

LOCAL MOVEMENTS OF HONEYEATERS IN A SUB-COASTAL VEGETATION MOSAIC IN THE NORTHERN TERRITORY

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We examined the local movements of honeyeaters in a vegetation mosaic near Darwin, Northern Territory over a 39-month period using mark-recapture banding and unquantified observations of nectar availability and the presence of birds. Thirty nectar source species provided nectar throughout the year, with the exception of interludes of several weeks between periods of prolific flowering during the Wet season. At least five species of honeyeater were present in the 470 ha study area throughout the study period. Banding returns suggest a moderate level of between-year site fidelity, as well as some local movements between nectar sources and habitats. Mark-resight techniques may prove more effective than mark-recapture techniques in further exploration of the patterns observed.

INTRODUCTION

There have been few studies of passerines in monsoonal Australia, even though this distinct climatic region covers 20 per cent of the Australian landmass and is a major centre of biodiversity. Banding studies have been especially scarce (Woinarski and Tidemann 1992; Tidemann and Woinarski 1994; Noske 1996; Franklin *et al.* 1998), the result of a scarcity of banders and perhaps also the often difficult conditions for banding. A consequence is that the natural history of Top End birds is poorly known, providing an inadequate foundation for more detailed ecological studies. Natural history remains the foundation stone of good ecology (James and McCulloch 1985). As Crawley (1993) stated, 'the best way to solve ecological problems is through a thoughtful blend of *observation*, theory and experiment' (our emphasis). Observation must come first.

A fundamental enigma of the ecology of bush (and aquatic) birds in monsoonal Australia is the nature of mobility and resource tracking in a predictably and intensely seasonal environment. There is a relative paucity of long-distance migrants. Many monsoonal Australian bush birds, and in particular nectarivores, appear to be highly mobile, tracking scattered resources in a vast landscape (Morton and Brennan 1991; Woinarski and Tidemann 1991; Woinarski 1992). However, in mangrove forest near Darwin, Noske (1996) found that the Red-headed Honeyeater *Myzomela erythrocephala* was relatively sedentary, with individuals moving only short distances when nectar was unavailable in their territories. In woodland near Darwin, Franklin and Noske (in press) found correlative evidence of resource tracking by a range of nectarivorous birds *within* a 107 ha study area over a six-month period.

In this study, we examine local movements of honeyeaters over a 39-month period, using banding and general observations of birds and their nectar sources. The study area was as for the six-month study of Franklin and

Noske (in press) but enlarged to 470 ha to embrace a wider range of habitats. We sought to determine which species (if any) were resident within the study area, to what extent resource tracking took the form of local movements between nectar sources and habitats, and whether mobile species exploited the predictable seasonality of the environment by returning to sites annually. In the process, we sought to determine the usefulness of mark-recapture banding in the study of these species.

STUDY AREA

The study was conducted at the 470 ha Territory Wildlife Park (12°45'S, 131°02'E) at Berry Springs in the Northern Territory. The climate is strongly monsoonal with a mean average rainfall of c. 1600 mm falling mostly from November to March. The Park comprises mostly undisturbed bushland, with zoo facilities and limited planting of nectar-sources in the south-eastern section only. Soils are lateritic gravels and sands. The area is low-lying (c. 8–20 m ASL) and substantial areas are subject to inundation in the Wet season. The vegetation (excluding treeless wetland) can be placed in five broad categories (Fig. 1): *a.* riparian open forest of Broad-leaved Paperbark *Melaleuca viridiflora* (rarely *M. cajaputi*) subject to inundation for approximately three to six months of the year; *b.* swamp woodland with a variable mixture of the following trees — Long-fruited Bloodwood *Corymbia polycarpa*, Fern-leaved Grevillea *Grevillea pteridifolia*, Yellow-barked Paperbark *M. nervosa* and Swamp Box *Lophostemon lactifluus* and subject to inundation for approximately one to three months of the year; *c.* eucalypt woodland/open forest of variable height and structure, featuring mainly Darwin Woollybutt *E. miniata*, Darwin Stringybark *E. tetradonta* and Apple Gum *C. polysciada*; *d.* a monsoon rainforest/open forest ecotone dominated by Black Wattle *Acacia auriculiformis* and Ghost Gum *C. arafurica*; and *e.* spring-fed monsoon rainforest. Most of the Park and all of the banding sites were unburnt throughout the study period. Bowman and Minchin (1987) provide greater detail of vegetation and soils of the Berry Springs area.

