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THE FORAGING BEHAVIOUR OF AVIAN NECTARIVORES IN A MONSOONAL AUSTRALIAN WOODLAND OVER A SIX-MONTH PERIOD

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The foraging behaviour of one lorikeet and six honeyeater species were compared over a six month period in tropical woodland near Darwin, Northern Territory. The study identified three broad groupings of nectarivores — the Rainbow Lorikeet, small honeyeaters (Brown, Dusky) and large honeyeaters (Silver-crowned and Little Friarbird, Blue-faced Honeyeater and Yellow-throated Miner). These groups were differentiated principally on relative dependence upon flowers and choice of flower types, but also on non-nectar foraging strategies. Larger nectarivores fed predominantly in eucalypts and smaller nectarivores at a greater variety of sources. There was surprisingly little variation between honeyeater species in their dependence upon flowers (54–74% of foraging observations), but the Rainbow Lorikeet fed almost exclusively at flowers. The study suggests several ways in which tropical Australian nectarivore communities may differ from their temperate-zone counterparts.

INTRODUCTION

Nectar-feeding bird communities often contain a considerable number of species, and the way these species partition resources has been the subject of considerable interest and research. Under conditions of superabundant food supply, communities may be relatively unstructured, but an identifiable community structure is normal and is probably a response to a combination of resource limitations (Carpenter 1978; Ford 1979; Ford and Paton 1982; McFarland 1986) and morphological variation (Ford and Paton 1977; Brown *et al.* 1978; Gill and Wolf 1978; Wooller 1984; Collins and Paton 1989).

The foraging behaviour of many avian nectarivore communities in temperate Australia has been described. However, in monsoonal Australia the only available data have been gathered in the course of studies covering entire avian communities (Keast 1985; Brooker *et al.* 1990; Noske 1996), with nectarivores a somewhat incidental (though major) component.

In this paper, I present foraging data for lorikeets and honeyeaters collected in a tropical woodland near Darwin, Northern Territory. The study spanned a six-month period from the late wet to the mid-dry seasons. I compared dependence upon nectar, choice of flower types and modes and substrates of non-nectar foraging. Of 11 species present in the community, seven species are examined in detail and four species which were infrequently observed are examined cursorily. In addition, I considered variation over time for the three more common species.

STUDY AREA AND METHODS

The 107 ha study area lies in the north-west corner of the Territory Wildlife Park (12°45'S, 131°02'E) at Berry Springs, 40 km south-west of Darwin, Northern Territory. It is a gently undulating plateau at 8–15 m above sea level. Soils are leached and infertile earths, sands and lithosols derived from Quaternary laterite. The climate is monsoonal with a mean annual rainfall of *c.* 1 500 mm. The landforms, soils and vegetation of the study area and relationships between them are described in detail by Sivertsen *et al.* (1980) and Bowman and Minchin (1987).

The vegetation was a floristically and structurally diverse woodland dominated variously by Darwin Woollybutt *Eucalyptus miniata*, Darwin Stringybark *E. tetrodonta*, Apple Gum *E. clavigera* or combinations of Fern-leaved Grevillea *Grevillea pteridifolia* and Yellow-barked Paperbark *Melaleuca nervosa* with scattered taller Long-fruited Bloodwood *E. polycarpa*. The understorey was mostly dominated by the

Spear Grass *Sorghum intrans*, but occasionally by shrubs such as Cunningham's Feather-flower *Verticordia cunninghamii* or Quinine Tree *Petalostigma pubescens*.

I collected data on 13 field trips at fortnightly intervals from mid-March to early September 1994. Foraging data were collected whilst walking slowly along a 2.5 km transect which follows a fire-access trail that loops through the study area. On each field trip I made three foraging traverses, one each in the early morning, at midday and in the late afternoon. Upon encountering a lorikeet or honeyeater I watched it for as long as required or possible, documenting only the first foraging act after locating it. For each foraging act I noted the bird species, substrate species, foraging substrate (foliage, bark, bud, flower or fruit) and foraging method. Foraging methods were categorised as *gleaned* — taken from a substrate whilst the bird was perched; *snatched* — taken from the air whilst the bird was perched; *hover-snatched* - taken from a substrate whilst the bird was in flight and *hawked* - taken from the air whilst the bird was in flight. For analysis, *snatching* and *hover-snatching* were combined.

