

Abundance, Zonation and Foraging Ecology of Birds in Mangroves of Darwin Harbour, Northern Territory

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Abstract

The density, seasonality, habitat utilisation and foraging ecology of birds in mangals (mangrove forests) at a site on the upper reaches of Darwin Harbour were investigated by transect censusing and colour-banding over three years. Despite having only 10 species of plants, the site supported 17 confirmed and five probable breeding resident species of birds, and was visited by 30 more. From variable-width transect censuses, the mean density of birds on a 4-ha plot was estimated to be 25 ha⁻¹, fairly consistent with densities obtained from territory mapping of colour-banded birds. Nearly 70% of the individuals belonged to just four species: two mangal-dependent species, the red-headed honeyeater, *Myzomela erythrocephala*, and the yellow white-eye, *Zosterops lutea*, and two more generalised species, the large-billed gerygone *Gerygone magnirostris*, and the brown honeyeater, *Lichmera indistincta*. Only the red-headed honeyeater showed significant seasonal variation in abundance, with highest numbers during the late dry season after breeding. This coincided with the period of greatest food (nectar) availability in the mangal, due to flowering *Bruguiera exaristata*. Lowest numbers of the red-headed honeyeater (and the brown honeyeater) occurred in the late wet season when nectar was scarce in the mangal but abundant in paperbarks, *Melaleuca cajuputi*, fringing the mangal. Several resident species held permanent territories, while others apparently shifted landward during the wet season, possibly due to the wetter conditions created by freshwater runoff and high spring tides.

Many species showed strong associations with particular mangal zones. Large-billed gerygones, grey whistlers, *Pachycephala simplex*, shining flycatchers, *Myiagra alecto*, and mangrove fantails, *Rhipidura phasiana*, were associated with the *Rhizophora* zone at the wetter (more frequently inundated) end of the plot; mangrove robins, *Eopsaltria pulverulenta*, and mangrove gerygones, *Gerygone laevigaster*, were encountered most in the *Ceriops* zone; and green-backed gerygones, *Gerygone chloronata*, strongly favoured the dry landward edge. Four foraging guilds were evident among 13 of the most abundant species, the largest of which was the insectivorous foliage-foraging guild. Species in this group partitioned resources by differential selection of mangrove species, heights and foraging techniques. The tiny (6.4 g) mangrove gerygone was the most specialised species, spending 80% of its time on *Avicennia marina*. Contrary to the literature, breeding of mangal-dwelling birds peaked during the dry season. The ecology, evolution and biogeography of mangrove-endemic birds is reviewed in the light of this study and recent information from Western Australia.

Introduction

North-western Australia supports more mangrove-endemic bird species than does any other region in the world. Found on coasts throughout the tropics, mangroves are thought to have originated in northern or western Australia (Mephram 1983), and they exhibit their greatest diversity in the South-east Asian–Australian region (Tomlinson 1986). In Peninsular Malaysia, where the diversity of mangroves is comparable to that in Australia, seven bird species are restricted to mangals (mangrove communities), although three of these extend into inland forests elsewhere in South-east Asia (Nisbet 1968; Wells 1985; Noske 1995). The floristically

poor mangals of Africa and South America each have only one bird species exclusive to this habitat (Cawkell 1964; Haverschmidt 1965; Ffrench 1966; Field 1968; Altenburg and Spanje 1989). Australia, however, has 14 species that are virtually confined to mangals, and at least six other species that depend on mangals in parts of their range (Ford 1982; Schodde *et al.* 1982).

Apart from Indonesia, Australia has the largest remaining area of mangal in the Indo-Pacific region (Saenger *et al.* 1983). These tracts are significant because they are largely unexploited by humans, in contrast to the situation in the rest of Asia and the Pacific (e.g. Budimen *et al.* 1987; Soepadmo 1987). Galloway (1982) estimated that the total area of mangal in Australia was 11 000 km², of which about 40% occurred in Queensland and a further 35% (4120 km²) in the Northern Territory. More recently, however, the area of mangal in the Northern Territory was estimated to be 1440 km² (Wilson *et al.* 1990). Stratigraphic and palynological evidence indicates that mangal was much more extensive in north-western Australia during the Pleistocene than today (Chappell and Grindrod 1985; Woodroffe *et al.* 1985a, 1985b, 1992; Clark and Guppy 1988). In terms of their floristics, the richest mangals in Australia are those of northern Queensland (Lear and Turner 1977; Bunt *et al.* 1982; Wells 1982, 1983), yet fewer mangal-endemic bird species occur there than in north-western Australia (Ford 1982; Schodde *et al.* 1982).

Given the interest that mangals have attracted from biologists in the last two decades, our understanding of their vertebrate fauna is surprisingly poor (Hutchings and Recher 1982; Milward 1982; Hutchings 1987). The literature on Australian mangal-dwelling birds is mainly concerned with their distribution, evolution and taxonomy (Ford 1982, 1983; Schodde *et al.* 1982; Johnstone 1990). Johnstone (1990) listed birds in 83 blocks of mangal between Cambridge Gulf and Shark Bay in Western Australia. Schodde *et al.* (1982) and Johnstone (1990) made general observations of the feeding behaviour, diet and habitat preferences of mangal-endemic birds, but there have been no quantitative studies of their abundance and foraging ecology.

The present study concerns the ecology of a bird community in mangals near Darwin, Northern Territory. The principal objectives of the study were to determine (1) the density, relative abundance and seasonality of all bird species inhabiting the mangal; (2) their spatial use of this habitat; and (3) their feeding ecology. These objectives were achieved by monthly bird censuses and spot-mapping of individually marked birds, observations of foraging behaviour and monitoring of floral (nectar) and insect food resources. It was assumed that the diet of each species was similar to that of its conspecifics in Western Australia (data in Johnstone 1990). The results of the studies of flowering phenology and insect abundance are summarised here, and will be detailed elsewhere.

Methods

Study Site

In June 1985, a study site was established adjacent to Palmerston Sewage Ponds (12°30'S, 130°57'E), 13 km east-south-east of Darwin Post Office, in mangals fringing Myrmidon Creek. This creek flows into the East Arm of Darwin Harbour near its junction with Elizabeth River (Fig. 1). This area was chosen because of its pristine condition, relative inaccessibility to the general public, and numerous abandoned survey lines cutting east-west through the mangal, providing easy access from the landward edge. The climate of the region is characterised by uniformly high temperatures and a highly seasonal rainfall. Some 90% of the rainfall (mean annual rainfall c. 1700 mm) falls during the wet season from November to April, while the dry season (May–October) is virtually rain-free. Darwin Harbour is macrotidal: the maximum range is 7.8 m; mean spring range is 5.5 m and mean neap range is 1.9 m (Darwin Tide Tables, 1988–90).

Vegetation at the site exhibited the zonation typical of mangals in northern Australia (Lear and Turner 1977; Semenuik *et al.* 1978; Davie 1985; Semenuik 1985; Wightman 1989) and that described for Creek 'H', only 4.5 km south of the study site (Woodroffe 1985). From the seaward or tidal river edge progressing inland, these zones were (i) a *Sonneratia* zone, represented by a narrow strip of *Sonneratia alba* fringing Myrmidon Creek; (ii) a zone dominated by *Rhizophora stylosa*, with distinctive stilt roots, occurring along all tidal channels; (iii) a relatively narrow zone dominated by *Bruguiera exaristata*; (iv) a wide zone

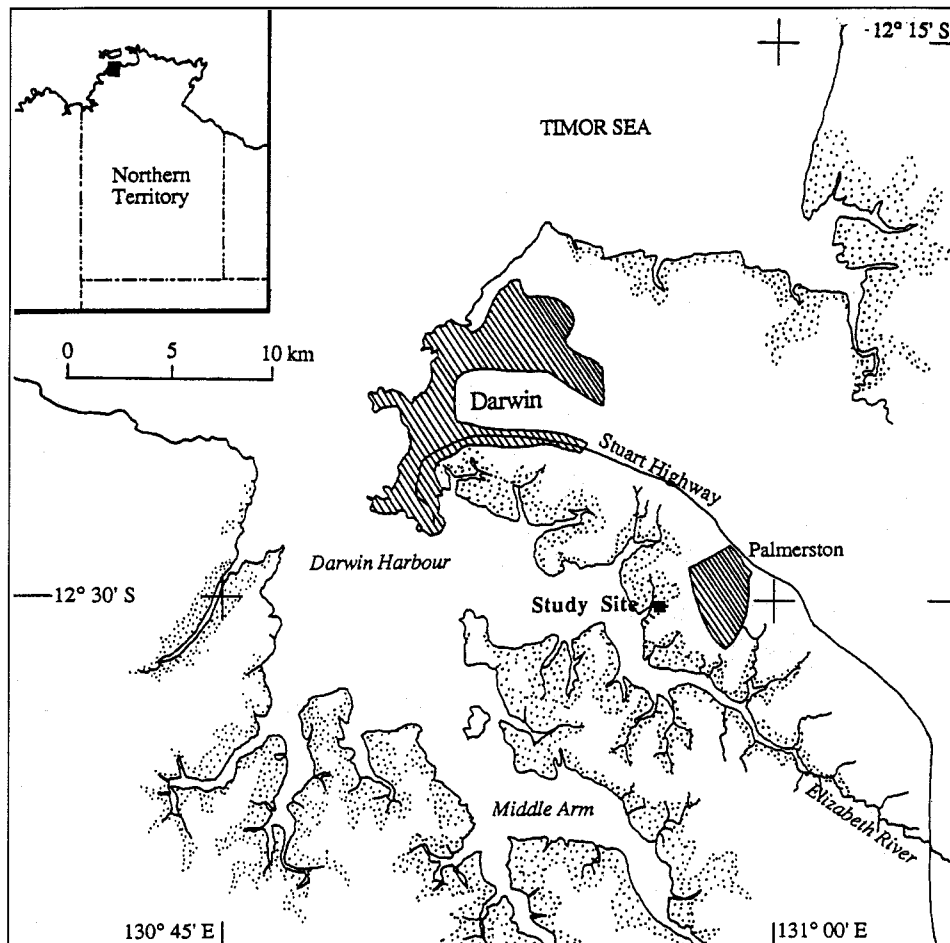


Fig. 1. Location of study site, in relation to Darwin and Palmerston. Stippled areas are mangals.

dominated by *Ceriops australis*, forming a virtual monoculture bisected by bare sandy saltflats into an inner *Ceriops* zone and an outer (often taller) *Ceriops* zone; and (v) a narrow zone dominated by *Lumnitzera racemosa*, marking the landward edge of the mangal (Fig. 2). The mangal was patchily fringed by paperbarks (*Melaleuca leucadendra* and *M. cajuputi*) and surrounded by savanna woodland dominated by *Pandanus spiralis*, *Planchonia careya*, *Hakea arborescens*, *Terminalia grandiflora* and *Cochlospermum fraseri*, with a well-developed grass layer.

The site contained many previously cut survey lines (1–1.5 m wide) extending west from the mangal–savanna boundary at 50-m intervals. A rectangular plot spanning four of these east–west lines was chosen for transect censuses and mist-netting. It included *Rhizophora*, *Bruguiera* and *Ceriops* zones (Fig. 2). The western edge of the plot was situated about 350 m from Myrmidon Creek, and the eastern edge 100–200 m from the mangal–savanna boundary. Five north–south lines were established, crossing the transects at 50-m intervals, to produce a grid of twelve 50 m × 50 m squares. The plot encompassed an area of 3 ha (200 m long × 150 m wide), but the censusing area extended 25 m south and north of the first and last transects, respectively, to make a total of 4 ha. The intersections of the lines were marked with flagging tape of two colours in unique combinations for mapping the locations of marked birds. The vegetation of the plot was quantified by identifying and recording approximate heights of all plants (>1 m high) counted within a belt 10 × 0.5 m wide at alternate 10-m intervals along one or both sides of each of the four cut transect lines.