METHODS

From October 1994 to December 1997 we visited the study area at monthly intervals (most months). On up to five (mostly two) days per month, we set from one to eight 9 m or 12 m mist nets

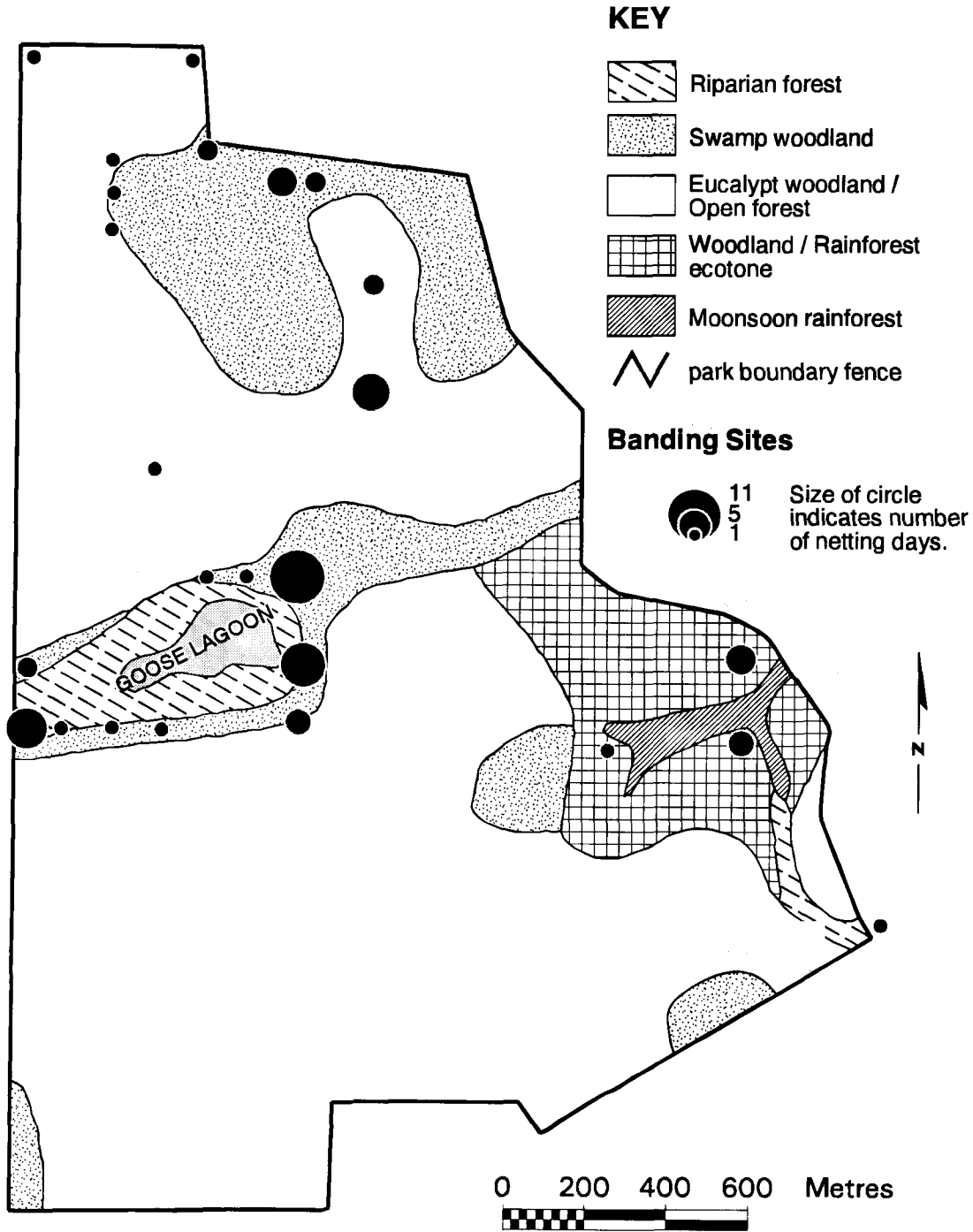


Figure 1. The Territory Wildlife Park, Berry Springs, Northern Territory, showing habitats and banding sites. The largest circle (near the centre of the Park) is the swamp woodland site that was netted on eleven days regardless of nectar availability.