The method of collecting observations emphasizes the independence of data points (group foraging may compromise independence, but this was considered to be a serious problem only with lorikeets), facilitating contingency analysis. Similarities in the foraging behaviour of the species were quantified using the Bray-Curtis dissimilarity index, and sorted using UPGMA (Unweighted Pair-Group Method using Arithmetic averages) (Krebs 1989). Because of sample size limitations, changes in foraging behaviour over time could be examined for only the three species for which I obtained the most foraging records by pooling data into six time periods. The diversity of nectar sources utilized by each species was evaluated using the Shannon-Weiner diversity index; a higher index score indicates that a bird species made relatively even use of a wide variety of nectar sources.

RESULTS

I obtained 1 181 foraging observations of two lorikeet and nine honeyeater species. All of the seven commonly observed species were observed foraging both at and away from flowers, and all except the Rainbow Lorikeet *Trichoglussus haematodus* and Blue-faced Honeyeater *Entomyzon cyanotis* were observed hawking (Table 1). The Rainbow Lorikeet differed markedly from all honeyeaters in its much greater dependence upon flowers. Amongst honeyeaters, the Dusky Honeyeater *Myzomela obscura* may have been more flower-dependant than other species (Table 1, Fig. 1a), but overall there was no significant difference between honeyeaters in their dependence upon flowers ($\chi^2 = 6.4$, d.f. $= 5$, $P > 0.25$).

All the major nectar sources were accessible to all nectarivore species. Most had 'cup-shaped' or soft 'brush' inflorescences (*sensu* Ford and Paton 1985). Like other members of its genus, *G. pteridifolia* has a 'gullet-shaped' flower, but may be unusual amongst grevilleas in presenting the nectar in the concavity at the distal end of the tepals, where it is visible externally. The flowers of *G. pteridifolia* were visited by the short-billed Rainbow Lorikeet as well as by the longer-billed honeyeaters (Table 1).

All species of nectarivore were observed feeding at the flowers of *Eucalyptus, Melaleuca* and *Grevillea*, the major nectar sources. However, based on patterns of flower choice, there were two distinct groups (Fig. 1b), the small honeyeaters (Brown Honeyeater *Lichmera indistincta* and Dusky Honeyeater) and the larger nectarivores including the Rainbow Lorikeet. The smaller honeyeaters had higher floral diversity indices (Table 1), and made much greater use of non-eucalypt flowers. Figure 2 confirms that the principal dichotomy is between the use of eucalypt and non-eucalypt flowers.

All but one of 730 formal observations of birds foraging at flowers were of perched individuals. The exception, along with four other observations noted whilst not formally recording foraging behaviour, were of Brown Honeyeaters hovering at the flowers of eucalypts and *V. cunninghamii* on four occasions, and one record of a Little Friarbird *Philemon citreogularis* which hovered at a eucalypt flower.

In nearly all cases where foraging at flowers was closely observed, birds probed the flowers, with no evidence that they were seeking pollen or insects or any food other than nectar. This was true for lorikeets as well as honeyeaters. The exceptions were: Rainbow Lorikeets sometimes placed their bills over the entire flower of *E. bleeseri* and pulled the anthers off; one Rainbow Lorikeet carefully worked over the anthers of *E. tetrodonta*; and Little Friarbirds were twice observed seeking insects from nectar-bearing flowers.

On the basis of mode of obtaining non-floral food, three species pairs are evident (Fig. 1c). Small honeyeaters again formed a markedly discrete group, infrequently foraging on eucalypts and rarely on bark, and fairly frequently snatching (*cf* gleaning) prey. Silver-crowned Friarbirds *(Philemon argenticeps)* and Little Friarbirds had very similar foraging modes featuring relatively

TABLE 1

Foraging behaviour of seven avian nectarivores, showing total number of observations (n), % use of major substrates, % use of nectar sources, the Shannon-Weiner floral diversity index (FDI) and non-flower vegetation foraging strategies.

