeyeater, but they show habitat differences — the Dusky is found in monsoon forest whereas the Bar-breasted is most common in riparian forest, especially paperbark (Storr 1977).

Five species-pairs in open forest-woodland were similar in feeding ecology, bodyweight and bill length; i.e. White-winged Triller and Rufous Whistler (dry season only); Weebill *Smicromis brevirostris* and Striated Pardalote *Pardalotus striatus*; Striated Pardalote and White-throated Honeyeater; Silver-crowned Friarbird *Philemon argenticeps* and Little Friarbird (dry season only); White-throated Honeyeater and Brown Honeyeater. Although overlapping

in our data, the Weebill uses flitting and hovering more often than the Striated Pardalote. There may be a floristic difference in preferred foraging sites as our observations associate pardalotes with *Eucalyptus* species (91% of records) compared with only 72% for Weebills. Similarly, Morton & Brennan (in press) found that, in northern Australia, Weebills are strongly associated with *Terminalia ferdinandiana*. This differs from the situation in eastern Australia where both Weebills and pardalotes feed almost exclusively on eucalypts (Woinarski 1985).

The relationships between estimated abundances of members of the species pairs identified above were examined using data from six censuses of 26 forest and woodland sites made during the Kakadu Fauna Survey (Brooker & Parker 1985). Of the correlations obtained, few were negative and all those significant were positive. Other evidence of interspecific competition for food resources was sought by calculating correlations of structural overlap for all species pairs with differences in some morphological characters which could be related to feeding ecology. The characters examined were bill, wing, tail and tarsus length and bodyweight, and the differences were expressed both as $A - B$ and as A / B where $A > B$. In monsoon forest, significant correlations ($P < 0.05$, $n = 120$) were obtained for actual and ratio differences in bodyweight and wing length. This relationship was strongest for species pairs ($n = 48$) containing an insectivore and a honeyeater (In/He) — correlations for In/In and He/He pairs alone were not significant ($P > 0.05$). No significant relationships were found for species pairs taking invertebrates in open forest-woodland.

Foraging diversity and morphological characters

The only significant correlations obtained between the physical attributes of a bird and our observed foraging diversities showed a positive relationship between tail length and structural (height and site) diversity in two sets of the data: monsoon forest in the dry season, $r = 0.497$, $P < 0.05$, $n = 17$; and open forest-woodland in the wet season, $r = 0.718$, $P < 0.01$, $n = 13$. This suggests that the greater manoeuvring ability of species with longer tails (Welly 1962) enables them to exploit a broader foraging niche than shorter tailed species. The correlations could be spurious since our comparisons are made across genera. However, the relationship holds for some comparisons within genera (Black-faced Cuckoo-Shrike and White-bellied Cuckoo-Shrike in the dry; Northern Fantail and Willie Wagtail in both wet and dry). In all three cases, the species with the longer tail or the higher tail length to cube root bodyweight ratio has the higher structural foraging diversity.

Diet

It was not possible to identify most of the invertebrate prey.

TABLE 8 The number of species of forest and woodland birds according to diet and modal foraging behaviour.

Modal foraging behaviour	Diet				Total
	Invertebrate	Invertebrate + nectar	Invertebrate + fruit/seed	Invertebrate + vertebrates	
Flitting	3				3
Gleaning	25	13	10	2	50
Hovering	0				0
Sallying	8		1	12	21
Hawking	13				13
Probing	0	1			1
Scratching	1		1		2
Total	50	14	12	14	90

The majority were small (bodylength < 20 mm) although ten of 32 bird species with > 10 records took some larger insects, the proportion of larger prey being less than 10% in all cases. Most of the heavier species (two cuckoo-shrikes, Rufous Whistler, Grey-crowned Babbler *Pomatostomus temporalis*, Black-tailed Treecreeper, two friarbirds) took some large insects, as did three of the smaller birds (Lemon-bellied Flycatcher *Microeca flavigaster*, Leaden Flycatcher, Northern Fantail). Other observations on the *Halcyon* kingfishers and the Black Butcherbird showed that they also include large insects in their diets (Brooker unpubl.).