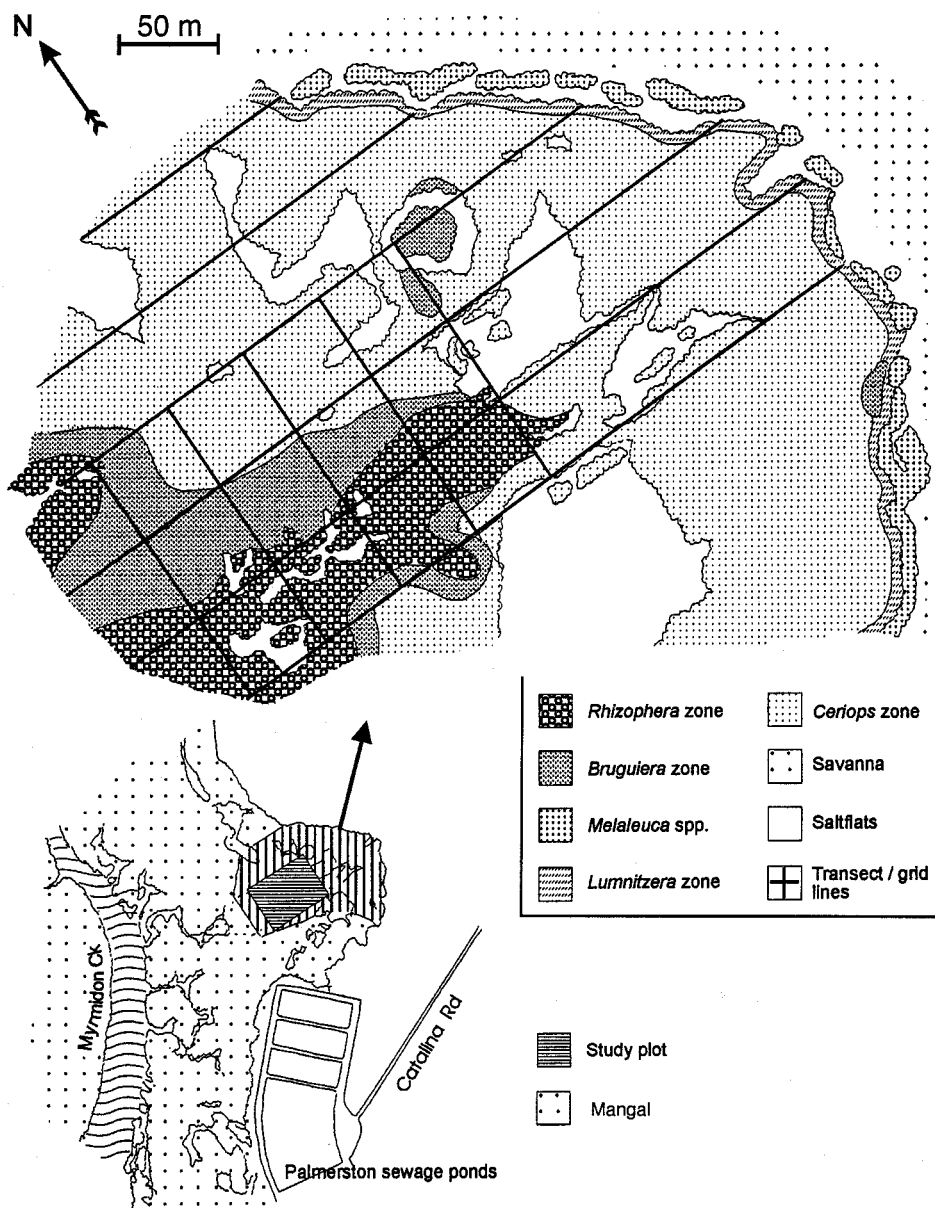


Fig. 2. Mangrove zonation at study site, showing gridded plot, and its relationship to mangal-savanna boundary and Myrmidon Creek.

Mist-netting

Netting and colour-banding of birds were conducted to enable recognition and mapping of individuals seen during censuses and other walks, and to provide additional locational and morphometrical data on each species. Mist-netting was conducted once a month on average from January 1986 to February 1990, and was usually restricted to mornings when tides did not exceed 3 m. Mist-net sites were numbered and, during the study period, nets were rotated over the four transects to ensure coverage of the plot. After 1990, nets were placed in locations outside the plot as well as inside, to maximise capture rates of one species (the red-

headed honeyeater). On each occasion, 4–6 nets were operated for 2–5 h, checked every 30 min to minimise the risks of dehydration and predation to captured birds. All captured birds were banded with a numbered metal band (supplied by the former Australian National Parks and Wildlife Service) on the left leg, and two coloured celluloid bands on the right leg.

Censusing and Spot-mapping

Once each month from August 1987 to July 1990, I counted birds seen or heard while walking slowly at 0.4 km h⁻¹ along each of the four 200-m east–west transect lines in sequence. Censuses were conducted only in the early morning between 0700 and 0900 hours, during fine weather, and were not undertaken during high tides because of the risk of predation of the author by crocodiles. As the habitat distribution and foraging behaviour of some bird species possibly vary with tidal state, my avoidance of high tides may have introduced some bias, but this was probably minimal since most high neap tides only affected the *Rhizophora* zone, whilst the *Ceriops* zone on the plot was affected for less than 2 h per day during maximum spring tides.

The location of each encountered bird was recorded by estimating its perpendicular distance up to 25 m (north or south) from the transect line, and distance from the nearest 50-m grid marker. These locations were subsequently transcribed onto maps for determination of territories. Where possible, sex and colour-band combination were also noted. As the transect lines were only 50 m apart, they were treated as a single transect 800 m long. In counting birds along closely spaced transects, care was taken to avoid multiple counting of individuals or groups, by noting the size of group and direction of travel on maps, and identifying any colour-banded members. Locations that appeared to refer to previously detected individuals or groups were ignored in data analyses. This problem is largely negated by the analysis, described below, in which data from beyond the first 5-m band were usually excluded. The difficulty of seeing birds in the mangal beyond 3 m from the transect line precluded a 'sight only' approach. Similarly, alternating the route of the walk was precluded because of rising tides affecting one end of the plot.

Transect census data were analysed by the variable-width procedure to compensate for variability in detectability of birds over different transect widths, as most species showed a consistent decline in detection over increasing distances from the transect line. This contradicts the assumption of equal detectability over the entire transect area inherent in the fixed-width density procedure. For simplicity, I used the technique outlined by Balph *et al.* (1977), in which, for each species in each census, densities are calculated separately for strips of increasing width (5, 10, 15, 20, 25 m; total areas 0.8, 1.6, 2.4, 3.2, 4 ha), and the strip with the highest density used for that census. This approach seemed justified given that transect methods invariably underestimate true densities (e.g. Emlen 1971; Eberhardt 1978; Franzreb 1981; Hilden 1981; Bell and Ferrier 1985; Ford *et al.* 1985), especially in dense habitats such as mangal. Transect density estimates were checked against densities determined for colour-banded species inhabiting the plot. To examine seasonal variation in abundance, density estimates were grouped into six bimonthly periods and analysed by one-way ANOVA, after data were transformed to $\log_{10}(x + 1)$.

Locational data were analysed to determine whether bird species had preferences for particular mangrove species or zones. Such data came from two sources: observations during censuses and other walks; and the locations of mist-nets where birds were caught. For observational data, a colour transparency map, showing the boundaries of the three mangal zones represented in the (4 ha) plot, was superimposed on bird-species maps so that each locational record could be assigned to a zone or zones. Where a bird location fell on the boundary between two zones, each zone would score 0.5 for that record. Records involving more than one bird were, except where indicated, treated as single records. Preferences for particular zones were investigated with chi-square tests by comparing the distribution of records between the three zones with the total area (in m²) of each zone on the plot, calculated from the vegetation map by means of a planimeter. Yates' correction factor was applied to 2 × 2 contingency tables. As sampling outside the plot was opportunistic and uneven, it was not valid to calculate expected values based on the area of zones so such data are used only in interspecific comparisons. Data on mist-net locations of each species were initially assigned to each of the five mangal zones (*Rhizophora*, *Bruguiera*, inner *Ceriops*, outer *Ceriops*, *Lumnitzera*) sampled up to February 1994, and compared with expectations based on the total net-hours devoted to each zone (number of nets × hours of operation) by means of chi-square tests.

Except where mentioned in the text, scientific names of birds are given in the Appendix.

Foraging Observations

Foraging observations of the four most abundant species were restricted to the site, but, for other species, observations were made at several sites around Darwin Harbour, to minimise the possibility of site

bias. For each foraging bird encountered, the following four niche dimensions were recorded: foraging site (leaf, branch, flower, ground), foraging height, foraging technique, and plant species used. Foraging techniques were categorised as follows: glean (attempting to obtain stationary prey while perched), snatch (acquiring stationary prey during short flight from perch), hover (hovering beside stationary food source), hawk (chasing flying prey), drill (repeatedly pecking at one location) or probe (inserting bill into cavity of flower or branch). No two observations were made consecutively; if an individual was observed more than once, observations were separated by at least 30 min.

For each species, niche breadth was calculated with the Shannon–Wiener index of diversity (Krebs 1989):

$$H' = -\sum p_i \log_e p_i,$$

where p_i is the proportion of foraging manoeuvres in each of n categories per niche dimension (substratum, height, technique, plant species). These values were standardised for interspecific comparisons by means of the Evenness measure (Krebs 1989):

$$J' = H' / H'_{\max},$$

where H'_{\max} is equivalent to $\log_e(n)$.

For each pair of species for each measured niche dimension, overlap was calculated with the Percentage Overlap formula (Krebs 1989):

$$P_{jk} = [\sum (\text{minimum } p_{ij}, p_{ik})] \times 100$$

where P is the percentage overlap between species j and k , and p_i is the proportion of observations in each category of each niche dimension (substratum, height, technique, plant species). As the foraging dimensions were not independent, overlaps for the four niche dimensions were averaged. Average overlap values for each pair of species were used to construct a dendrogram to delineate guilds of species that resembled each other in foraging behaviour, by the method of Cody (1974). Differences between species in foraging behaviour were examined with chi-square tests, Yates' correction factor being applied to all 2×2 comparisons. Statistical comparisons between species were mainly restricted to pairs of congeners. Nesting data were collected opportunistically.

Birds of Australian mangals are known to eat nectar, insects, spiders, crustaceans, fish and molluscs (Johnstone 1990). To assess the temporal and spatial variation in availability of these resources, insect and floral resources at the study site were regularly monitored over at least one full year. Monitoring of the crustacean, molluscan and fish fauna was outside the scope of this study. Flying insects were sampled with stationary Malaise and window interception traps at three locations, representing three mangrove zones, from May 1990 to February 1993. Stationary arthropods were sampled by bagging foliage clipped from branches of each of the five major mangrove species once a month from October 1989 to April 1991. Data relating to insect availability will be presented elsewhere.

The availability of nectar resources was assessed by monitoring the flowering phenology of all mangrove species that had flowers visited regularly by birds, viz. *R. stylosa*, *B. exaristata*, *C. australis* and *L. racemosa*. For each of these species, 12–20 individual plants were tagged and the following recorded each month for each tree: (i) the proportion of shoots ($n = 20$ –50) with buds or flowers; and (ii) the stages (buds, fresh or old flowers) of all flowers counted within 12 views through 10× binoculars at a distance of 10 m, four from each of three height strata (upper, middle and lower). Except for *L. racemosa*, the tagged plants were spread over the entire length of two or more transects to avoid bias associated with particular edaphic or tidal conditions. As the paperbark *M. cajuputi* on the mangal edge was found to be an important nectar source for mangal-dwelling birds at times, 15 individuals of this species were tagged and monitored as above.

Results

Vegetation and Flowering Phenology

Eight species of plants, all obligate mangroves (*sensu* Tomlinson 1986), occurred on the plot, while another two mangroves (*L. racemosa*, *Excoecaria ovalis*) were confined to the landward edge, east of the plot. Transect 1 exhibited fairly typical zonation from east to west, from the landward *C. australis* zone with an increasing amount of *B. exaristata*, to the twice-

daily inundated *Rhizophora* zone with co-dominant *Bruguiera parviflora* (Fig. 3; Table 1). The eastern (drier) end of Transect 2 was dominated by short (2–5 m) *R. stylosa*, with some *B. exaristata*, surrounding a shallow channel just south and parallel to the transect line; further west, where the creek widened considerably, *R. stylosa* (mixed with *B. parviflora*) reached heights of 13 m. This was the only transect with virtually no *C. australis*. Transects 3 and 4, however, were dominated by *C. australis*, which were taller on the latter transect (mean heights 2.9 and 3.5 m, respectively) (Table 1). *B. exaristata* reached its tallest also at the western end of Transect 4, near the mouth of another tidal channel. Other species confined to the wet, western end of the plot were *Aegiceras corniculatus* (2–3 m tall) and the prostrate *Camptostemon schultzei* (1–2 m), although the latter was absent from quadrats. *Avicennia marina* was scattered thinly throughout the plot, often as large trees (up to 10 m) adjacent to tidal channels. *Aegialitis annulata* formed a sparse ground cover to 0.5 m at the eastern end of Transects 1 and 2.