(depending on the anticipated bird activity and the availability of banders) from before sunrise until midday or until it was too hot. Honeyeaters caught were banded and released. In total, we netted birds on 66 days during 30 (of 39 possible) months.

Nets were set at or close to nectar sources on 50 days, mostly where a nectar source was attracting honeyeaters to a nettable height. Sites were chosen on a daily basis after examining the availability of nectar and the concentration of bird activity within the Wildlife Park during the previous afternoon(s). At one site in swamp woodland (Fig. 1) that was favoured by small honeyeaters we attempted to net birds every two to three months regardless of

nectar availability. In the absence of suitable nectar sources, nets were set wherever there was a concentration of bird activity. We mostly chose banding sites in the centre and north of the Park, both because they were generally more suitable for our purposes and to avoid the disturbance associated with zoo and visitor facilities.

All capture locations were plotted on a base map and attributed to a 125 m x 125 m cell. Distances to recaptures have been estimated using distances between the centres of cells. The maximum distance between banding sites was 3.2 km, with most nectar source sites within 1.6 km of each other (Fig. 1). For

analysis, distances of less than 200 m have been pooled and treated as 'no movement' so as to include all immediately adjacent and diagonal cells.

On each visit we kept a list of honeyeaters observed and made notes on the flowering of nectar sources and their use by honeyeaters. Additional flowering data for the period March-September 1994 were taken from Franklin (1994) and Franklin and Noske (in press).

The term 'eucalypt' is taken to include members of the genera *Eucalyptus* and *Corymbia* (Hill and Johnson 1995).

RESULTS

Nectar sources

Honeyeaters were recorded using 30 species of flowers as nectar sources at the Territory Wildlife Park. Species that provided the most significant nectar supplies occur in all habitats except monsoon rainforest (which however,

was inadequately surveyed), but with the greatest variety in swamp and eucalypt woodland (Fig. 2). Seasonal patterns of availability were similar in swamp and eucalypt woodland, some nectar sources being available in every month, but variety being greatest from August to November. Availability in both habitats was particularly high during June, July and August due to the prolific flowering of Darwin Woollybutt, Fern-leaved Grevillea, Darwin Stringybark and Yellow-barked Paperbark (see also Franklin and Noske, in press).

In contrast, riparian and ecotone forests provided few nectar sources with intermittent availability (Fig. 2). However, riparian forest made a significant contribution to the seasonal pattern of availability through its dominant plant species, the Broad-leaved Paperbark, which flowered prolifically during the Wet season when there was a paucity of alternative nectar sources.