Some of the insectivores and honeyeaters also take food items other than invertebrates and nectar. There was one record each of a White-bellied Cuckoo-shrike and an Australian Magpie-lark preying on small lizards. Several species included fruit in their diets: White-bellied Cuckoo-shrike (3/64 feeding records), White-winged Triller (1/38), Little Friarbird (1/52), Blue-faced Honeyeater (1/15) and Striated Pardalote (1/34). In all cases, the fruit was a *Ficus* sp. except for the Striated Pardalote (*Amyema* sp.). Silver-crowned Friarbirds and White-gaped Honeyeaters also occasionally feed on fruit (Pyke 1980). Sources of nectar for lorikeets and honeyeaters are shown in Figure 3. The genera exploited agree with those considered by Taylor & Dunlop (1985) to be the most favoured sources of nectar in this region; i.e. *Syzygium*, *Eucalyptus*, *Melaleuca*, *Xanthostemon*, *Grevillea*, *Planchonia*, *Erythrophleum*, *Lophos-temon* and *Hakea*. Other nectarivorous taxa in the region which may compete with the honeyeaters and lorikeets are the Northern Blossom-bat *Macroglottus lagochilus* (body-weight 14 g, Strahan 1983), two species of flying-fox *Pteropus scapulatus* (360 g) and *P. alecto* (600 g) and the arboreal rodents *Mesembriomys gouldii* (600 g) and *Coni-lurus penicillatus* (150 g).

Manna, honeydew and lerp (as defined by Yen [1983])

and sap, as well as nectar, are important energy sources in the diet of honeyeaters and pardalotes in south-eastern Australia (Recher *et al.* 1985). We have only two records of feeding on lerp (Varied Lorikeets and Little Friarbirds) which suggests that it is less important as a food source in the Northern Territory than in southern Australia, at least during the months when our observations were made.

Discussion

Foraging strategies

Our results show that most species of insectivores and honeyeaters tend to have generalised feeding ecology; only a small number show specialisation in foraging height, site or behaviour. Levins (1968) suggested that species with broad niches are more likely to be found in climatically variable environments than are those with narrow niches. Therefore the paucity of specialists in our habitats may reflect the unpredictable and relatively harsh climate. The long, hot dry season and wet season alternate annually, but the wet season varies considerably in commencement time, length and intensity (Ridpath 1985; Taylor & Tulloch 1985), as does the fire regime (Braithwaite & Estbergs 1985). Fire intensity is largely determined by the phenological state of the vegetation and prevailing weather conditions over the long fire season from March to December. However, the abundance of different animal species is affected by their vulnerability to this range of fire regimes (e.g. Braithwaite 1987).

Although there are no detailed studies of any of the 60 species of insectivorous and nectarivorous birds in this region, available information can be used to classify species according to broad foraging zones. Figure 4 illustrates such a system for the insectivores found in monsoon forest, open forest and woodland habitats in Kakadu National Park. This provides a preliminary description of