Avicennia marina formed a thin band around the bare sandy saltflats, which occupied large areas landward of Transects 2 and 3, and south of Transect 1. Further inland, *C. australis* occurred as a monoculture until the mangal-savanna boundary, where *L. racemosa* formed a dense, narrow (10–20 m wide) fringe (Fig. 2). This broad *Ceriops* zone was subdivided into inner (wetter) and outer (drier) zones, west and east of the saltflats, respectively, for describing bird locations. Apart from its occurrence on all transect lines within the plot, *B. exaristata* occurred in a small monospecific stand at the inland end of Transect 4, marginally overlapping the north-eastern corner of the plot.

The major mangrove species flowered at discrete, predictable times of the year at the study site. *R. stylosa* and *L. racemosa* flowered during the wet season, mainly from December to February, while *B. exaristata* flowered during the dry season, from May to October (Fig. 4).

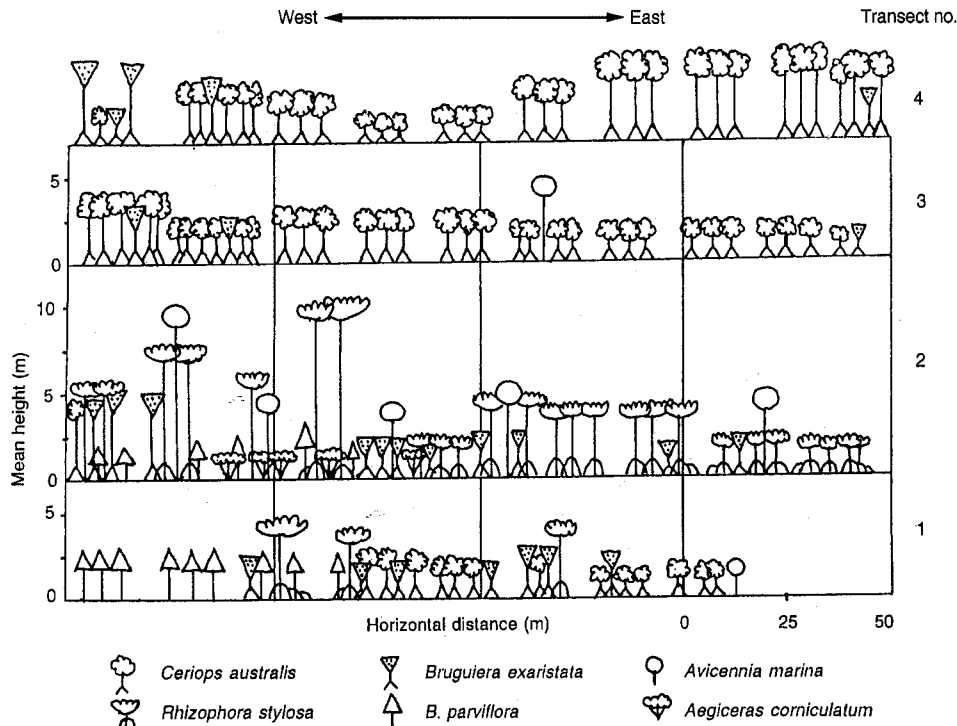


Fig. 3. Vegetation of study plot, showing relative abundance of mangroves along the four east-west transects. The northernmost transect is at the top of diagram; distances between transects (50 m) are not to scale.

Table 1. Relative abundance, height and density of plants on the Palmerston mangal plot

Transect	Relative abundance (%) and mean height (m; in parentheses)					n	Plant density (m ⁻²)	
	<i>Rhizophora stylosa</i>	<i>Bruguiera parviflora</i>	<i>Aegiceras corniculatus</i>	<i>Bruguiera exaristata</i>	<i>Ceriops australis</i>	<i>Avicennia marina</i>	Mean	s.d.
1	5.8 (4.0)	32.0 (3.0)	1.8 (2.6)	12.2 (2.6)	47.0 (2.2)	1.2 (2.1)	3.73	1.66
2	68.6 (4.5)	9.3 (2.0)	5.1 (1.8)	11.9 (3.1)	0.9 (5.0)	4.2 (5.8)	1.07	0.27
3	0	0	0	3.6 (2.8)	95.4 (2.9)	1.0 (4.5)	3.58	1.76
4	1.7 (1.4)	0	0	5.0 (4.8)	93.3 (3.5)	0	2.18	1.06

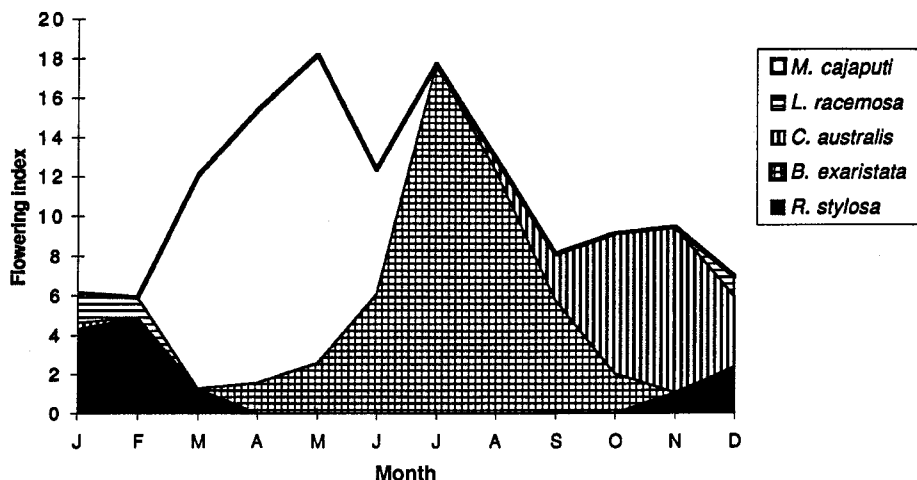


Fig. 4. Flowering phenology of four major mangrove species, and *Melaleuca cajuputi*, at the study site. *M. cajuputi* is on the seasonally inundated landward edge of the mangal.

C. australis flowered mostly from October to December, plants from the landward (drier) end of the gradient starting and finishing later than those from the inner mangal (R. A. Noske, P. Donaldson and M. Bezuijen, unpublished data). On the landward edge of the mangal, *M. leucadendra* flowered profusely but briefly during February, while *M. cajuputi* flowered from March to May, when freshwater runoff from the hinterland peaked, and flowering of mangroves was least (Fig. 4).

Flying insects were trapped throughout the year, but fluctuated both within and between years (R. A. Noske, P. Donaldson and M. Bezuijen, unpublished data). There was no consistent seasonality in insect numbers or biomass. All three zones sampled (*Rhizophora*, *Bruguiera*, *Ceriops* and *Lumnitzera* *Melaleuca*) produced similar total numbers and biomass of insects, but there were differences in taxonomic composition of insects. The highest numbers of stationary invertebrates were found in *A. marina*, and the lowest in *R. stylosa*. Again, the abundance of invertebrates fluctuated, but seasonal variation was inconsistent between mangrove species.

Bird Species Richness, Density and Relative Abundance

Excluding migratory waders, herons and aerial insectivores (martins and swifts), 54 species of birds were recorded in mangal at the study site within 200 m of the plot. However, only 31 species (including the aerial rainbow bee-eater, which foraged within the mangal) were recorded on 10 or more occasions (Table 2). Less-frequently recorded species included several mangal-specialists (e.g. the mangrove golden whistler and white-breasted whistler), as well as many visitors to the landward edge from the adjoining savanna (e.g. little friarbirds and double-barred finches; see Appendix). The granivorous peaceful and bar-shouldered doves were recorded in the mangal on almost every visit, and both species nested within the mangal, but as their food occurred outside this habitat they made frequent excursions to the adjoining savanna. Of the 31 most-frequently recorded species (≥ 10 records), 17 were known to breed on the site and another five species probably bred closer to the river edge (Table 2). Among the remaining eight species, several were distinctly seasonal (see below).

In all, 36 bird species were recorded on the 4-ha plot during censuses. By summing the mean densities for each species, the total density of birds on the plot was estimated to be 24.8 ha^{-1} (Table 2). In comparisons of bimonthly samples there was no significant seasonal variation in the density of all species combined (log-transformed, $F_{5,30} = 0.751$, $P > 0.5$), but mean density (\pm s.d.) was lowest in the late wet season (March–April, $20.7 \pm 4.98 \text{ ha}^{-1}$), and highest in the late dry season (September–October, $28.6 \pm 4.36 \text{ ha}^{-1}$).

Table 2. Density, seasonality and breeding status of most-frequently recorded birds at Palmerston mangal site*n*, number of times encountered on censuses (max. 36); *N*, number of months recorded at site (max. 54)

Species	<i>n</i>	Plot (4 ha)		Site (8 ha)	
		Density (birds ha ⁻¹)		<i>N</i>	<i>N</i>
		Mean	s.e.	Dry	Wet
Red-headed honeyeater ^A	36	5.5	0.63	27	27
Yellow white-eye ^A	36	5.02	0.6	25	26
Large-billed gerygone ^A	36	3.89	0.41	26	27
Brown honeyeater ^A	31	2.31	0.38	25	25
Mangrove robin ^B	35	2.12	0.29	23	26
Mangrove gerygone ^A	26	0.91	0.17	20	22
Grey whistler ^B	27	0.71	0.11	21	21
Shining flycatcher ^A	26	0.61	0.1	17	19
Bar-shouldered dove ^A	13	0.48	0.18	18	21
Peaceful dove ^A	14	0.38	0.1	20	20
Black butcherbird ^A	16	0.32	0.09	20	21
Silver-crowned friarbird ^A	8	0.3	0.16	13	7
Lemon-bellied flycatcher ^C	11	0.27	0.08	11	17
Northern fantail ^A	6	0.26	0.11	9	19
Sacred kingfisher	13	0.19	0.05	19	14
Green-backed gerygone ^A	11	0.17	0.05	19	20
Leaden flycatcher	9	0.16	0.06	18	7
Helmeted friarbird ^A	5	0.16	0.08	4	7
Varied triller	6	0.14	0.06	15	20
Broad-billed flycatcher ^C	6	0.13	0.05	12	14
White-bellied cuckoo-shrike	4	0.09	0.05	12	13
Cicadabird	4	0.08	0.05	5	20
Little kingfisher ^C	6	0.08	0.04	11	14
Dusky honeyeater	3	0.06	—	10	4
Mangrove fantail ^C	3	0.15	—	7	13
Little bronze-cuckoo ^A	2	0.01	—	13	22
Little shrike-thrush ^C	2	0.03	—	2	9
Rainbow bee-eater	2	0.09	—	14	17
White ibis	2	0.04	—	6	6
Chestnut rail ^A	0	—	—	15	22
Rufous whistler	0	—	—	8	2
Other species (7) censused	9	0.2	—	—	—
Total	36	24.84			

^ANests recorded on or close to plot.^BJuveniles seen on plot.^CKnown to breed in Darwin mangals.

Over three-quarters (77%) of the birds counted belonged to just five species; in order of decreasing abundance, these were the red-headed honeyeater, the yellow white-eye, the large-billed gerygone, the brown honeyeater and the mangrove robin. Mist-netting statistics showed consistent trends (Table 3). Up until February 1990, 379 individuals of 28 species (516 captures) were netted on the plot, of which the above five species comprised 81%. Although fewer yellow white-eyes and more red-headed honeyeaters were caught than expected according to estimated densities, the combined relative abundance of these two species was about the same (42% and 45% of all birds from censuses and mist-netting respectively). The density of chestnut rails was obviously underestimated because they were never encountered on the plot during censuses, which were conducted at low tides. In fact, this species was often heard on the plot at other times, and even nested within it during the study (Table 2).