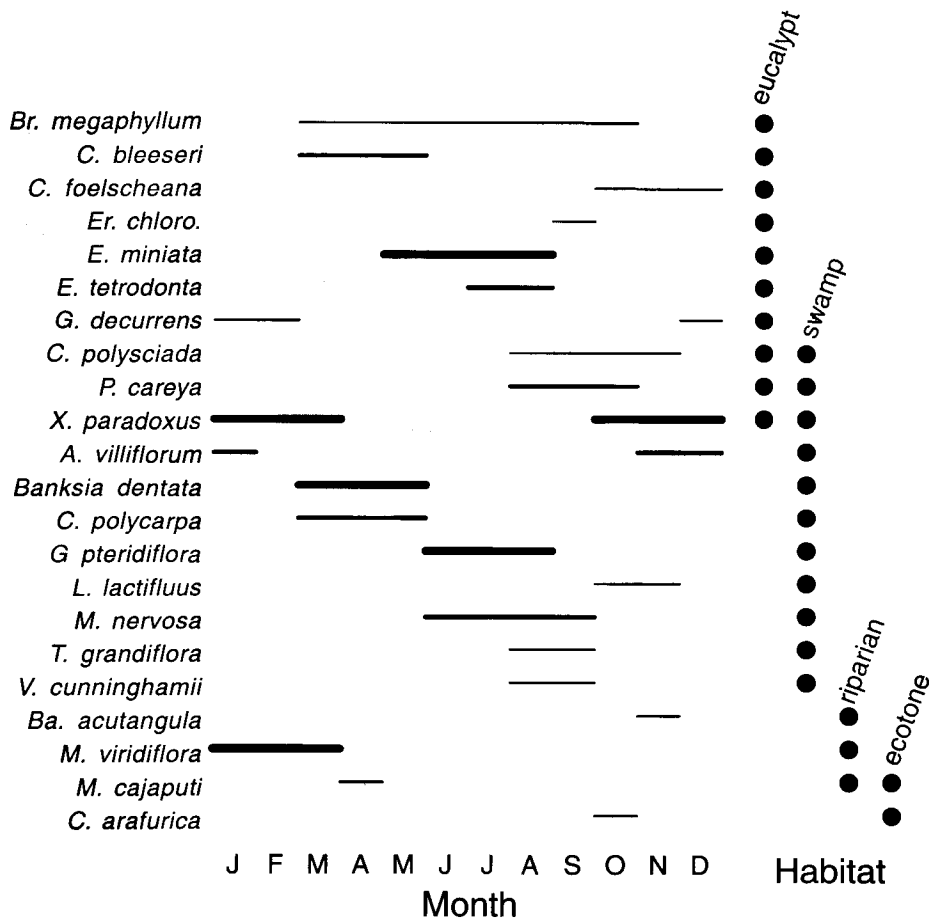


Figure 2: Flowering times and habitats of the main nectar sources of the Territory Wildlife Park. Generic abbreviations: A. = *Amyema* (Loranthaceae), Ba. = *Barringtonia* (Lecythidaceae), Br. = *Brachychiton* (Sterculiaceae), C. = *Corymbia* (Eucalyptus, Myrtaceae), E. = *Eucalyptus* (Myrtaceae), Er. = *Erythrophleum* (Caesalpiniaceae), G. = *Grevillea* (Proteaceae), L. = *Lophostemon* (Myrtaceae), M. = *Melaleuca* (Myrtaceae), P. = *Planchonia* (Lecythidaceae), T. = *Terminalia* (Combretaceae), V. = *Verticordia* (Myrtaceae), X. = *Xanthostemon* (Myrtaceae). Heavy lines are flowering times for nectar sources that made a major contribution to supporting the nectarivore community in each of the four study years; medium lines are for sources that made a major contribution in at least one year; fine lines are for other significant nectar sources. Habitats are as defined in the study area description.

Flowering times were broadly consistent between years but the intensity of flowering was more variable. Fern-leaved Grevillea, Broad-leaved Paperbark and the Tropical Banksia *Banksia dentata* were extremely dependable from year to year. Darwin Woollybutt flowered every year, but varied considerably in its intensity. Shiny-leaved Bloodwood *Corymbia bleeseri* and Long-fruited Bloodwood flowered heavily only in 1994; in 1997 the former did not flower at all and the latter only very poorly.

Most species displayed unimodal annual peaks of flowering activity, but the two major nectar sources of the Wet season were exceptions. Bridal Tree *Xanthostemon paradoxus* flowered throughout the Wet season and especially from October to December and again in March, but did so in short, repeated and sometimes dramatic pulses that varied between patches and years. Broad-leaved Paperbark consistently flowered twice per year, with very dramatic but short-lived pulses (the peaks lasted no more than several weeks) usually in January and again in March. Thus the Wet season was characterized by periodic flushes of abundant flowering separated by periods of several weeks or more when it was sometimes difficult to find a nectar source anywhere.

The honeyeaters

Thirteen species of honeyeater were recorded at the Territory Wildlife Park. Of these, five species — Silver-crowned Friarbird *Philemon argenteiceps*, Blue-faced Honeyeater *Entomyzon cyanotis*, Yellow-throated Miner *Manorina flavigula*, White-gaped Honeyeater *Lichenostomus unicolor* and Dusky Honeyeater *Myzomela obscura* and possibly a sixth, the White-throated Honeyeater *Melithreptus albogularis* — were present in the Park throughout the study period. The Brown Honeyeater *Lichmera indistincta* was usually present in the study area in good numbers at sites with shrubs or dense

low trees (see also Franklin and Noske, in press). However, in mid-October 1994, early- and mid-November 1995, early- and mid-November 1996 and mid-October 1997 it was absent from or scarce in the study area. The Little Friarbird *P. citreogularis* was usually present, but its numbers were highly variable (see also Franklin and Noske, in press). The Rufous-banded Honeyeater *Conopophila albogularis*, Rufous-throated Honeyeater *C. rufogularis*, Banded Honeyeater *Certhionyx pectoralis* and Red-headed Honeyeater were relatively infrequent and/or irregular visitors to woodland and riparian forest. We have insufficient data to state whether the Bar-breasted Honeyeater *Ramsayornis fasciatus* was consistently present.