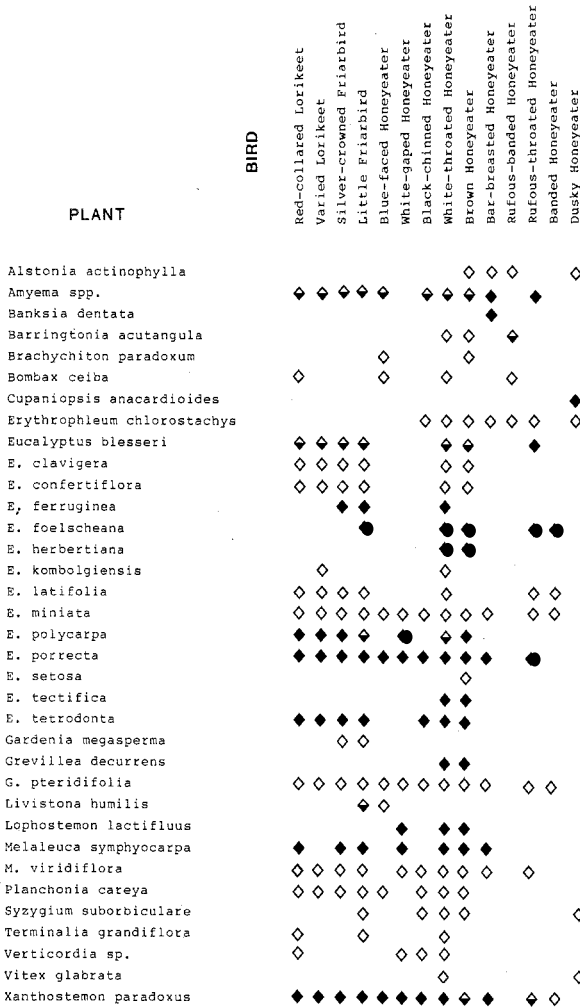


FIGURE 3 Species of trees and shrubs used as sources of nectar by lorikeets and honeyeaters (◆ = dry season; ◆ = wet season; ◆ = both seasons).

the system and suggests management options. More than half of the insectivores take some or all of their prey from the ground or from shrubs and grass. For all open forest and woodland species, 30% feed almost exclusively on the ground and a further 25% obtain part of their diet there (Brooker *et al.* 1985). The lower strata are the most affected by fire and fluctuations in water availability thus maximising their impact on the avifauna. The needs of this large ground and shrub-foraging guild should therefore be considered in the formulation of fire management plans in this region. A range of fire types throughout the year might increase the habitat diversity within open forest and woodland with a positive effect on the diversity of bird species.

An examination of bird lists provided for forests in south-eastern Australia (Nix & Brooker 1978; Lyon 1980; Brooker 1981, Smith 1984, Recher *et al.* 1985) and for Jarrah forest in the south-west (Kimber 1972) shows that the proportion of the insectivorous guild which feeds to some extent on the ground is approximately half of that found in Kakadu open forest and woodland. However, the number and percentage of species which feed exclusively on the ground are higher in the south-east forests (12-14, 30-33%) than at Kakadu (8, 20%), whereas the figures for the south-west Jarrah forest (6, 21%) are comparable to Kakadu. The south-west Jarrah forests probably experience a fire frequency regime more like that of Kakadu than does south-eastern Australia. However, a number of factors other than fire regime could explain these differences (e.g. biogeography, soil, climate, topography), further discussion of which is beyond the scope of this paper.

Insectivores vs. honeyeaters

The main structural difference between the foraging of insectivores and honeyeaters is that the latter rarely feed on the ground. Similar results have been obtained for honeyeaters in temperate Australian habitats (e.g. Ford & Paton 1976; Collins & Briffa 1982).

Honeyeaters in monsoon forests of the Northern Territory confined their foraging for invertebrates to higher vegetation strata than did the insectivores, which used all heights. This observation agrees with Frith (1984) who found that 'mixed feeders' which included honeyeaters, foraged higher than insectivores in upland tropical rainforest in North Queensland and with the data of Crome (1978, Table 3) which show the same trend in lowland rainforest in north Queensland. However, Bell (1982) recorded significant foraging activity by at least four species of honeyeater in his lowest stratum (0-1 m) in New Guinea lowland rainforest.

When taking invertebrate prey, honeyeaters have a narrower spectrum of foraging behaviours than insectivores. No honeyeaters were true aerial predators and none used terrestrial behaviours such as scratching. Honeyeaters were not exploited by insectivores which feed commensally with other species, possibly because of the interspecific aggression sometimes shown by honeyeaters (e.g. Dow 1977).