Seasonality of Individual Species

There was considerable variability over the year in densities on the plot for most species, but only the red-headed honeyeater showed significant seasonal variation between bimonthly periods ($F_{5,30} = 7.01$, $P < 0.001$). The mean density of this species on the plot was significantly lower in March–April than in each of the other bimonthly periods except January–February (Fig. 5a) (Tukey test, $P < 0.05$). Peak mean densities occurred from July to November,

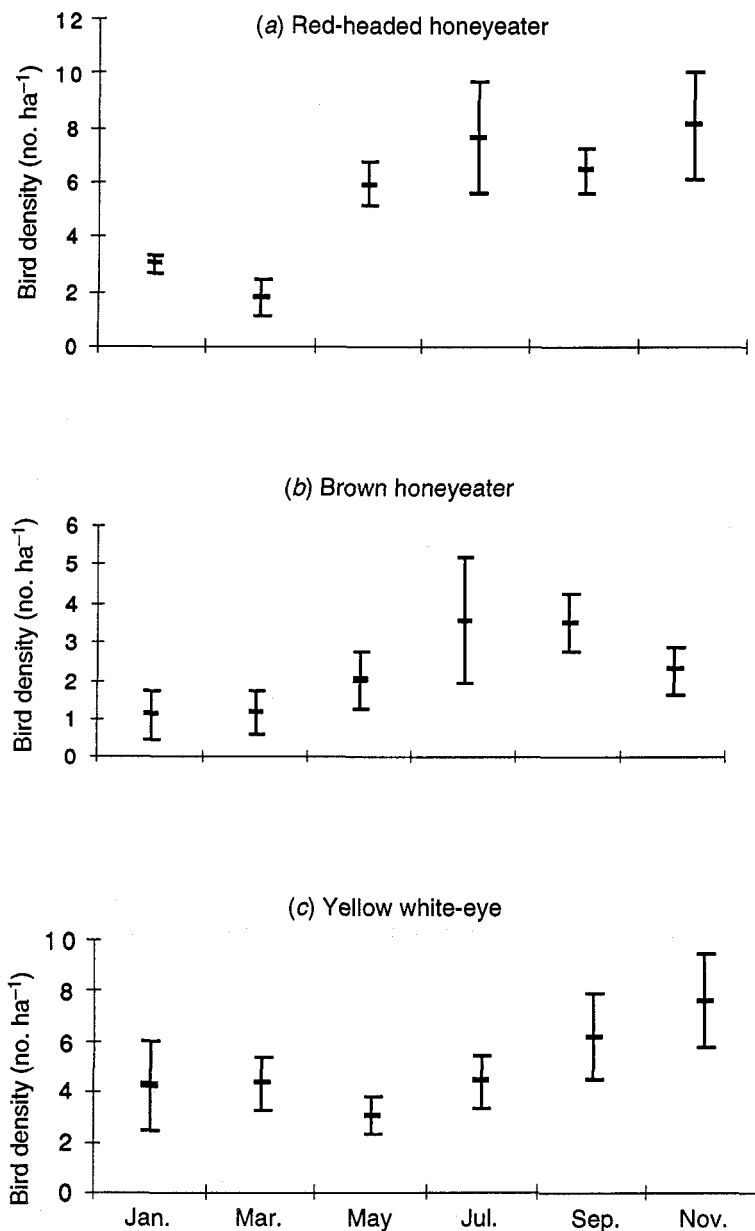


Fig. 5. Estimated densities of (a) the red-headed honeyeater, (b) the brown honeyeater, and (c) the yellow white-eye over the year. Values are means with standard errors.

Table 3. Trapping statistics and masses of birds mist-netted on the Palmerston mangal plot
Banding data from February 1986 to February 1990, plot only. Mass data to February 1993, from
Palmerston unless otherwise stated; includes birds caught outside the plot; nr, not recorded

Species	No. banded	Trapped (% of all species)	Retrapped (%)	Mass (g)		n
				Mean	s.d.	
Red-headed honeyeater	133	35.09	23.3	7.52	0.73	524
Large-billed gerygone	59	15.57	28.8	7.06	0.61	68
Yellow white-eye	49	12.93	32.7	9.14	1.65	110
Brown honeyeater	46	12.14	19.6	9.76	1.57	132
Mangrove robin	19	5.01	57.9	18.84	2.51	39
Grey whistler	12	3.17	41.7	16.25	0.96	27
Shining flycatcher	10	2.64	20.0	18.3	0.92	21
Sacred kingfisher	12	3.17	0	39.89	5.44	15
Mangrove gerygone	6	1.58	16.7	6.41	0.30	9
Green-backed gerygone	5	1.32	0	6.07	0.40	11
Broad-billed flycatcher	3	0.79	0	11.34	0.47	8
Leaden flycatcher	3	0.79	33.3	10.95	0.89	10
Mangrove fantail	3	0.79	0	6.98	1.28	6
Azure kingfisher	3	0.79	0	28.27	0.87	3
Little shrike-thrush	2	0.53	0	37.05	1.22	4
Little kingfisher	2	0.53	0	13.25	1.99	4
Dusky honeyeater	1	0.26	100.0	11.7	1.16	5
Helmeted friarbird ^A	1	0.26	100.0	90.23	6.35	4
Black butcherbird ^B	1	0.26	0	198.54	12.88	5
Lemon-bellied flycatcher	1	0.26	0	12.06	0.72	5
Little bronze-cuckoo ^C	1	0.26	0	15.1	nr	5
White-bellied cuckoo-shrike	1	0.26	0	65.5	3.54	2
Northern fantail	1	0.26	0	11.65	1.31	4
Silver-crowned friarbird	1	0.26	0	75.07	1.7	3
Others (4 spp.)	4	1.06	0			
Total	379	100				

^AHall (1974) (populations from the Kimberley and/or the Northern Territory only included).

^BHall (1974) and Noske (unpublished data).

^CJohnstone (1990).

coinciding with the breeding season and dispersal of young (see below). The brown honeyeater showed a similar but more gradual seasonal trend, with highest mean densities during the mid-to-late dry season (Fig. 5b), but differences were not significant ($F = 2.28$, $P > 0.05$). The mean density of yellow white-eyes peaked in the early wet-season months of November and December (Fig. 5c). The sacred kingfisher was significantly more abundant in the dry season than in the wet ($F_{1,34} = 4.81$, $P < 0.05$), whereas the reverse was true for the black butcherbird, although this difference was not significant ($F_{1,34} = 3.53$, $P > 0.05$). The large-billed gerygone, mangrove robin and mangrove gerygone showed no consistent seasonal pattern of abundance, suggesting year-round residence (see below).

Of the 25 records of cicadabirds, 22 (88%) fell between October and April, suggesting regular movement out of the mangal in the dry season. The mangrove fantail and the little shrike-thrush were also recorded most frequently in the wet season. By contrast, the dusky honeyeater, the leaden flycatcher and the rufous whistler were predominantly dry-season visitors to the site (Table 2). None of these species is considered migratory in the Northern Territory (Crawford 1972; Storr 1977), but records from the Darwin region since 1990 suggest

movement of the last two species inland during the wet season (R. A. Noske and N. M. McCrie, unpublished data). Three of the four records of the mangrove golden whistler were of immature birds in the wet-season months of February and March.

Territory Mapping

Each year, adult red-headed honeyeaters held territories in flowering *B. exaristata* for much of the dry season, while during the wet they moved locally between other nectar sources. Several colour-banded males occupied a core area year-round, except during the period of food shortage from March to May, when they established small feeding territories in *M. cajuputi* on the landward edge of the mangals, up to 500 m from their core areas. In the small patch of *B. exaristata* (0.3 ha) just outside the study plot, 7–10 colour-banded pairs occupied territories in flowering trees during the dry seasons of 1988–90, giving densities of about 47–66 birds ha⁻¹. These values exclude unbanded non-breeders and young birds, which at times were as numerous as the residents (R. A. Noske and M. Bezuijen, unpublished data). Even higher densities of red-headed honeyeaters were recorded in flowering *M. cajuputi* during the late wet season each year. Despite the low recapture rate compared with other common residents (Table 3), unbanded birds comprised 61, 53 and 31% of the birds sighted on the plot during all censuses in 1987, 1988 and 1989, respectively ($n = 46, 64, 52$), indicating that a large proportion of the population on the plot had been banded by the end of the study period, although new individuals were still entering.

Unlike the solitary or paired red-headed honeyeaters, yellow white-eyes frequently occurred in tight flocks of six or more birds, which moved rapidly through the plot. These birds were typically unbanded, suggesting they were vagile non-breeders. Fourteen colour-banded individuals, including five breeding pairs, were recorded repeatedly on the plot and just beyond it, over at least two years, but home ranges appeared to overlap. Assuming that the four 'unpaired' birds had unbanded partners, an average density of 5 birds ha⁻¹ (Table 2), including subadults, seems reasonable. Sightings of unbanded birds on the plot during censuses dropped from 71% in 1987 to 36% in 1988 and 15% in 1989–90 ($n = 14, 28, 20$, respectively), but members of flocks were rarely seen sufficiently well for identification.

Territorial interactions and mapping suggest that the large-billed gerygone holds year-round territories. In 1988, at least six colour-banded pairs were known to inhabit the plot. However, banding statistics (Table 3) and the sighting rate of unbanded birds, which increased from 41% in 1988 to 64% and 76% in 1989 and 1990, respectively ($n = 54, 25, 21$), suggest that mortality was high and/or that many non-territorial birds were present. Few colour-banded brown honeyeaters were permanent residents on the plot, although four individuals were sighted repeatedly over 2- or 3-month periods. The recapture rate for this species was the lowest of the seven most abundant species (Table 3). As did red-headed honeyeaters, brown honeyeaters moved to flowering *B. exaristata* and *Melaleuca* spp. as they became available, but in much smaller numbers.

Two groups of colour-banded mangrove robins, each comprising three adults, held permanent territories within the plot, while most of the territory of a third pair was outside the plot. Thus, the plot usually contained 5–7 banded adults, and one or more juveniles at times. The density estimate of this species from transect censuses (Table 2) was slightly exaggerated as it predicts 8.5 individuals on the plot. This overestimation may be due to groups of robins splitting up, resulting in double-counting of individuals. Despite a moderate recapture rate for grey whistlers (Table 3), over half of the sightings of this species were of unbanded birds, suggesting high mortality and/or large, overlapping home ranges. Two colour-banded pairs of mangrove gerygones were regularly sighted on the south-eastern periphery of the plot, mainly on the edge of saltflats. Similarly, one colour-banded pair of shining flycatchers was seen over much of the plot, although other unbanded individuals were occasionally seen. For the latter three species, estimates of 2.8, 3.7 and 2.4 birds, respectively, over the 4-ha plot (derived from densities in Table 2) appear valid.

Zonation of Birds

The mapped locations of sighted and mist-netted birds of the common species suggested associations with particular mangrove zones. Red-headed honeyeaters were encountered and mist-netted in the *Bruguiera* zone more often than expected, according both to the area of zones within the plot and to netting time allocated to each zone ($\chi^2 = 150.6$ and 87.2 , respectively, d.f. = 1, $P < 0.001$ for both) (Tables 4, 5). From sightings over the entire site, significant differences in zonation were found between each bimonthly period (Fig. 6), except between the early (November–December) and mid (January–February) wet-season periods ($\chi^2 = 7.79$,

Table 4. Use (%) of mangal zones by most-abundant bird species, according to observations within the Palmerston plot

Bold value, most-frequently used zone; total plot area = 40287 m². *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant

Species	Zone			n	χ^2_1	P
	<i>Rhizophora</i>	<i>Bruguiera</i>	<i>Ceriops</i>			
Red-headed honeyeater	38.7	46.2	15.1	523	150.58	***
Yellow white-eye	50.2	25.3	24.5	312	70.07	***
Large-billed gerygone	57.1	29.0	13.9	264	103.50	***
Brown honeyeater	30.1	46.1	23.9	178	50.66	***
Mangrove robin	34.1	34.1	31.8	157	8.85	**
Grey whistler	48.7	31.6	19.7	76	8.29	**
Mangrove gerygone	7.3	12.1	80.6	62	32.58	***
Shining flycatcher	51.1	34.8	14.1	46	6.39	*
Sacred kingfisher	53.1	20.4	26.5	25	3.81	n.s.
Black butcherbird	52.2	26.1	21.7	23	3.20	n.s.
Area of plot (%)	28.5	23.2	48.3			

Table 5. Location (%) of birds captured in mist-nets according to zones

Zones: 1, *Rhizophora*; 2, *Bruguiera*; 3, inner *Ceriops*; 4, outer *Ceriops*; 5, *Lumnitzera/Melaleuca*. Bold values are most-frequently used zones. **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant; n.a., not applicable

Species	Zones					n	χ^2_1	P
	1	2	3	4	5			
Red-headed honeyeater	13.7	63.3	7.0	8.5	7.6	615	87.22	***
Brown honeyeater	11.3	42.4	10.2	22.6	13.6	77	96.23	***
Yellow white-eye	26.3	37.1	9.0	5.4	22.2	167	13.35	***
Large-billed gerygone	49.1	34.5	12.7	0.9	2.7	110	16.89	***
Mangrove robin	23.5	45.1	31.4	0	0	51	8.50	**
Grey whistler	33.3	38.1	19.0	4.8	4.8	42	0.11	n.s.
Shining flycatcher	50.0	22.7	18.2	9.1	0.0	22	3.32	n.s.
Sacred kingfisher	30.0	15.0	30.0	0	25.0	20	0.05	n.s.
Mangrove gerygone	13.3	33.3	46.7	6.7	0	15	n.a.	n.a.
Dusky honeyeater	10.0	60.0	0	0	30.0	10	n.a.	n.a.
Broad-billed flycatcher	33.3	33.3	0	0	33.3	9	n.a.	n.a.
Mangrove fantail	85.7	0	14.3	0	0	7	n.a.	n.a.
Northern fantail	16.7	33.3	50.0	0	0	6	n.a.	n.a.
Little kingfisher	80.0	0	0	0	20.0	5	n.a.	n.a.
Net-hours (%)	29.7	39.9	15.0	3.7	11.6	1395		

d.f. = 3, $P > 0.05$). The *Rhizophora* zone was favoured over this period, with moderate use of *L. racemosa* (in the *Melaleuca* zone) in December and January (Fig. 6). During the late wet (March–April), the landward edge was most important, because of the attraction of flowering *Melaleuca* spp. The *Bruguiera* zone was favoured for most of the dry season owing to the long flowering season of *B. exaristata*, but in October and November the *Ceriops* zone became important owing to flowering of *C. australis*.