		Major substrates (%)			Nectar sources (%)											Vegetation foraging		
Species	n	flowers	veg.	air	*Eb*	*Em*	*Ep*	*Et*	*Gp*	*Mn*	*Mv*	*Pc*	*Xp*	OT	FDI	% euc	% fol	% gl
Rainbow Lorikeet *Trichoglossus haematodus*	200	94	6	0	29	32	31	3	3	0	1	0	0	1	.60	58	83	100
Silver-crowned Friarbird *Philemon argenticeps*	113	64	29	7	16	50	21	7	3	0	3	0	0	0	.58	91	91	76
Little Friarbird *Philemon citreogularis*	463	57	31	12	12	49	27	3	3	3	2	1	<1	<1	.63	85	85	79
Blue-faced Honeyeater *Entomyzon cyanotis*	40	65	35	0	4	65	12	8	4	0	4	0	4	0	.52	93	43	100
Yellow-throated Miner *Manorina flavigula*	119	54	39	7	13	45	23	5	2	0	3	2	6	2	.71	94	61	91
Brown Honeyeater *Lichmera indistincta*	169	56	34	10	4	17	33	0	14	4	13	5	1	9	.88	21	96	75
Dusky Honeyeater *Myzomela obscura*	27	74	22	4	0	20	30	0	5	0	15	5	5	20	.78	33	100	66

"veg." = vegetation excluding flowers. *'Eb'* = *Eucalyptus bleeseri* (Shiny-leaved Bloodwood); *'Em'* = *E. miniata* (Darwin Woollybutt); *'Ep'* = *E. polycarpa* (Long-fruited Bloodwood); *'Et'* = *E. tetrodonta* (Darwin Stringybark); *'Gp'* = *Grevillea pteridifolia* (Fern-leaved Grevillea); *'Mn'* = *Melaleuca nervosa* (Yellow-barked Paperbark); *'Mv'* = *M. viridiflora* (Broad-leaved Paperbark); *'Pc'* = *Planchonia careya* (Cocky Apple); *'Xp'* = *Xanthostemon paradoxus* (Bridal Tree); 'OT' = Others (*Brachychiton paradoxus*, Red-flowered Kurrajong, five records; *E. clavigera*, Apple Gum; one record; *Lophostemon lactifluus*, Swamp Box, three records; *Terminalia grandiflora,* Nut Tree, two records; *Verticordia cunninghamii*, Cunningham's Feather-flower, five records). 'Vegetation foraging' acts classified in three independent ways — '%euc' is the percentage that was on eucalypts; '%fol' is the percentage on foliage including buds, fruits and twigs, the contrast being with bark; and '%gl' is the percentage gleaned, here defined broadly as foraging whilst perched, contrasting with snatching and hover-snatching.