Most of the honeyeaters have longer bills relative to size than the insectivores (Fig. 5). The position of four species (Black-chinned Honeyeater *Melithreptus gularis*, White-throated, Rufous-banded and Rufous-throated Honeyeaters) on the regression line suggests that they are the most insectivorous of the honeyeater guild (see Ford & Paton 1977). The figure also demonstrates the paucity of smaller long-billed honeyeater genera (e.g. *Acanthorhynchus* and *Phylidonyris*) in this region where many of the flowers are

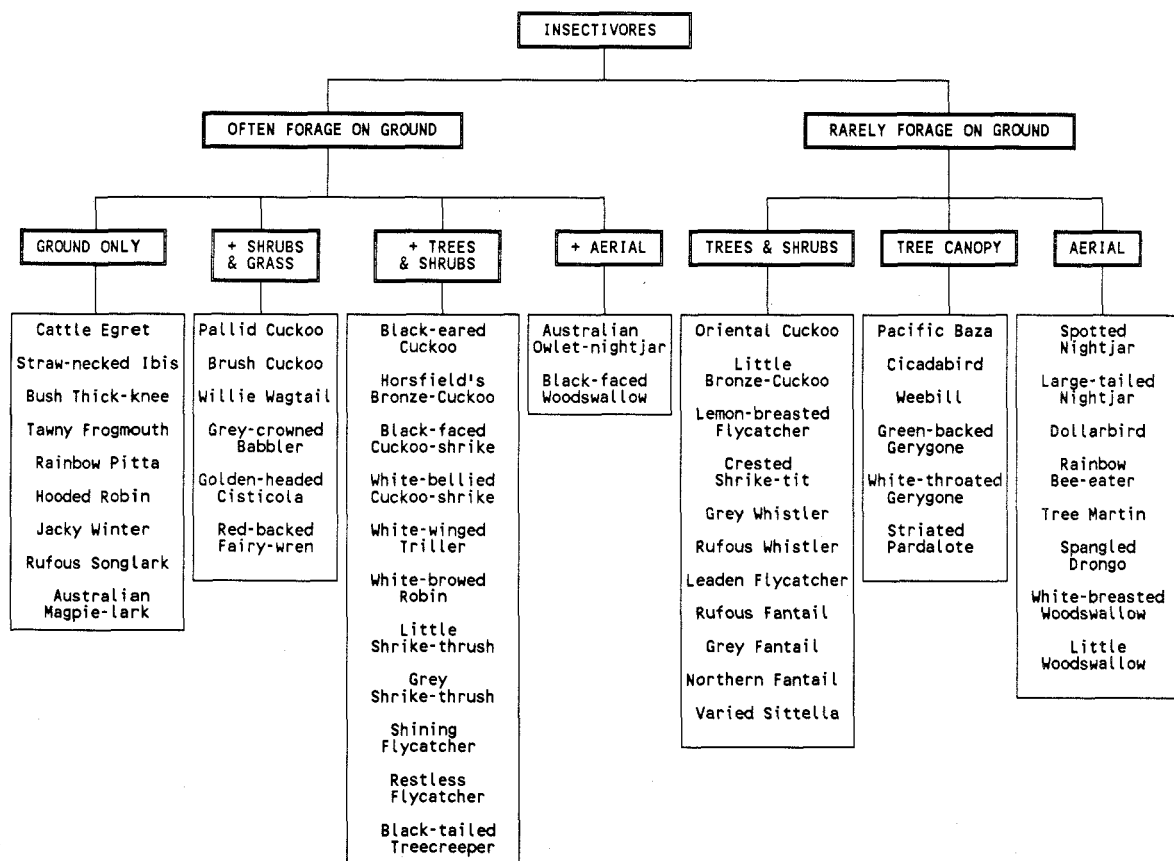


FIGURE 4 Species composition of foraging zones for all insectivorous birds in monsoon forest, open forest and woodland.

large and shallow with an open structure, compared to southern Australia where tubular flowered heaths are more abundant.

Structural overlap and competition

An examination of structural overlaps has identified pairs of species potentially in competition for food resources but provides little evidence that competition is, in fact, occurring. Species pairs with high structural overlap and similar morphology showed no inverse relationship in abundance, nor were positive correlations obtained between the foraging overlap of a pair and food-related morphological similarities. In a variable environment, species of birds may tend to be opportunistic in their foraging and diet selection (Rotenberry 1980) and therefore may not partition the resources as finely as they would in a more stable environment. However, our inability to find evidence of competition could also be due to a more subtle selection of food items not identified by our observations.