The brown honeyeater was mist-netted in all five zones, but disproportionately in the outer *Ceriops* (Table 5) mainly because of large numbers exploiting *C. australis* in October–November. Within the plot, it was seen most in the *Bruguiera* zone (Table 4), but over the entire site, this preference was manifested only in the dry season (Table 6), when *B. exaristata* flowered. During the wet season this species, like the red-headed honeyeater, increased use of the *Lumnitzera* zone (Table 6). Within the plot, yellow white-eyes were encountered most often in the *Rhizophora* zone (Table 4), but over the entire site there was significant seasonal variation in zones used (Table 6). This species was mist-netted more often than expected in the *Lumnitzera* zone (Table 5), mostly in the wet season (Table 6), when *L. racemosa* and adjacent *Melaleuca* spp. flowered.

The large-billed gerygone was encountered most in the *Rhizophora* zone in both seasons (Tables 4, 6), and was disproportionately mist-netted in this zone (Table 5). Mangrove robins were encountered more than expected in the *Bruguiera* zone (Table 4), yet were mist-netted disproportionately in the inner *Ceriops* zone (Table 5). In sightings, both the grey whistler and the shining flycatcher showed significant preferences for the *Rhizophora* zone (Table 4), although neither showed significant zonation according to locations of mist-netted birds (Table 5). Mangrove gerygones favoured the *Ceriops* zone within the plot, but too few were caught to test for differences in capture locations. The sacred kingfisher and black butcherbird did not show any significant zonation (Tables 4, 5).

The green-backed gerygone and mangrove gerygone differed significantly in their locations ($\chi^2 = 44.61$, d.f. = 1, $P < 0.001$), the former showing a distinct preference for the landward edge of the mangal, including the *Lumnitzera* zone (Fig. 7a). The mangrove fantail was more strongly tied to the *Rhizophora* zone than was the northern fantail ($\chi^2 = 7.23$, $P < 0.01$) (Fig. 7b).

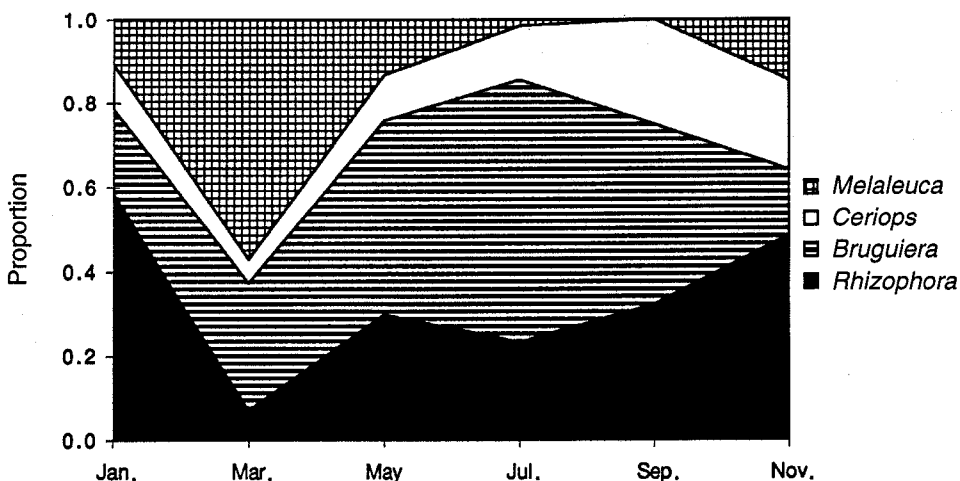


Fig. 6. Seasonal variation in use of zones by red-headed honeyeaters. *n*: January–February, 75; March–April, 91; May–June, 134; July–August, 128; September–October, 99; November–December, 103. Of 15 chi-square pairwise comparisons of the six periods, 13 were significantly different at the $P < 0.001$ level, one at $P < 0.01$, and the remaining one was non-significant (see text). The *Melaleuca* zone includes *Lumnitzera racemosa*.

Table 6. Seasonal variation in use of mangal zones (%) from observational data over the entire site. Zones: 1, *Rhizophora*; 2, *Bruguiera*; 3, inner *Ceriops*; 4, outer *Ceriops*; 5, *Lumnitzera/Melaleuca*. Bold values indicate zones in which significant seasonal increase in use occurred. ***, $P < 0.001$; n.s., not significant

Season	1	2	Zones			n	χ^2_1	d.f.	P
			3	4	5				
Yellow white-eye									
Dry	38.5	26.4	28.3	3.7	3.1	161	17.86	3 ^A	***
Wet	44.4	17.1	19.2	4.2	15.0	213			
Total						374			
Large-billed gerygone									
Dry	58.3	22.8	16.5	0.8	1.6	127	4.02	2 ^B	n.s.
Wet	53.3	33.1	11.5	2.1	0	144			
Total						271			
Brown honeyeater									
Dry	19.0	36.3	22.5	2.9	19.3	171	34.92	3 ^A	***
Wet	19.4	18.5	7.4	3.7	50.9	108			
Total						279			

^AZones 4 and 5 combined for chi-square analysis. ^BZones 4 and 5 ignored for analysis.

Foraging Ecology

Cluster analysis of foraging behaviour of 13 of the most regularly encountered species at the Palmerston site (Fig. 8) suggests a fairly simple community of one large foliage-foraging guild and three small ones, foraging mainly (1) on the ground (two species of robin-flycatchers); (2) in the air (two species of fantails); or (3) on flowers (two species of honeyeaters). The red-headed honeyeater and the brown honeyeater showed the greatest similarity in overall foraging behaviour. The two ground-foragers were the heaviest of the 13 species (both >18 g). The foliage-foraging guild divided into two groups, the smaller one (lower cluster in Fig. 8) comprising the two *Myiagra* flycatchers and the large-billed gerygone, species that tended to use *R. stylosa* and snatching techniques (unlike the species in the other group), and levels higher than did those in the other, larger group. Both groups contained small, fine-billed gerygones, and larger, more robust-billed whistler/flycatchers.

The tiny mangrove gerygone was the most specialised of the species examined, especially in its selection of plant species (Table 7). This species used *A. marina* significantly more than did the similar-sized green-backed gerygone ($\chi^2 = 52.11$, d.f. = 1, $P < 0.001$), while the latter foraged more often on *L. racemosa* and *C. australis* ($\chi^2 = 25.51$ and 6.34, d.f. = 1, $P < 0.001$ and 0.05, respectively) (Fig. 9b). These differences reflected differential use of zones by these two species (Fig. 7a), as *A. marina* was most abundant around the saltflats within the *Ceriops* zone. The slightly larger-bodied (Table 3) large-billed gerygone snatched prey significantly more than did the mangrove gerygone ($\chi^2 = 4.88$, d.f. = 1, $P < 0.05$) (Table 8) and foraged more in *R. stylosa* than did either the mangrove or green-backed gerygones ($\chi^2 = 57.34$ and 38.68, respectively, d.f. = 1, both $P < 0.001$) (Fig. 9b).

The yellow white-eye was a generalised forager (Table 7), actively gleaning arthropods from leaves and twigs (Tables 8, 9), and probing flowers of most mangrove species (viz. *R. stylosa*, *B. exaristata*, *C. australis*, *L. racemosa*, *Av. marina*, *Ae. corniculatus*), as well as *M. cajuputi*, presumably for nectar. It was also observed eating seeds and pulp from wild passionfruit, *Passiflora foetida*, growing on the edge of mangals (Noske, personal observation). The largest of the foliage-searchers, the grey whistler, was also a generalised forager, but foraged more often on bark than did other foliage-foragers (Table 9).

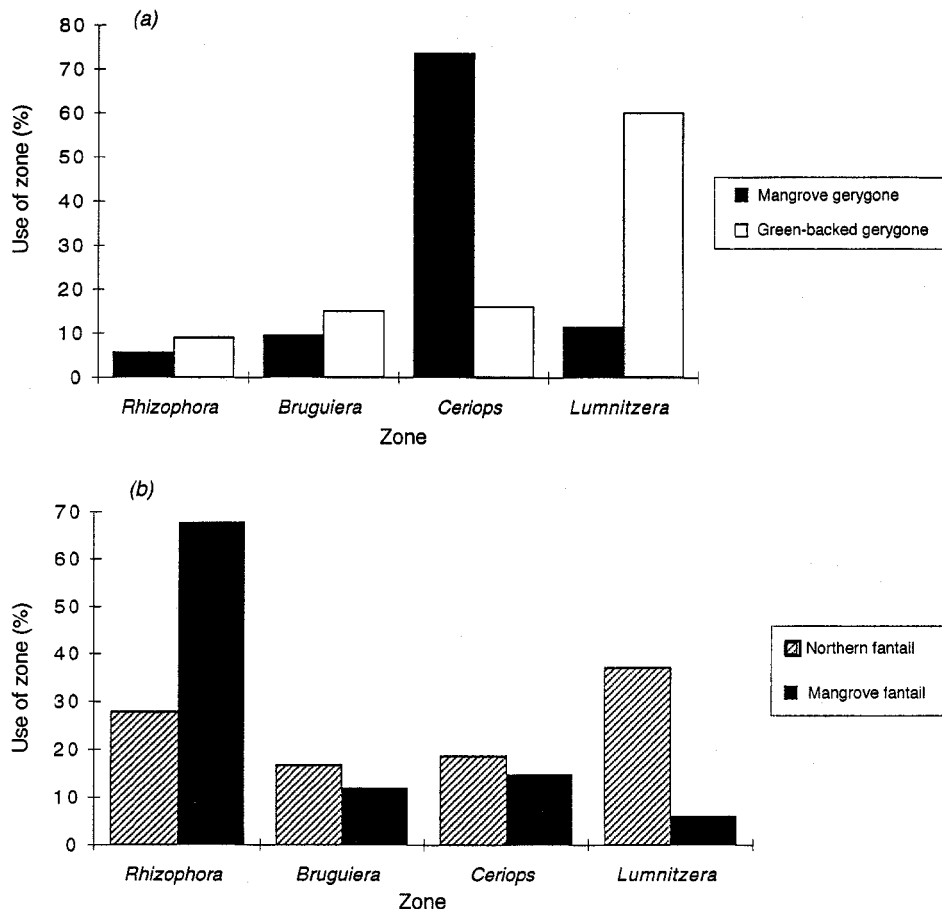


Fig. 7. Differential use of mangal zones by (a) mangrove and green-backed gerygones ($n = 79$ and 50 , respectively); and (b) northern and mangrove fantails ($n = 27$ and 17 , respectively).

The morphologically near-identical broad-billed and leaden flycatchers were among the most generalised foragers of the species examined (Table 7). The broad-billed flycatcher spent more time at lower levels (< 2 m) than did the narrower-billed leaden flycatcher ($\chi^2 = 7.80$, d.f. = 1, $P < 0.01$) (Table 10). The leaden flycatcher also appeared to hover more frequently and use *C. australis* less frequently (Table 10; Fig. 9c) than the broad-billed flycatcher, but these differences were not significant. The two aerial-hawking fantails were also partitioned vertically (Table 10), the mangrove fantail spending most of its time below 2 m, while the larger northern fantail was significantly more often at higher levels ($\chi^2 = 15.13$, d.f. = 1, $P < 0.001$). Both the mangrove robin and the shining flycatcher foraged mostly within 1 m of the ground (Table 10), and, although there were no significant differences in substrata or techniques, they differed in their general foraging strategy. The mangrove robin obtained prey principally by pouncing on the ground from a low perch, then hopping slowly over the mud for short distances, gleaning ants and probing crab burrows. The more-agile shining flycatcher moved more rapidly over mud and logs, and under the stilt-roots of *R. stylosa*, sometimes snatching insects from low foliage.