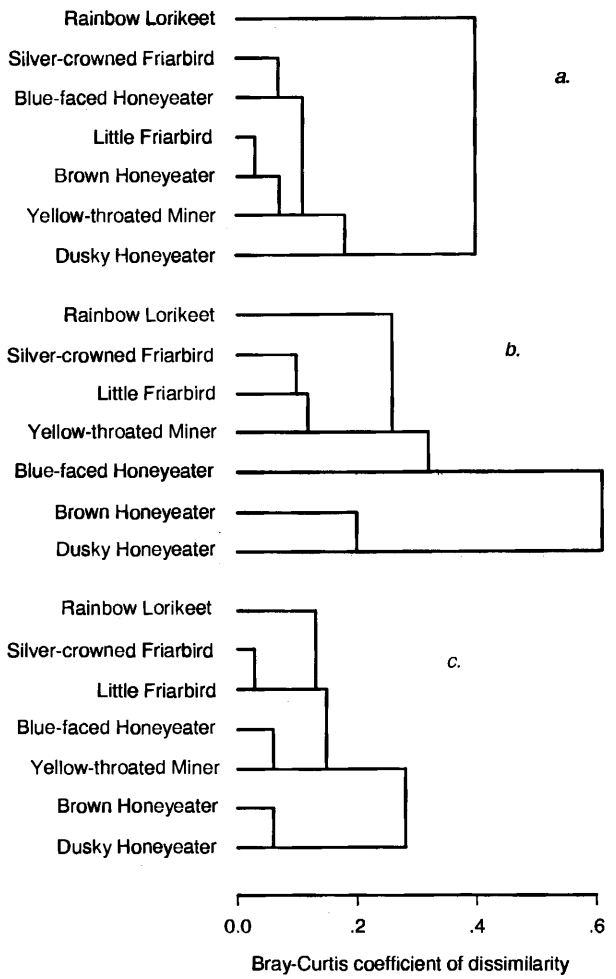

Figure 1. *Nectarivores grouped by similarities in foraging behaviour: a. by proportional use of major substrates (flowers, other vegetation, air); b. by proportional use of flower types (as grouped in Table 1); and c. by non-nectar foraging strategies at vegetation (as presented in Table 1).*

high rates of use of eucalypts, foliage and prey-snatching. Prey-snatching commonly consisted of visually locating prey amongst foliage at fairly close range (typically about 30 cm), then leaping or fluttering at the prey in what appeared a rather uncontrolled manner, often tumbling through the foliage with or in pursuit of it. The third pair, the Blue-faced Honeyeater and Yellow-throated Miner *Manorina flavigula*, were noteworthy for their more frequent use of bark, eucalypts and gleaning.

Invertebrates appeared to be the main non-flower foraging target, but on five occasions I noted birds licking *E. miniata* branches of *c.* 5–15 mm diameter, as if obtaining manna or honeydew. On at least two occasions, both in the late afternoon, loose mixed aggregations of Little Friarbirds and Yellow-throated Miners were observed sallying after flying arthropods at tree-top height.

Seasonal patterns

The Rainbow Lorikeet consistently used flowers at high rates, declining somewhat from mid-August to early September (Fig. 3a) when they were observed eating the dry fruits of Turkey Bush *Calytrix exstipulata* and apparently chewing a dead leaf of *G. pteridifolia*. In contrast, rates of flower use fluctuated markedly for both the Little Friarbird ($\chi^2 = 25.4$, d.f. = 5, $P < 0.001$) and the Brown Honeyeater ($\chi^2 = 24.7$, d.f. = 5, $P < 0.001$), being particularly low from late-June to the end of July.

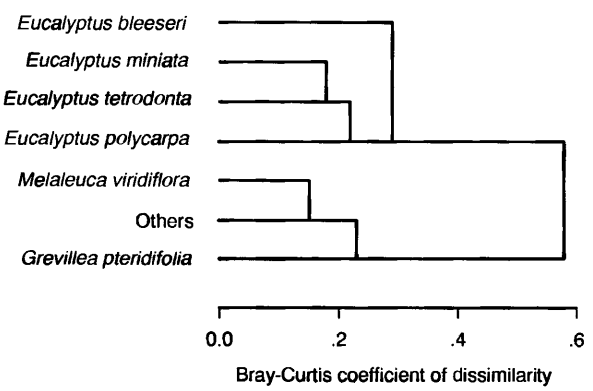

Figure 2. *Nectar sources grouped according to similarities in the birds feeding at them. Data for each plant have been converted to proportions prior to analysis. 'Others' includes all species for which I obtained less than 25 observations (Table 1).*

Both the Rainbow Lorikeet and Little Friarbird had consistently high rates of use of eucalypt flowers compared to other flower types (Fig. 3b). In contrast, the relative use of eucalypt flowers by the Brown Honeyeater dropped dramatically in mid-June and remained low thereafter, the variation being statistically significant ($\chi^2 = 33.5$, d.f. = 5, $P < 0.001$).