Morphology

In our samples there were few close relationships between the morphology of bird species and their foraging ecology. Wiens & Rotenberry (1980) obtained a similar result for grassland and shrub-steppe birds in North America. Their explanation, that sporadic stresses obscure the expected associations, may also apply in our area where possible stresses include temporal variations in the patterns of rainfall and fire.

Some studies (e.g. Ricklefs & Cox 1977) have shown that foraging overlap is related to morphological similarity. However, we found few strong relationships between indices of similarity and overlap as has been reported for other passerine communities (see Wooller & Calver 1981, Saether 1982). Significant correlations were found only for bodyweight and wing length with foraging overlap for monsoon forest species containing an insectivore and a honeyeater. Because honeyeaters can exploit food resour-

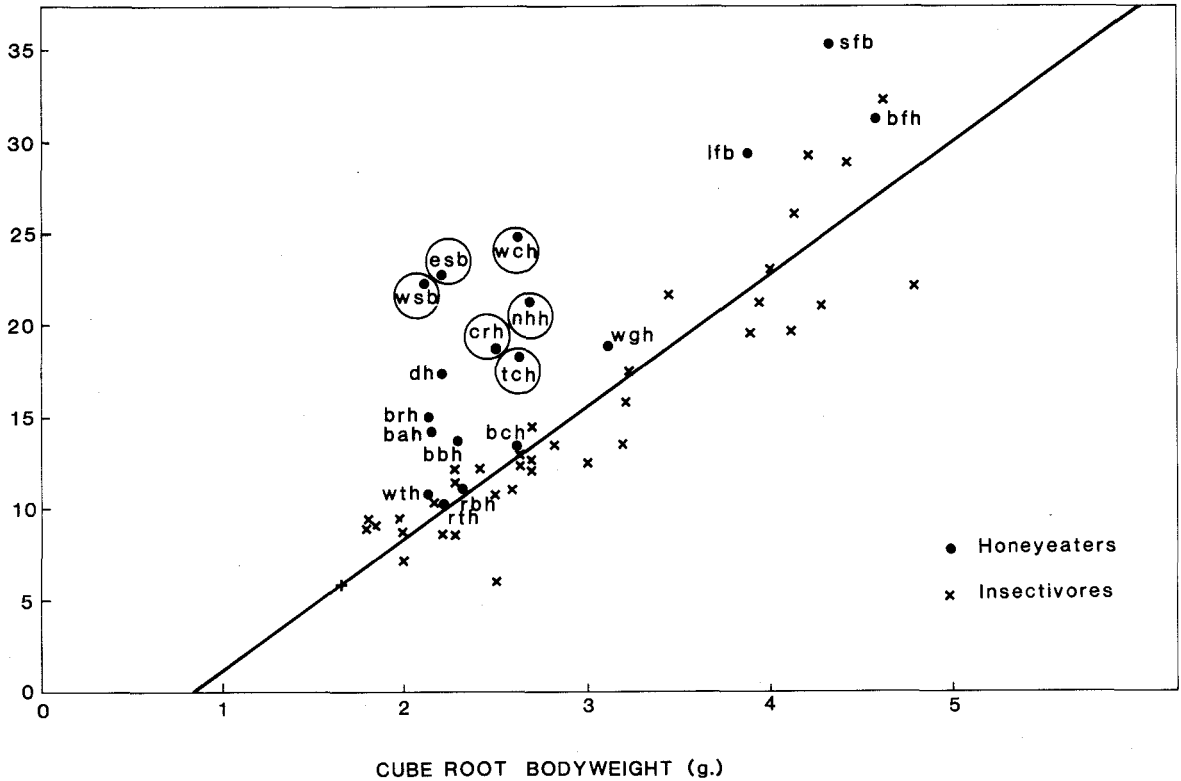


FIGURE 5 The relationship between bill length (L) and cube root bodyweight (B) for (a) all insectivorous forest and woodland passerines (x) in the study area ($L = 7.2 B - 6.1$, $r = 0.93$, $n = 37$); (b) study area honeyeaters (•) and (c) honeyeaters from elsewhere (circled) (data for *Acanthorhynchus* and *Phylidonyris* from Ford 1979 and Tullis *et al.* 1982). Honeyeaters: bah = Banded, bbh = Bar-breasted, bch = Black-chinned, bfh = Blue-faced, brh = Brown, crh = Crescent, dh = Dusky, nhh = New Holland, rbh = Rufous-banded, rth = Rufous-throated, tch = Tawny-crowned, wch = White-cheeked, wgh = White-gaped, wth = White-throated, lfb = Little Friarbird, sfb = Silver-crowned Friarbird, esb = Eastern Spinebill, wsb = Western Spinebill.

ces (nectar, fruit) not used by insectivores, any competition for invertebrate prey is more likely to be tolerated. We found significant negative relationships between bodyweight and the various measures of foraging diversity. This is contrary to the results of Morse (1974) who found that large species tended to be more specialised feeders than small species.

Conservation