The red-headed and brown honeyeaters had very similar niche breadths (Table 7), related to their mutual requirement for available nectar sources. Over 80% of foraging observations for

Table 7. Niche breadth of mangal birds, in order of decreasing mean breadth
 Values are H/H_{\max} (see text); n , range of observations for all foraging dimensions

Species	Foraging dimension				Mean breadth	n	
	Substrata	Heights	Techniques	Tree spp.		Min.	Max.
Broad-billed flycatcher	0.582	0.801	0.596	0.619	0.650	24	36
Leaden flycatcher	0.298	0.858	0.629	0.755	0.635	13	18
Yellow white-eye	0.435	0.886	0.328	0.885	0.634	108	156
Grey whistler	0.341	0.855	0.439	0.770	0.601	21	42
Brown honeyeater	0.267	0.907	0.320	0.907	0.600	55	79
Red-headed honeyeater	0.282	0.916	0.290	0.858	0.587	315	394
Northern fantail	0.339	0.656	0.256	1 ^A	0.563	17	18
Shining flycatcher	0.511	0.168	0.534	1 ^A	0.553	13	26
Large-billed gerygone	0.082	0.944	0.549	0.630	0.551	69	101
Mangrove fantail	0.244	0.329	0.244	1 ^A	0.454	15	18
Green-backed gerygone	0	0.728	0.528	0.537	0.448	33	43
Mangrove robin	0.263	0.189	0.255	1 ^A	0.427	14	22
Mangrove gerygone	0.062	0.854	0.383	0.251	0.388	48	63

^AMaximum diversity because trees were rarely used as foraging surfaces.

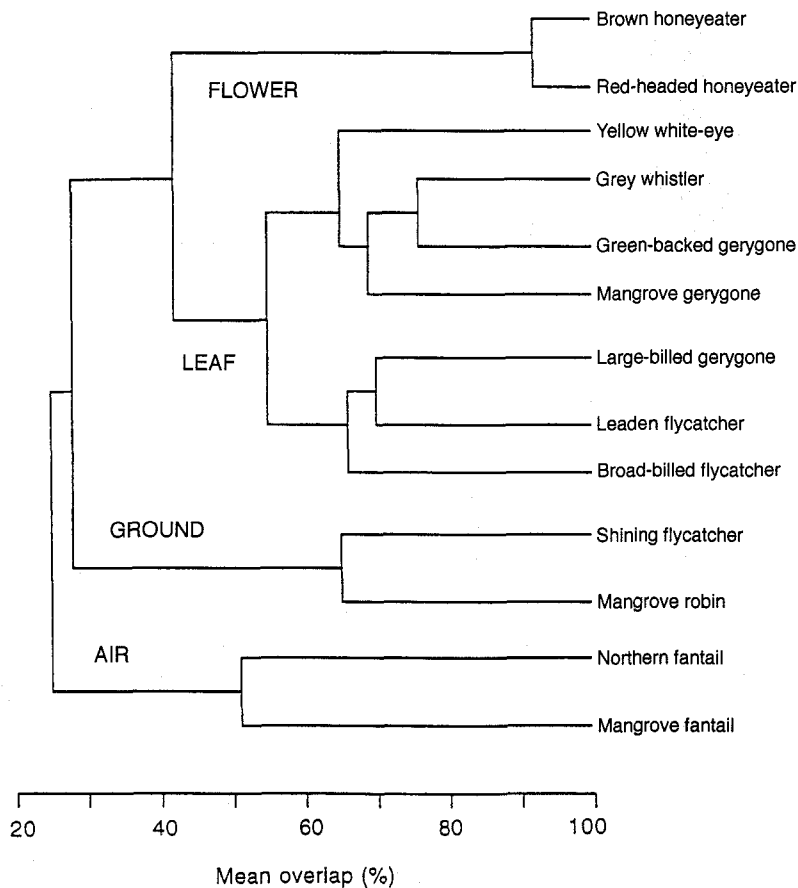


Fig. 8. Dendrogram of foraging behaviour of 13 mangal-dwelling bird species near Darwin, Northern Territory.

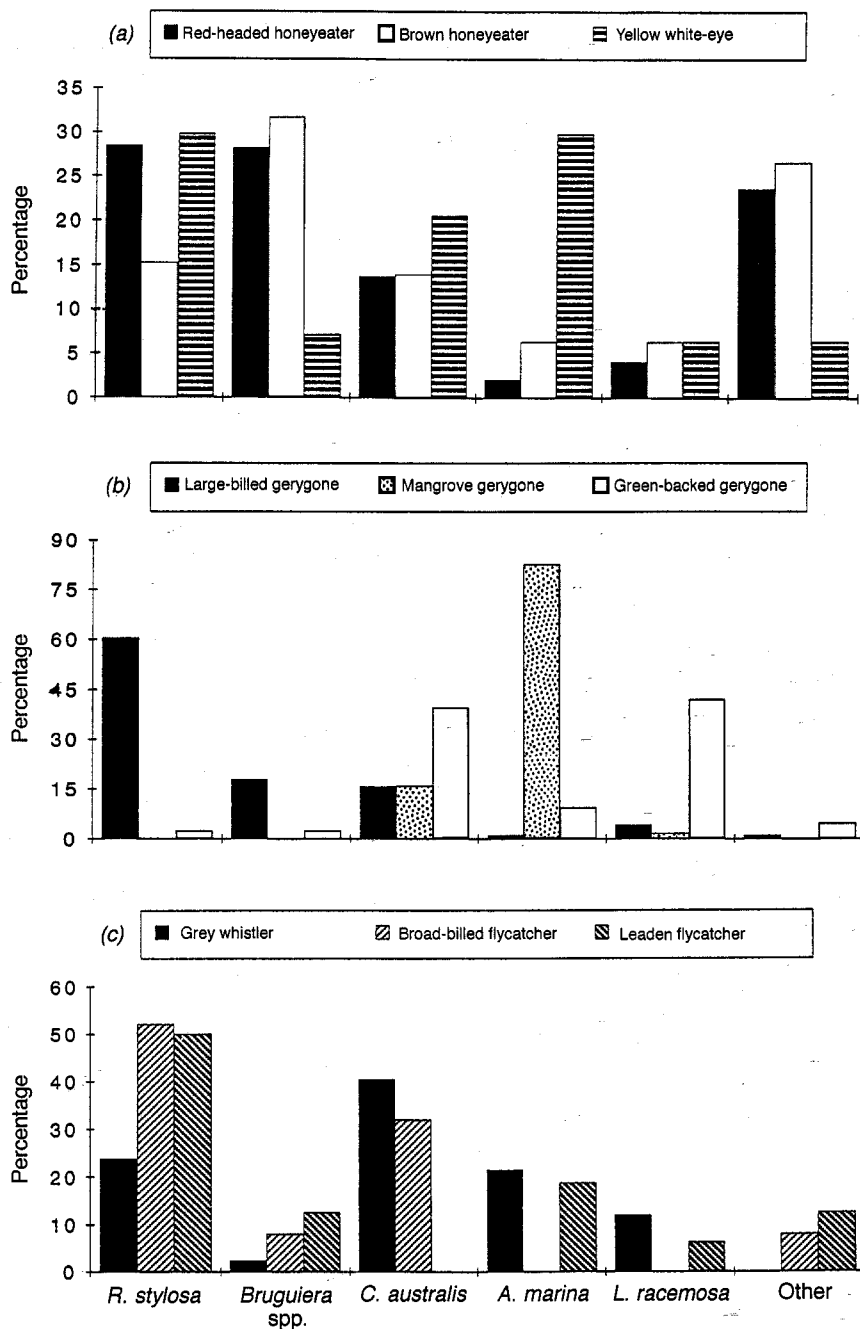


Fig. 9. Choice of foraging plant species within three guilds: (a) partial nectarivores; (b) small leaf-gleaning insectivorous warblers; and (c) medium-sized flycatching insectivores. *n*: red-headed honeyeater, 291; brown honeyeater, 78; yellow white-eye, 131; large-billed gerygone, 82; mangrove gerygone, 48; green-backed gerygone, 36; grey whistler, 23; broad-billed flycatcher, 25; leaden flycatcher, 13.

Table 8. Foraging techniques (%) of mangal-inhabiting birds

Species	Foraging technique					n
	Glean	Snatch	Hover	Hawk	Probe	
Red-headed honeyeater	14.1	0	0.3	0.8	84.9	391
Brown honeyeater	11.5	0	3.8	0	84.6	78
Yellow white-eye	77.9	0	0	0	22.1	131
Large-billed gerygone	56.1	36.6	7.3	0	0	82
Mangrove gerygone	79.2	16.7	4.2	0	0	48
Green-backed gerygone	63.9	27.8	8.3	0	0	36
Grey whistler	39.1	52.2	8.7	0	0	23
Shining flycatcher	61.5	30.8	0	7.7	0	13
Mangrove robin	85.7	0	0	0	14.3	14
Northern fantail	0	11.8	5.9	82.4	0	17
Mangrove fantail	0	13.3	0	86.7	0	15
Broad-billed flycatcher	8	68.0	8.0	16.0	0	25
Leaden flycatcher	0	38.5	46.2	15.4	0	13

Table 9. Use (%) of foraging substrata (%) by mangal-dwelling birds

Species	Foraging substratum					n
	Leaf/twig	Branch	Ground	Air	Flower	
Red-headed honeyeater	14.3	0	0	0.8	84.9	391
Brown honeyeater	15.4	0	0	0	84.6	78
Yellow white-eye	70.4	2.8	0	0	26.9	108
Large-billed gerygone	97.1	2.9	0	0	0	69
Mangrove gerygone	98.0	2.0	0	0	0	49
Green-backed gerygone	100.0	0	0	0	0	33
Grey whistler	76.2	23.8	0	0	0	21
Shining flycatcher	18.2	4.5	72.7	4.5	0	22
Mangrove robin	0	15.0	85.0	0	0	20
Northern fantail	23.5	0	0	76.5	0	17
Mangrove fantail	13.3	0	0	86.7	0	15
Broad-billed flycatcher	66.7	4.2	8.3	20.8	0	24
Leaden flycatcher	78.6	0	0	21.4	0	14

both red-headed and brown honeyeaters involved flower-probing (Tables 8, 9). In *B. exaristata*, 93% of observations of red-headed honeyeaters were of birds probing flowers, whilst in *R. stylosa* 33% of feeding actions involved leaf-gleaning (R. A. Noske, unpublished data). Red-headed honeyeaters visited *R. stylosa* more often than did brown honeyeaters ($\chi^2 = 5.30$, d.f. = 1, $P < 0.05$) (Fig. 9a), yet the two birds were often encountered together in the other major flowering plants. Both intraspecific and interspecific aggression was common at flowering trees, neither species consistently dominating the other. The foraging ecology of these species will be detailed elsewhere.