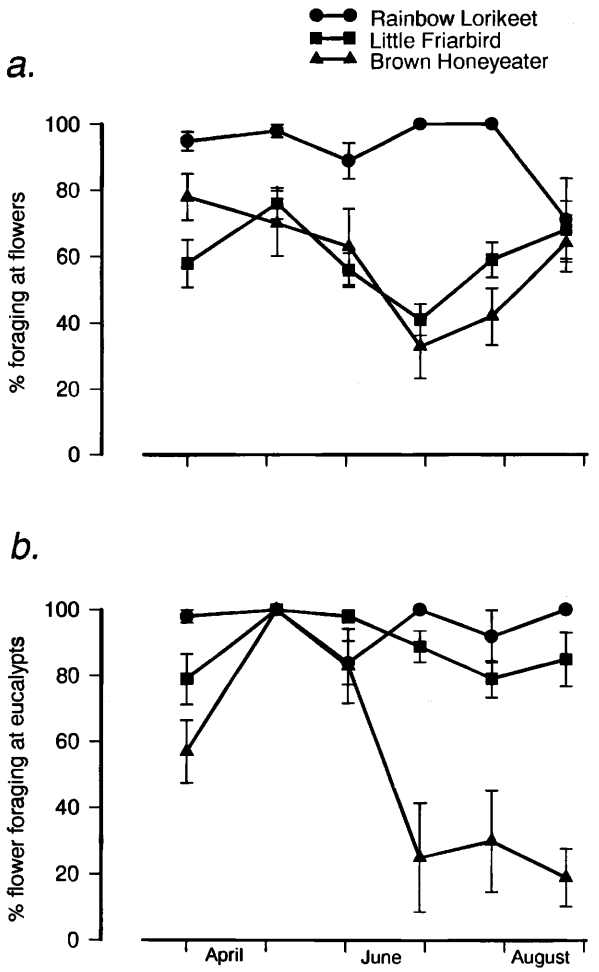

Figure 3. *Seasonal variation in foraging behaviour of three species of nectarivorous birds over a six month period (% ± s.e.). a. variation in the proportion of foraging acts that were at flowers; and b. variation in the proportion of flowers visited that were eucalypts.*

The uncommon species

Fourteen feeding observations of the Varied Lorikeet *Psitteuteles versicolor* were all at the flowers of eucalypts. Of 13 feeding observations of the White-gaped Honeyeater *Lichenostomus unicolor*, seven were at flowers and six of these at *G. pteridifolia*. All non-flower foraging of the White-gaped Honeyeater was by gleaning, with five of six observations being at plants other than eucalypts. Only five of 12 feeding observations of the White-throated Honeyeater *Melithreptus albogularis* were at flowers (all eucalypts), the lowest proportion of any species at the site. Of 11 feeding observations of the Red-headed Honeyeater *Myzomela erythrocephala*, 10 were at flowers, of which nine were at eucalypts.

DISCUSSION

This study identified a range of foraging strategies amongst the nectarivorous birds of a tropical woodland. Based on these findings, three broad groupings of species are recognized, the Rainbow Lorikeet, and the small and large honeyeaters.

The Rainbow Lorikeet made much more frequent use of flowers, predominantly eucalypts, than did any of the honeyeaters, apparently harvesting both nectar and pollen, and this behaviour was relatively consistent through the study period. In tropical eucalypt woodland, open forest and monsoon forest, Brooker *et al.* (1990) reported the species feeding at the flowers of eight eucalypt and nine other plant species, but did not quantify relative usage nor state whether other food sources were exploited. In sub-tropical Queensland and New South Wales, Cannon (1984) found that the Rainbow Lorikeet made extensive use of eucalypt flowers, but also exploited a range of other nectar sources as well as fruit and leaf buds. She attributed the dietary diversity observed to the semi-urban nature of the population studied, as it contrasted with the greater dependence upon eucalypt flowers observed in the less urban Scaly-breasted Lorikeet *Trichoglossus chlorolepidotus*.