Most of the species examined by us utilise a wide spectrum of habitats and have wide geographical ranges. However, two of the more specialised foragers (Large-tailed Nightjar *Caprimulgus macrorus*, an aerial feeder; Rainbow Pitta, a terrestrial feeder) were placed in Class 1 Rarity Category by Brooker & Parker (1985) (small geographic range, narrow habitat specificity, small local population). The Crested Shrike-tit *Falcunculus frontatus* was not recorded during the Kakadu Fauna Survey but occurs in this area

and fits the Class 1 Rarity Category. It is a specialised exploiter of exfoliating bark in other regions (see Holmes & Recher 1986) and its rarity here could be due to the lack of trees which shed bark.

The monsoon forest of the Northern Territory occupies only 0.5% of the total land area and is highly fragmented, with patch sites generally between 1 and 200 ha. In many cases, it has been modified by the activities of the introduced Water Buffalo (Braithwaite *et al.* 1984). It is therefore not surprising that most of its present insectivorous avifauna are generalist foragers. The arboreal insectivores studied in north Queensland rainforests by Crome (1978) and Frith (1984) also foraged over a broad spectrum of heights and sites and in New Guinean lowland rainforest most of the species in this group foraged at three or more height categories and sites (Bell 1982). However, many of the species referred to in these studies are restricted to rainforest and utilise the different regeneration stages

within the forest. Kikkawa *et al.* (1981) found that many of the common bird species of the Northern Territory monsoon forest also occur in Cape York where they were found in open forest rather than in monsoon forest. In the Northern Territory, monsoon forest patches are mostly found in the margin between upland eucalypt forests and sedgeland. Most of the species of insectivorous birds found in these patches forage extensively in surrounding habitats and can be regarded more accurately as margin species. However, for some, notably the Large-tailed Nightjar, Rainbow Pitta and Green-backed Gerygone, monsoon forest provides essential foraging resources.

Acknowledgements

The authors wish to thank Billie Gill who contributed to the foraging observations during the Survey, Helen Mason for processing the data, Lesley Brooker for analysing the data, drawing the figures and typing the manuscript, Harry Recher, Michael Ridpath and two anonymous referees for their helpful comments and the Australian National Parks and Wildlife Service for financial support.