Breeding

Over 60 nests belonging to 13 species were found at the site (Table 11), including two species of doves that did not forage in the mangal to any extent. There were significantly more breeding records in the dry season than in the wet (Mann-Whitney $U = 1.5$, $P < 0.05$), but there was no seasonal difference in the number of species breeding (Mann-Whitney $U = 6$, $P > 0.05$). The red-headed honeyeater clearly bred in the mid-to-late dry season, during the flowering season of *B. exaristata*. The brown honeyeater also bred during the early and mid dry

Table 10. Use (%) of foraging heights by mangal-inhabiting birds

Species	Height (m)					n
	0-1.0	1.1-2.0	2.1-4.0	4.1-8.0	>8.0	
Red-headed honeyeater	4.4	16.8	27.3	32.4	19.0	315
Brown honeyeater	5.5	18.2	32.7	30.9	12.7	55
Yellow white-eye	6.4	14.7	28.8	39.1	10.9	156
Large-billed gerygone	10.9	15.8	20.8	36.6	15.8	101
Mangrove gerygone	14.3	39.7	25.4	19.0	1.6	63
Green-backed gerygone	2.3	34.9	37.2	25.6	0	43
Grey whistler	7.3	26.8	41.5	19.5	4.9	41
Shining flycatcher	92.3	7.7	0	0	0	26
Mangrove robin	90.9	9.1	0	0	0	22
Northern fantail	0	33.3	22.2	27.8	16.7	18
Mangrove fantail	77.8	22.2	0	0	0	18
Broad-billed flycatcher	41.7	25.0	22.2	11.1	0	36
Leaden flycatcher	0	22.2	22.2	27.8	27.8	18

Table 11. Breeding records of mangal-inhabiting birds in Darwin Harbour, Northern Territory

Values are estimated egg dates derived from nests or interpolated from building or fledgling records

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	n
Red-headed honeyeater	-	-	-	-	-	6	3	2	4	2	-	-	17
Large-billed gerygone	1	1	3	-	1	-	1	3	3	1	-	-	14
Yellow white-eye	2	1	-	1	1	2	1	-	2	2	-	1	13
Green-backed gerygone	1	2	-	-	4	3	1	1	-	-	-	-	12
Mangrove gerygone	-	-	2	5	-	-	-	1	-	2	1	-	11
Brown honeyeater	-	-	-	1	1	3	-	4	-	-	-	-	9
Mangrove robin ^A	2	1	1	-	2	-	-	-	1	-	-	1	8
Chestnut rail ^B	1	-	-	-	-	-	-	-	-	1	-	4	6
Peaceful dove	-	-	1	1	-	1	1	-	1	-	-	-	5
Helmeted friarbird	-	2	-	-	-	1	-	-	-	1	-	-	4
Grey whistler ^{AC}	-	-	-	-	-	1	1	2	-	-	-	-	4
Silver-crowned friarbird	-	-	-	-	-	-	-	-	2	1	-	-	3
Black butcherbird ^A	2	-	-	-	-	-	-	-	-	-	1	-	3
Shining flycatcher	1	1	-	-	-	-	-	-	1	-	-	-	3
Bar-shouldered dove	-	-	-	-	-	1	-	-	-	-	-	-	1
Broad-billed flycatcher ^{AC}	-	-	-	-	1	-	-	-	-	-	-	-	1
Northern fantail	-	-	-	1	-	-	-	-	-	-	-	-	1
Little bronze-cuckoo ^A	-	-	-	-	-	-	-	-	-	1	-	-	1
No of breeding records	10	8	7	8	10	18	9	13	14	10	2	6	115
No. of species breeding	7	6	4	4	6	8	7	6	7	7	2	3	17

^AEgg dates based on fledgling or building dates (otherwise based on nests).^BD. Franklin and T. Barnes, personal communication and observations.^CData from Rix (1970).

season, while most nests of friarbirds were in the late dry (although data are few). The generalised yellow white-eye showed no obvious seasonality in breeding. Large-billed gerygones also bred over the year, with a distinct peak in the late dry season, in contrast to the mangrove and green-backed gerygones, which bred mostly in the late wet and early dry seasons, respectively. Although nests of the mangrove robin were never found, most young birds were found in the wet season.

Table 12. Distribution of mangal-dependent bird taxa in Australia, and habitat of closest relatives
 Partly adapted from Ford (1982) and Schodde *et al.* (1982). WA, Western Australia; NT, Northern Territory; NE Qld, North-east Queensland; NSW, New South Wales. Taxonomy follows Christidis and Boles (1994). Status: E, species (e, subspecies) endemic to mangals in at least part of range. Mangal-dependence: A, virtually confined to mangal; B, found in a variety of closed habitats, including mangal; A/B, mangal is the principal habitat. Habitat of closest relative: R, rainforest; S, sclerophyll forest; W, woodland; if closest relative not identified, then main habitat of species (if not mangal)

Species	Status	Mangal-dependence over range				Origin or closest relative	Habitat of closest relative
		WA	NT	NE Qld	NSW		
Great-billed heron	E	A	A/B	A	—	Sundas	—
Striated heron	e	A	A/B	A	A	Sundas	—
Chestnut rail	E	A	A	—	—	<i>E. plumbeiventris?</i>	R
Collared kingfisher	e	A	A	A	A	Sundas	—
Mangrove robin	E	A	A	A	—	<i>E. australis?</i>	S,R
Kimberley flycatcher	e	A	—	—	—	<i>E. flavigaster</i>	S,W
White-breasted whistler	E	A	A	—	—	<i>P. rufiventris</i>	W,S
Mangrove golden whistler	e	B	A/B	A	—	<i>P. pectoralis</i>	R,S
Little shrike-thrush	—	B	B	A/B	B	—	R
Broad-billed flycatcher	e	B	A/B	—	—	<i>M. rubecula?</i>	S,W
Shining flycatcher	—	A/B	B	A/B	—	—	R
Mangrove fantail	E	B	A	—	—	<i>R. fuliginosa</i>	W,S,R
Rufous fantail	—	A/B	B	B	B	Sundas	?
Dusky gerygone	E	A	—	—	—	<i>G. magnirostris</i>	R
Large-billed gerygone	—	A	B	B	—	—	R
Mangrove gerygone	E	B	A	A	A	<i>G. fusca</i>	W
Yellow white-eye	E	A	A	—	—	Sundas	—
Red-headed honeyeater	E	A	A	—	—	<i>M. adolphinae</i>	R
Mangrove honeyeater	E ^A	—	—	A	A	<i>L. virescens</i>	W
Varied honeyeater	E ^A	—	—	B	—	<i>L. virescens</i>	W
Helmeted friarbird	—	—	B	B	—	Sundas	—
Black butcherbird	—	A	A	B	—	—	R

^AFormerly conspecific.

Discussion

Avian Community

The avifauna of the mangals was surprisingly rich given its depauperate flora. Over 50 species of birds (excluding waders and aerial species) were encountered at the site, which supported only 10 species of plants. All 11 mangal-dependent species of the region (Table 12) were recorded during the study period, although only half of these were encountered regularly. Of the less-frequently recorded mangal-dependent species, five (the great-billed heron, the striated heron, the chestnut rail, the collared kingfisher and the mangrove fantail) are apparently commonest in, or restricted to, the seaward edge or margins of tidal rivers, while two others (the white-breasted whistler and the mangrove golden whistler) are generally scarce in Darwin Harbour (see below). Although the majority of birds was breeding residents, several species (e.g. the cicadabird and the leaden flycatcher) appear to be seasonal visitors to mangals from other habitats, while others may move within mangals.

In terms of species, the mangal avifauna is dominated by insectivores mostly less than 10 g in mass (Table 3), which may be related to the year-round availability of aerial insects such as mosquitos, as well as foliage-dwelling arthropods (R. A. Noske, P. Donaldson and M. Bezuijen,

unpublished data). In contrast to monsoon rainforests, mangals in the Darwin region lack frugivores, doubtless owing to the lack of edible fruits among mangroves (Tomlinson 1986), except where the mangrove mistletoes *Amyema* spp. or *Diospyros maritima* occur (personal observation). Apart from the ground-feeding doves that nest and roost in mangals, granivores are also conspicuously absent. Raptors are rare, although I have recorded grey goshawks hunting in mangal several times (see also Johnstone 1990), and mist-netted them on the study plot. Black butcherbirds are known predators of fish (especially mudskippers) and crabs, as well as insects (Johnstone 1990), but may also take bird nestlings. Specialised trunk- or bark-foragers are virtually absent from Australian mangals, in stark contrast to mangals of South-east Asia, where woodpeckers are a conspicuous and important element of the avifauna (e.g. Nisbet 1968; Noske 1995). This is despite the fact that the mangrove trees upon which woodpeckers forage, and doubtless many of their prey items (e.g. ants), are the same species as those in Australia.

The nectarivore guild is depauperate compared with that in surrounding savannas where up to seven species of honeyeaters and two species of lorikeets often co-occur (personal observation; D. Franklin, unpublished data). This is probably due to the lack of plant species with large nectariferous flowers in mangals, the major exceptions being large-flowered *Bruguiera* and *Sonneratia* species (Tomlinson *et al.* 1979; Noske 1993). The very small size of the red-headed honeyeater (7.5 g), apparently the smallest honeyeater in Australia, may well be related to the tiny size of, and minute amounts of nectar in, flowers of most mangroves (e.g. *C. australis*, *R. stylosa*, *L. racemosa*, *A. corniculatus*) (R. A. Noske and T. Schultz, unpublished data). However, lorikeets and several species of honeyeaters typical of savanna visit the flowers of the river-fringing *S. alba* (personal observation). More nectarivores are probably supported where there are *Bruguiera* species (e.g. *B. gymnorhiza*) with flowers larger than those of *B. exaristata*. In Peninsular Malaysia, up to four species of sunbirds were observed feeding concurrently on a few individuals of the large-flowered *Bruguiera sexangula* (Noske 1993, 1995). In eastern Australia, the red-headed honeyeater is replaced by the larger varied honeyeater, *Lichenostomus versicolor*, or mangrove honeyeater, *L. fasciogularis* (Table 12), but both of these species appear to be more insectivorous than the former (Hall 1974). Primack and Tomlinson (1978) reported honeyeaters feeding on a sugary secretion from terminal stipules of *R. stylosa* in northern Queensland; however, this was not observed in the present study.

Densities and Seasonality

Contrary to some of the literature (e.g. MacNae 1968; Hutchings and Recher 1982), the density of birds in mangals is moderately high (see also Woinarski *et al.* 1988). The estimates of total bird density on the Palmerston plot (24 ha⁻¹) are probably reasonably accurate. Although the densities of some species (viz. the yellow white-eye, the mangrove robin) were marginally overestimated according to mapping of marked individuals, rarer species (e.g. the chestnut rail, the broad-billed flycatcher) were probably under-estimated. These estimates are twice those reported by Woinarski *et al.* (1988) for subcoastal mangal on the Howard Peninsula (only about 20 km north-east of the Palmerston site), where mean density of non-aerial birds in April–May was 12–13 ha⁻¹ (v. 20.7 ha⁻¹ for Palmerston for March–April). These values are not entirely comparable, however, as Woinarski *et al.* (1988) used quadrats for censusing rather than transects. Arnold (1983) found that stationary observers at the centre of 1-ha plots recorded significantly lower numbers of most species than did observers walking transects. In addition, neither *B. exaristata* nor *M. cajuputi* occurred in the mangal plots of Woinarski *et al.* (1988), and flowering of these species was the major factor contributing to the rise in density of nectarivores (which accounted for nearly a third of all birds) over this period at Palmerston. With conservative fixed-width transect censuses, total bird density at three mangal sites with similar mangrove diversity in Peninsular Malaysia ranged from 15 to 26 ha⁻¹ (Noske 1995).

Seasonal variation in the abundance of red-headed honeyeaters on the plot can be readily attributed to local movements, related to available nectar sources, and to its breeding biology. Minimum densities on the plot occurred in March–April, when flowering within mangals had

virtually ceased, while on the landward edge *Melaleuca* spp. flowered profusely. The peak abundances of the species during the mid dry and early wet seasons coincide with the production of young and the flowering season of *C. australis*, which provides an extensively distributed nectar source for dispersing young. Low densities in January–February suggest high juvenile mortality and/or movement out of the mangal to savanna–woodland nectar sources (e.g. *Amyema* spp., *Grevillea decurrens*, *Melaleuca viridiflora*). The seasonal pattern of abundance of brown honeyeaters is similar, except that this species relies less on *R. stylosa*, so proportionately more probably move out of the mangal during the wet season. That the pattern of abundance of yellow white-eyes is dissimilar to that of the two honeyeater species suggests that nectar sources are not as limiting for this species.

Most records of the little shrike-thrush, the mangrove fantail, the lemon-bellied flycatcher and the mangrove golden whistler at the site were in the late wet season, when landward areas were often shallowly inundated with freshwater runoff from the hinterland. Such conditions may make landward zones temporarily favourable to specialists of the river or seaward edge, enabling those species to broaden or shift their home ranges.

Without documenting evidence, Schodde *et al.* (1982) claimed that many mangal-dependent species breed in the wet season, with a hiatus during late November–January, ‘when there are spring tides’. Data presented here suggest, on the contrary, that breeding in mangals of Darwin Harbour peaks in the dry season. Although nesting is least common during the early wet, maximum spring tides (>7 m) in this region are most frequent in February–March and October–November, when one such tide occurs once every two days, on average (Darwin Tide Tables, 1988–90). Yet such tides inundate higher ground for short periods only, and are matched by equally impressive low tides (<1 m). Of more significance to the ecology of mangal-dwelling animals, freshwater runoff in the region is greatest in February–March (Chappell and Ward 1985). This, combined with high spring tides, may flood large areas, reducing the area available for foraging by ground-dwelling species in the latter half of the wet season. Perhaps this is why the terrestrial, crab-eating chestnut rail nests in the first half of the wet season [October–January; records from the Kimberley are from Johnstone (1990); local records from T. Barnes and D. Franklin (personal communication) and personal observation]. However, both the shining flycatcher and the mangrove robin, which are also ground-foragers, breed in the late wet season both locally (personal observation) and in the Kimberley (Johnstone 1990).