Few studies have compared the foraging behaviour of lorikeets with honeyeaters, even though they frequently coexist and share flowers. In a temperate woodland, Ford *et al.* (1986) recorded the Little Lorikeet *Glossopsitta pusilla* feeding only at eucalypt flowers, whereas all honeyeaters species fed at a range of flower and non-flower substrates.

The Brown and Dusky Honeyeaters exhibited fairly similar foraging behaviour, with moderately high rates of flower use and relatively low rates of use of eucalypts. The high rate of nectarivory of the Dusky Honeyeater in this study stands in marked contrast to Crome's (1978) data from lowland tropical rainforest in Queensland, where only 26 per cent of 148 foraging observations were

at flowers. The Brown Honeyeater bred throughout the study period (the only other species to do so was the Blue-faced Honeyeater), which may have contributed to its comparatively low rate of nectarivory and preference for non-eucalypt nectar sources. Its dramatic move away from eucalypt nectar sources mid-way through the study did not correspond with any change in its micro-habitat choice, and probably reflects spatio-temporal variation in the relative availability of eucalypt and non-eucalypt nectar, and perhaps also avoidance of larger honeyeaters present in the canopy (Franklin 1994).

Consistent with Collins' (1980) observation, I found that the Brown Honeyeater used a wider range of nectar sources than other species (the Dusky Honeyeater possibly excepted in this study). But in this study it was somewhat less nectarivorous than found by Newland and Wooller (1985), and markedly less so than described by Collins and Briffa (1982). There is also much variation between studies in its mode of non-nectar foraging. In this study as well as the tropical woodland studies of Keast (1985) and Brooker *et al.* (1990) it was primarily a foliage gleaner, whereas in Collins and Briffa's (1982) temperate zone study it was recorded equally often hawking as gleaning. These differences are consistent with the described relationship between hawking and very high levels of nectarivory (Recher and Abbott 1970; Ford and Paton 1976), but may also represent a fundamental difference between the ecology of the species in temperate and tropical areas.

There were surprisingly few differences in the foraging behaviour of the larger honeyeaters, especially between the two friarbird species. All were moderately dependent upon flowers, and all made heavy use of eucalypts both as a nectar source and for other foraging. However, the Blue-faced Honeyeater was not observed hawking, and both this species and the Yellow-throated Miner gleaned and made much greater use of bark than other species. The distinctive prey-snatching behaviour of the friarbirds was also noted by Brooker *et al.* (1990), who used the term 'flit'.

The seasonal change in rates of use of flowers by the Little Friarbird and Brown Honeyeater but not the Rainbow Lorikeet is at first sight perplexing, especially so as the period of low use coincides with a major peak in nectar availability (Franklin 1994). Low rates of flower use, however, also coincided with the sharp reduction in arthropod availability characteristic of the Australian monsoonal tropics during the cool dry season of June and July (e.g. Woinarski and Tidemann 1991; Churchill 1994). Thus the data may reflect the relatively greater time needed to obtain arthropods than nectar during the cool dry season, rather than any change in the proportion of nectar consumed. The late decline in the observed rate of nectarivory by the Rainbow Lorikeet coincides with a marked reduction in nectar availability from its preferred sources (Franklin 1994).

A feature of the honeyeater community was that all species exhibited moderate dependence upon flowers (range 54–74% of foraging observations). This contrasts with a temperate woodland honeyeater community (Ford *et al.* 1986), where the species ranged from 8 per cent at flowers (Brown-headed Honeyeater *Melithreptus brevirostris*) to 90 per cent (Scarlet Honeyeater *Myzomela sanguinolenta*). However, partitioning between nectar sources was particularly marked between small and larger honeyeaters. Like Brooker *et al.* (1990), I found little evidence that non-nectar carbohydrates were an important alternative to nectar for birds in tropical woodland.

This study has provided a small window into the ecology of a tropical woodland community of lorikeets and honeyeaters. The similarities and differences between these communities and those of their taxonomic and ecological counterparts in temperate Australia remain largely unexplored.

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