References

- Bell, H.L. (1982). A bird community of New Guinean lowland rainforest. 3. Vertical distribution of the avifauna. *Emu* **82**, 143-162.
- Blakers, M., Davies, S.J.F. & Reilly, P.N. (1984). *The Atlas of Australian Birds*. RAOU and Melbourne Univ. Press, Melbourne.
- Braithwaite, R.W. (1985). *Kakadu Fauna Survey An ecological survey of Kakadu National Park*. Consultancy Report to A.N.P.W.S. 6 Vols.
- Braithwaite, R.W. (1987). Effects of fire regimes on lizards in the wet-dry tropics of Australia. *J. Trop. Ecol.* **3**, 265-275.
- Braithwaite, R.W. & Estbergs, J.A. (1985). Fire patterns and woody vegetation trends in the Alligator Rivers region of northern Australia. In: *Ecology and Management of the World's Savannas* (eds J.C. Tothill & J.J. Mott) pp. 359-364. Australian Academy of Science, Canberra.
- Braithwaite, R.W., Dudzinski, M.L., Ridpath, M.G. & Parker, B.S. (1984). The impact of water buffalo on the monsoon forest ecosystem in Kakadu National Park. *Aust. J. Ecol.* **9**, 309-319.
- Braithwaite, R.W., Wood, J.T., Fogarty, P. & Millar, L. (1985). Ecological spatial units for the management of faunal assemblages. In: *The Kakadu Fauna Survey: An ecological survey of Kakadu National Park*. (ed. R.W. Braithwaite) pp. 471-519. Consultancy Report to A.N.P.W.S., Canberra.
- Brooker, M.G. (1981). The vegetation and terrestrial vertebrate fauna of the proposed Welcome Reef Dam site on the Shoalhaven River near Braidwood, N.S.W. *CSIRO Wildl. Res. Tech. Memo* 17.
- Brooker, M.G. & Braithwaite, R.W. (1988). The Kakadu Fauna Survey: Description and evaluation of methodology for the census of vertebrates. *CSIRO Tech. Memo*. No. 29.
- Brooker, M.G. & Parker, B.S. (1985). The birds of Kakadu National Park. In: *The Kakadu Fauna Survey: An ecological survey of Kakadu National Park* (ed. R.W. Braithwaite) pp. 327-388. Consultancy report to A.N.P.W.S., Canberra.
- Brooker, M.G., Braithwaite, R.W. & Estbergs, J.A. (1985). Resource partitioning of forest and woodland birds in Kakadu National Park — An interim report. In: *The Kakadu Fauna Survey: An ecological survey of Kakadu National Park* (ed. R.W. Braithwaite) pp. 520-556. Consultancy report to A.N.P.W.S., Canberra.
- Collins, B.G. & Briffa, P. (1982). Seasonal variation of abundance and foraging of three species of Australian honeyeaters. *Aust. Wildl. Res.* **9**, 557-569.
- Crome, F.H.J. (1978). Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. *Aust. J. Ecol.* **3**, 195-212.
- Dow, D.D. (1977). Indiscriminate interspecific aggression leading to almost sole occupancy of space by a single species of bird. *Emu* **77**, 115-121.
- Ford, H.A. (1979). Interspecific competition in Australian honeyeaters — depletion of common resources. *Aust. J. Ecol.* **4**, 145-164.
- Ford, H.A. & Paton, D.C. (1976). Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Aust. J. Ecol.* **1**, 281-287.
- Ford, H.A. & Paton, D.C. (1977). The comparative ecology of ten species of honeyeaters in South Australia. *Aust. J. Ecol.* **2**, 399-407.
- Frith, D.W. (1984). Foraging ecology of birds in an upland tropical rainforest in north Queensland. *Aust. Wildl. Res.* **11**, 325-347.
- Hespenheide, H.A. (1971). Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* **113**, 59-72.
- Holmes, R.T. & Recher, H.F. (1986). Search tactics of insectivorous birds foraging in an Australian eucalypt forest. *Auk* **103**, 515-530.
- Keast, A. (1985). Bird community structure in southern forests and northern woodlands: a comparison. In: *Birds of the Eucalypt Forests and Woodlands: Ecology, Conservation and Management* (eds A. Keast, H.F. Recher, H. Ford and D. Saunders) pp. 97-116. Surrey Beatty & Sons, Sydney.
- Kikkawa, J., Webb, L.J., Dale, M.B., Monteith, G.B., Tracey, J.G. & Williams, W.T. (1981). Gradients and boundaries of monsoon forest in Australia. *Proc. Ecol. Soc. Aust.* **11**, 39-52.
- Kimber, P. (1972). Birds of the Jarrah forest. *Forest Focus* **7**, 5-7.
- Levins, R. (1968). *Evolution in Changing Environments*. Princeton University Press, Princeton.
- Loyn R.H. (1980). Bird populations in a mixed eucalypt forest used for production of wood in Gippsland, Victoria. *Emu* **80**, 145-156.
- Morse, D.H. (1974). Niche breadth as a function of social dominance. *Amer. Nat.* **108**, 818-830.
- Morton, S.R. & Brennan, K.G. (in press). Birds. In: *Monsoonal Australia: Landscape Ecology and Man in the Northern Lowlands* (eds C.D. Haynes, M.G. Ridpath & M.A.J. Williams). A.A. Balkema, Rotterdam.
- Nix, H.A. & Brooker, M.G. (1978). Part 3. Birds. In: *Land use on the south coast of N.S.W. Vol 2. Bio-physical background studies* (ed R.H. Gunn) pp. 74-80. CSIRO, Melbourne.
- Pyke, G.H. (1980). The foraging behaviour of Australian honeyeaters: a review and some comparisons with hummingbirds. *Aust. J. Ecol.* **5**, 343-369.
- Recher, H.F., Holmes, R.T., Schulz, M., Shields, J. & Kavanagh, R. (1985). Foraging patterns of breeding birds in eucalypt forest and woodland of southeastern Australia. *Aust. J. Ecol.* **10**, 399-419.
- Ricklefs, R.E. & Cox, G.W. (1977). Morphological similarity and ecological overlap among passerines on St. Kitts, British West Indies. *Oikos* **29**, 60-66.
- Ridpath, M.G. (1985). Ecology in the wet-dry tropics: how different? In: *Ecology in the Wet-Dry Tropics* (eds M.G. Ridpath & L.K. Corbett). *Proc. Ecol. Soc. Aust.* **13**, 3-20.