Most species were found across the range of habitats available in the Park. Exceptions were the White-gaped Honeyeater, which was common in riparian and ecotone forests but rare elsewhere; the Bar-breasted Honeyeater, which was mostly seen in riparian forest; and the Yellow-throated Miner which was mostly seen in swamp and eucalypt woodlands. No species regularly occurred in the monsoon rainforest, although Dusky and White-gaped Honeyeaters were common along the fringe and in the broad ecotone between monsoon rainforest and the eucalypt woodlands.

Banding and recapture data

We banded 526 honeyeaters of 12 species, and recaptured 64 individuals (Table 1), means of 8.0 and 1.0 respectively per banding day. Daily capture tallies varied from 0 to 35 honeyeaters. Consistently high capture rates were achieved at Tropical Banksia inflorescences, and by netting in the understorey of riparian forest when the Broad-leaved Paperbarks were in heavy blossom, even though this meant setting and checking nets in up to a metre of water. Netting at the flowers of Bridal Tree

TABLE 1

Summary of banding results for honeyeaters at the Territory Wildlife Park for the 39 months from October 1994 to December 1997. For individuals captured more than once, the distance to recapture and time elapsed is from the initial capture to the last recapture.

Species	No. banded	Number of individuals recaptured (% of number banded)				Time elapsed (months)	
		Recaptured once or twice	Recaptured twice	Distance		<200 m	>200 m
				<200 m	>200 m		
Silver-crowned Friarbird	37	4 (11)	3 (8)	3	1	11, 24, 36	27
Little Friarbird	63	1 (2)	0 (0)	1	0	1	
Blue-faced Honeyeater	26	3 (12)	2 (3)	2	1	13, 23	5
Yellow-throated Miner	7	0 (0)	0 (0)	0	0		
White-gaped Honeyeater	19	3 (16)	0 (0)	1	2	15	3, 5
White-throated Honeyeater	67	3 (4)	0 (0)	3	0	1, 8, 23	
Brown Honeyeater	137	28 (20)	4 (3)	22	6	median = 11 range <1–32	median = 14 range 1–20
Bar-breasted Honeyeater	9	2 (23)	1 (11)	1	1	13	17
Rufous-throated Honeyeater	5	0 (0)	0 (0)	0	0		
Banded Honeyeater	3	0 (0)	0 (0)	0	0		
Dusky Honeyeater	149	20 (13)	4 (3)	11	9	median = 9 range 1–15	median = 11 range 2–29
Red-headed Honeyeater	4	0 (0)	0 (0)	0	0		
TOTAL	526	64 (12)	14 (3)	44	20		

produced highly variable results, being most successful when there were few inflorescences overall but a good concentration low on a few trees. Other major nectar sources, e.g. all eucalypts and many flowers of the Fern-leaved *Grevillea*, were generally too high for successful netting. Moderate capture rates were achieved at relatively minor, localised and low nectar sources such as the Freshwater Mangrove *Barringtonia acutangula* and the Pink *Grevillea G. decurrens*.

At one swamp woodland site that appeared particularly favoured by small honeyeaters (Brown Honeyeaters especially) we attempted to net at intervals of two to three months regardless of nectar availability and did so on a total of 11 days. Capture rates varied from 3 to 22 honeyeaters per day, but were generally low and we eventually abandoned the site.

Twelve per cent of individuals banded were recaptured, and 22 per cent of individuals recaptured were recaptured again (Table 1). Most recaptures (69%) were at the site of banding or in an adjacent or diagonal cell (i.e. <200 m). Six individuals were recaptured 1 km or more from the site of banding: Brown Honeyeaters at 1.0, 1.4 and 1.4 km; Dusky Honeyeaters at 1.0 and 1.2 km and a Blue-faced Honeyeater at 1.3 km, the latter being subsequently recaptured close to the original banding site. Nine of 20 birds recaptured more than 200 m from their banding site had changed habitat, with movements occurring between each combination of riparian forest, swamp woodland and eucalypt woodland.

Samples sizes for individual species were small, and comparisons are further complicated by temporal and spatial differences in the patterns of capture. Nevertheless, two comparisons are worth noting. Silver-crowned and Little Friarbirds were frequently seen and captured together. Eleven per cent of Silver-crowned Friarbirds banded were recaptured, and three of the four individuals involved were recaptured again. The time elapsed from first to last capture was more than 300 days in all cases, and all recaptures were within 300 m of the original capture site. In contrast, only one of 63 Little Friarbirds banded was recaptured, and this was a short-term recapture. The difference in recapture rates was marginally non-significant (two-tailed Fishers Exact Test, $P = 0.06$).