- Robbins, M.B. (1981). Two cases of commensal feeding between passerines. *Wilson Bull.* **93**, 391-392.
- Rotenberry, J.T. (1980). Dietary relationships among shrubsteppe passerine birds: Competition or opportunism in a variable environment. *Ecol. Mono.* **50**, 93-110.
- Saether, B.E. (1982). Foraging niches in a passerine bird community in a grey alder forest in Central Norway. *Ornis. Scand.* **13**, 149-163.
- Smith, P. (1984). The forest avifauna near Bega, New South Wales. I. Differences between forest types. *Emu* **84**, 200-210.
- Storr, G.M. (1977). Birds of the Northern Territory. W.A. *Mus. Spec. Publ.* No. 7.
- Strahan, R. (Ed.) (1983). *The Australian Museum Complete Book of Australian Mammals*. Angus & Robertson, Sydney.
- Taylor, J.A. & Dunlop, C.R. (1985). Plant communities in the wet-dry tropics of Australia: the Alligator Rivers region, Northern Territory. In *Ecology in the Wet-Dry Tropics* (eds M.G. Ridpath and L.K. Corbett). *Proc. Ecol. Soc. Aust.* **13**, 83-127.
- Taylor, J.A. & Tulloch, D. (1985). Rainfall in the wet-dry tropics: Extreme events at Darwin and similarities between years during 1870-1983 inclusive. *Aust. J. Ecol.* **10**, 281-295.
- Tullis, K.J., Calver, M.C. and Wooller, R.D. (1982). The invertebrate diets of small birds in Banksia woodland near Perth, W.A. during winter. *Aust. Wildl. Res.* **9**, 303-309.
- Welty, J.C. (1962). *The Life of Birds*. W.B. Sanders: Philadelphia.
- Wiens, J.A. & Rotenberry, J.T. (1980). Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.* **50**, 287-308.
- Woinarski, J. (1985). Foliage gleaners of the treetops, the Pardalotes. In: *Birds of the Eucalypt Forests and Woodlands: Ecology, Conservation and Management* (eds. A. Keast, H.F. Recher, H. Ford & D. Saunders), pp. 165- 175. Surrey Beatty & Sons, Sydney.
- Wooller R.D. & Calver, M.C. (1981). Feeding segregation within an assemblage of small birds in the Karri forest understorey. *Aust. Wild. Res.* **8**, 401-410.
- Yen, A.L. (1983). Honeydew, manna, scale and lerp. *Vict. Nat.* **100**, 244-245.