Brown and Dusky Honeyeaters were often seen and captured together, and sample sizes for both species are moderately large. Recapture rates did not differ significantly (two-tailed Fishers Exact Test, $P = 0.12$). It appeared that Brown Honeyeaters (79%) were more likely to be recaptured within 200 m of the banding site than were Dusky Honeyeaters (55%), but the difference was not significant (two-tailed Fishers Exact Test, $P = 0.12$). There was no significant difference in the time elapsed until recapture between birds that moved and those that were recaptured within 200 m of the banding site for either the Brown or Dusky Honeyeater (Mann-Whitney U-tests, P both > 0.2). Nor was there any significant relationship between the time elapsed until recapture and the distance between capture and recapture site for individuals that moved greater than 200 m (Brown Honeyeater, $r_s = 0.30$, $n = 6$, $P > 0.5$; Dusky Honeyeater, $r_s = -0.10$, $n = 9$, $P > 0.5$).

Although most Brown Honeyeaters left the study area for 1–2 months each year (see above), 13 individuals were recaptured at intervals of greater than one year and nine of these were recaptured within 200 m of the original banding site. Of the four Brown Honeyeaters that were recaptured more than 300 m from the banding site, all were either banded or recaptured during the period August to December, which is the non-breeding period for the species (unpubl. data).

Four Brown Honeyeater recaptures fall outside the scope of Table 1 and the summary of results in the previous paragraph. A bird banded by D. Geering in July 1989 at one end of the Goose Lagoon riparian forest was recaptured by us at the other end, approximately 800 m away, more than six years later. Three birds banded by us at the flowers of Tropical Banksia were recaptured by Territory Wildlife Park staff, all within 200 m and also at the flowers of Tropical Banksia, at intervals of one, two and three years later. For the latter two birds, this was their third recapture, all being within 200 m of the banding site.

DISCUSSION

Banding as a tool in the monsoonal tropics

The consistently hot weather in monsoonal Australia poses special problems for bird banding and in particular the use of mist nets. Without adequate care, heat stress and subsequent mortality of birds can readily occur. The risk is particularly acute in woodlands (which constitute 95% of the Top End's vegetation) where shade is limited, and especially in the 'build-up' months of October and November. No heat-stress mortalities occurred during this study, but we were obliged to close our nets or severely restrict our activities by 1100 hours almost throughout the year. In inland areas during the 'build-up', closure of nets within two hours of sunrise may be necessary (DCF, pers. obs.). Temperatures are generally lower in the middle of the Dry season (June and July in particular) and during heavily overcast weather during the peak of the Wet season, but the advantage for netting in the former is generally undermined by the predictable mid-morning breezes. The cooler period in the evening is usually short, and as darkness descends rapidly after sunset in the tropics, we generally did not attempt to net then.

Yet another limitation for mark-recapture studies (excluding netting at water holes) in the monsoonal woodlands in particular is the low density of birds (in general and of understorey insectivores in particular, Woinarski and Tidemann 1991), leading to low capture rates. In the many frequently burnt areas, there is little understorey to provide low cover for either birds or mist nets. High levels of avian mobility and/or large home ranges make prediction of good banding sites difficult and recapture rates low. Some of these problems may also limit banding studies in other habitats including temperate grassy woodland. Our choice of study area minimised these problems but, despite active selection of sites on the basis of bird-attracting blossom and/or bird activity, capture rates averaged only eight honeyeaters and three

non-honeyeaters per day, though our honeyeater recapture rate was moderately high at 12 per cent. Previous bush bird-community banding projects in monsoonal Australia have been few and have achieved higher capture rates by operating in low, dense vegetation where bird numbers are higher than in the woodlands (i.e. mangrove communities, Noske 1996), or by netting at waterholes where birds congregate in large numbers (e.g. Woinarski and Tidemann 1992; Tidemann and Woinarski 1994; Franklin *et al.* 1998).

The combination of low capture rates but high recapture rates suggests that future ecological studies of resident and locally mobile nectarivorous birds in Top End woodlands and open forests may be more profitably undertaken at carefully-selected sites using colour-banding and/or radio telemetry (e.g. Noske 1996). This study and that of Franklin and Noske (in press) suggest a considerable number of candidate species for such approaches, including the Silver-crowned Friarbird, Blue-faced Honeyeater, Yellow-throated Miner, White-gaped Honeyeater, White-throated Honeyeater, Brown Honeyeater, Dusky Honeyeater and Rainbow Lorikeet.

The Brown Honeyeater

Our most informative species-specific data set refers to the Brown Honeyeater. The species mostly left the Territory Wildlife Park for a short period during October or November each year, sometimes in spite of the continuing presence of at least some blossom, but displayed a marked tendency to return to the same sites within the Park in successive years. Some of these sites were nesting territories (pers. obs.) and some were sources of nectar, particularly Tropical Banksia, that were available reliably at the same time each year. In November 1997 when Brown Honeyeaters were scarce in the Park we found a localised concentration in a small swamp forest adjacent to the Park where they were attracted to the flowers of the Freshwater Mangrove. The Darwin Harbour mangrove communities are also a possible refuge for the species, although the seasonality of occurrence observed by Noske (1996) in a mangrove area 24 km north of our study area is not complementary to our observations. Recaptures of banded birds in south-west Western Australia and south-eastern Queensland have demonstrated movements of up to 33 km (Collins and Briffa 1982; Liddy 1989; Saunders and de Rebeira 1991).

In a range of environments throughout Australia, Brown Honeyeaters are usually present throughout the year but numbers fluctuate in response to nectar availability (Robertson and Woodall 1983; Collins *et al.* 1984; Liddy 1989; Noske 1996). Our recapture rate of 20 per cent is almost identical to that achieved by Noske (1996) in Darwin Harbour mangroves, both comparing favourably with 12 and 14 per cent achieved for the species respectively by Robertson and Woodall (1987) and Liddy (1989). The evident predictability of their occurrence in our study area also contrasts with the pattern of movements described for the species in Kakadu National Park by Morton and Brennan (1991). It seems likely that

the Wildlife Park provides favourable habitat for the species both because of the near-complete continuity of nectar availability, and because, unlike much of the region, it is infrequently burnt, allowing the development of the shrubs and small trees favoured by the species (Franklin and Noske, in press).

Honeyeater movements

At a spatial scale of less than 470 ha, five and possibly six species of honeyeater were present throughout the year, as was also the nectarivorous Rainbow Lorikeet (DCF, unpubl. data). Banding returns suggested that individuals of a number of species are either highly localised within the study area over periods often greater than a year, or that they return to specific sites at intervals when food is available. Unfortunately, the data are mostly inadequate to distinguish between these hypotheses. However, limited evidence suggests that some individual Silver-crowned Friarbirds were sedentary, and that Dusky Honeyeaters may occupy larger home ranges within the study area than Brown Honeyeaters. Little Friarbirds, on the other hand, were rarely recaptured, and mobility at a spatial scale larger than the study area is a likely explanation for this (Franklin and Noske, in press). Rufous-throated and Banded Honeyeaters were uncommon but clearly irruptive visitors to the study site (as also was the Varied Lorikeet), possibly arriving from the drier inland tropical woodlands. The Red-headed Honeyeater was also an uncommon visitor, probably travelling from the extensive Darwin Harbour mangrove communities which commence within 300 metres of the study site.

High levels of residency amongst honeyeaters in the study area may be facilitated by small-scale habitat heterogeneity. A diversity of sources provided nectar almost throughout the year and this availability was facilitated by the juxtaposition of several habitats. Although eucalypt and swamp woodlands provided the greatest variety and continuity of nectar, riparian forest was especially important during the Wet season. Honeyeaters moved between the available habitats. However, short periods during the Wet season in which virtually no nectar was available were not matched by an exodus of otherwise resident honeyeater (and lorikeet) species. Diet switching would appear a likely explanation, but this remains to be investigated.

Small-scale heterogeneity of forest and woodland habitats is a feature of many near-coastal areas in the Top End (e.g. Woinarski *et al.* 1988). Elsewhere in the Top End and throughout much of monsoonal Australia, floristically heterogeneous woodlands are the vastly predominant habitat, but the scale at which heterogeneity occurs is mostly much larger than in our study area. Many woodland areas are also subject to annual wildfires that may disrupt the continuity of nectar supply and reduce habitat structural diversity. In a semi-deciduous Top End woodland well away from the coast, Woinarski and Tidemann (1991) noted extreme fluctuations in avian nectarivore abundance. It may be only in heterogeneous near-coastal areas that a variety of nectarivorous honeyeaters can persist locally throughout the year.

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