The lack of breeding records in the early wet season may be partly due to uneven sampling. Nests of neither the grey whistler nor the mangrove fantail were found, both of which reputedly breed in the wet season (Storr 1977; Johnstone 1990). Breeding seasons of mangal-inhabiting birds may also vary markedly between regions with different tidal regimes and rainfall (e.g. Kimberley and Pilbara), and within regions varying in topography and hydrology.

Foraging Ecology and Zonation

Schodde *et al.* (1982) compared the niches of congeners in mangals based on unquantified observations. They noted that the riverine azure and little kingfishers differ in size, and thus probably take prey of differing size. The paucity of observations and captures of the azure kingfisher in this study suggests these species also show zonation within mangals, the smaller (13.3 g) little kingfisher occupying narrow tidal creeklets in the mangal interior, and the azure kingfisher (28 g) apparently preferring larger tidal rivers (personal observation). The collared kingfisher (69 g) and the smaller sacred kingfisher (40 g) show more-obvious zonation, the former being largely restricted to the *Sonneratia* zone fringing the harbour and major rivers, and the latter occurring in the *Rhizophora* and more landward zones (Schodde *et al.* 1982; personal observation).

Among the three fantails occurring in mangals, Schodde *et al.* (1982) considered the northern fantail to occupy mainly the landward edge, while in the seaward mangal the rufous fantail foraged lower than did the smaller mangrove fantail. In the present study, northern fantails occurred in all zones, including the *Rhizophora* zone. Indeed, the northern and

mangrove fantails appeared to be vertically segregated, the former hawking in wide sweeps in higher situations where the canopy is patchy (in tall, well-spaced *R. stylosa* with no understorey, and river edges), while the latter makes short sallies among the dense, low vegetation fringing tidal creeks. In Western Australia, Johnstone (1990) recorded the widely distributed mangrove fantail at all levels in mangals, as well as in paperbark thickets up to 3 km from mangal. This 'relaxed' niche may relate to the absence of the northern fantail over much of Western Australia. Rufous fantails were infrequent visitors to the Palmerston mangal plot, appearing to prefer *R. stylosa* closer to large tidal rivers (Johnstone 1990; personal observation). In both Northern Territory and Western Australia, this species is commoner in vine forests and wetland thickets (Crawford 1972; Storr 1977; Johnstone 1990).

Schodde *et al.* (1982) suggested that the leaden flycatcher keeps mainly to the landward fringe of mangals, while the other two *Myiagra* flycatchers are separated by foraging heights. In this study, all three species were recorded in all zones, including the landward fringe, but the shining and broad-billed flycatchers showed a significant affinity for the *Rhizophora* zone. Although both of these species preferred lower levels, the former was largely a ground-forager and the latter a foliage-snatcher. The shining flycatcher is abundant in monsoon vine and riparian forests, both in the Northern Territory and Western Australia (Crawford 1972; Storr 1977; Johnstone 1990). The broad-billed flycatcher is primarily a mangal species, yet also occurs patchily in monsoon thickets and *Melaleuca* swamps (Crawford 1972; Johnstone 1990). The leaden flycatcher, by contrast, is common in open forest and woodland, and in mangals in the Darwin region may avoid potential competition with the morphologically near-identical broad-billed flycatcher by greater use of the canopy (and hovering techniques), and by moving to woodland during the wet season (R. A. Noske and N. McCrie, unpublished data). A fourth flycatcher species, the lemon-bellied flycatcher, was uncommon on the mangal plot, but is common in the *Sonneratia* zone close to the sea or river edge in the Darwin region (personal observation), as well as in riparian and open forests (Crawford 1972). It forages mainly by sallying for aerial insects from exposed perches, but also gleans insects from branches (Johnstone 1990; personal observation).

The three gerygone species in this study, being very similar in foraging techniques and substrata, were segregated by choice of plant species, which probably accounted for differences in height selection and zonation. As noted by Schodde *et al.* (1982), the mangal-endemic mangrove gerygone prefers low thickets of *Avicennia*, particularly those surrounding saltflats near the landward fringe. This species is among the most specialised of Australian birds, spending over 80% of its time in *A. marina*, even in zones where only a few individuals of this mangrove are present. This association with the most wide-ranging mangrove in Australia may partly explain why the mangrove gerygone is the most widespread Australian mangal-endemic bird species. This association breaks down, however, in the southern Kimberley, where it is commoner in *Melaleuca* woodland and thickets backing mangal (Ford 1982; Johnstone 1990), perhaps owing to competition with the sympatric mangal-endemic dusky gerygone, *Gerygone tenebrosa*.

Both the large-billed and the green-backed gerygones occur in vine and riparian forests, as well as mangals, in the Northern Territory. Although Schodde *et al.* (1982) contend that both of these species prefer tall, dense forests of *Rhizophora-Bruguiera*, and that the green-backed gerygone is only a temporary visitor to mangals abutting rainforest, in this study the latter species clearly favoured the landward *Lumnitzera* zone and fringing *Melaleuca*, nesting usually in *L. racemosa* (unpublished data). This site and many others of the species are at least 10 km from the nearest vine forest or thicket. The green-backed gerygone foraged equally frequently in *C. australis* and *L. racemosa*, which have fairly clustered, obovate, isobilateral leaves of similar size. By contrast, the foliage of *A. marina*, favoured by the mangrove gerygone, has widely spaced, lanceolate-to-elliptic, strongly dorsiventral leaves. Recher (1989) found strong differential selection of two co-dominant species of eucalypts by five co-existing acanthizid warblers in open forest near Sydney, New South Wales. This differentiation was related to

disparate densities of invertebrate prey, as well as to different foliage characteristics of the two trees, one having narrower and more tightly clustered leaves than the other (Recher and Majer 1994). The foliage of *A. marina* supported more stationary invertebrates than did four other dominant mangroves, on a weight-to-weight basis (R. A. Noske, P. Donaldson and M. Bezuijen, unpublished data).

Biogeography of Mangal-dependent Birds

The dependence of Australian mangal-specialised birds varies geographically (Ford 1982; Schodde *et al.* 1982) (Table 12). In Western Australia, 16 species of birds are virtually confined to mangals (Johnstone 1990), but many of these species occur in other habitats, notably monsoon vine (or rain) forests and paperbark forests in the Northern Territory and Queensland. Johnstone (1990) contended that most or all of the mangal-dependent species would not persist in Western Australia without mangal, because of its large area (c. 2000 km²) compared with that of vine forest (c. 50 km²). On islands without mangals off north-eastern Arnhem Land, by contrast, mangrove golden whistlers and yellow white-eyes are common in heaths and open woodlands, and chestnut rails and striated herons are very common on boulder-strewn reefs (J. C. Z. Woinarski, personal communication). Mangrove robins occur in vine forests on small islands in the Gulf of Carpentaria (M. Fleming, personal communication). Such habitat flexibility in one region and specialisation in another makes it difficult to describe any particular species as 'mangal-dependent', and the term 'mangal-specialised' is used here to denote specialisation in at least part of the range of a species.

The mangal-specialised white-breasted whistler and mangal-associated mangrove golden whistler were virtually absent from the study site, and are scarce in Darwin Harbour generally, but occur patchily in mangals on the adjacent coastline (H. Thompson, A. Hertog, personal communication; personal observation). The break in the range of the large white-breasted whistler (37 g, Johnstone 1990) in Western Australia from Cambridge Gulf to St George Basin has been attributed to competition from the morphologically similar (37 g, Table 3) and phylogenetically related little shrike-thrush (Ford 1982). Further south, where the white-breasted whistler is common, the shrike-thrush is absent. Although this whistler occurs in a wide variety of mangals in Western Australia, it prefers those dominated by tall forests of *A. marina*, although it also occurs in extensive stands of pioneering *A. marina* (Johnstone 1990). The absence of extensive stands of *A. marina* in Darwin Harbour may thus contribute to its scarcity here.

In Western Australia, the mangrove golden whistler favours *Rhizophora* forest, but often wanders up to 10 km from mangals into neighbouring vine forest and *Melaleuca* thickets (Johnstone 1990). Similarly, in the Northern Territory the species occurs in vine forests and bamboo thickets along rivers well inland, and even in heaths on small islands off the coast of Northern Territory (A. Hertog, J. C. Z. Woinarski, personal communication; personal observation). It is tempting to suggest that the scarcity of the mangrove golden whistler in Darwin Harbour mangals is related to the abundance of the similar sized grey whistler [19.1 v. 16.3 g, respectively: data from Johnstone (1990) and Table 3]. Conversely, the ubiquity of mangrove golden whistlers in Western Australia may relate to the absence of the grey whistler from that State (Blakers *et al.* 1984).

In this study, the mangrove robin was found in the *Bruguiera* and inner *Ceriops* zones more than in the *Rhizophora* zone, and observations at many other sites around Darwin Harbour confirm that this species commonly occurs in both the inner and outer *Ceriops* zones. Johnstone (1990) found this species only in mangals with extensive *Rhizophora* forest, which he attributed to (1) the provision of numerous low-level perches on prop roots of *Rhizophora*, and (2) the apparently greater density of insects and other invertebrates in *Rhizophora* than in other mangroves. Among five species of mangroves at the Palmerston plot, however, stationary insects were least abundant on *Rhizophora* foliage (R. A. Noske, P. Donaldson and M. Bezuijen, unpublished data). I suggest that mangrove robins generally favour mangals having a well-developed *Rhizophora* zone, because such mangals are typical of large estuaries

with sufficient silt to form many zones. Interestingly the species is absent from the south-west Kimberley, where there are no large watercourses, few stands of *R. stylosa*, and the substratum typically contains more sand than mud. These characteristics contrast with those of mangals in the north-west Kimberley and Pilbara regions, where the robin does occur. Moreover, conditions such as those of the south-west Kimberley may not favour small crabs, a known food source of mangrove robins (Hall 1974; Johnstone 1990).

Johnstone (1990) noted that Eighty Mile Beach, which is devoid of mangals, marked the southern limit of the red-headed honeyeater in Western Australia. He suggested that this physical break in the distribution of mangals had prevented this species (and three others) from colonising mangals further south. This is an unlikely explanation, however, given the high vagility of this species (Ford 1982) relative to other species that have successfully straddled the gap. It seems more likely that its southern limits relate to lack of reliable nectar sources both within and adjacent to mangals. Although *B. exaristata* occurs sparingly in mangals south of the Eighty Mile Beach gap (Pilbara region), these mangals are not fringed with *Melaleuca acacioides* as are those to the north of the gap (Johnstone 1990). Moreover, the flowering seasons of other nectar-bearing mangroves in the Pilbara may be considerably shorter than those in the Kimberley, given its drier climate (300 mm at Port Hedland v. 540 mm at Broome), further reducing its potential for successful colonisation by nectarivores.

Evolution of Mangal-specialised Birds

In terms of their floristics, the richest mangals in Australia are those of north-eastern Queensland (Lear and Turner 1977; Bunt *et al.* 1982; Wells 1982, 1983), yet fewer mangal-specialist bird species occur there than in north-western Australia (Table 12). Ford (1982) and Schodde *et al.* (1982) argued that many Australian mangal-specialists originated in Australian rainforests, with subspecies or closely related species still in rainforests today. As the continent dried out during Pleistocene glacial periods, rainforests contracted and fragmented into patches that were too small to support viable populations of these species. Many of these isolated taxa then adapted to mangals, possibly because it represented the only closed habitat available, in stark contrast to the savanna-woodland surrounding them. The widespread contraction of monsoon rainforests in north-western Australia during the Pleistocene glacials accords with the lack of distinctive rainforest forms among its present avifauna.

This scenario provides a convenient explanation for the differences between north-western and north-eastern Australia in number of mangal-specialists. However, it ignores the fact that several mangal-specialists may have closer affinities with open forest or even inland forms, viz. the mangrove fantail, the broad-billed flycatcher, the Kimberley flycatcher, *Microeca (flavigaster) tormenti*, the mangrove gerygone and the mangrove honeyeater (Table 12). This suggests that mangals may have offered an attractive refuge during the arid conditions of the Pleistocene even for woodland-adapted forms, perhaps because of greater or more stable food resources. In addition, mangals were far more extensive up to 6000 years ago (Woodroffe *et al.* 1985b, 1992; Clark and Guppy 1988). Schodde *et al.* (1982) suggested that the maximum extent of mangals may have been in the Carpentarian Basin before (or during) its inundation, as the sea level rose between 15000 and 8000 years ago. Perhaps as the sea flooded mangals and coastal vine thickets on islands in this region (and off Arnhem Land), mangal-specialised species were forced to adapt to other habitats, facilitated by lack of competitors. This may explain the apparent enigma of some mangal-'specialists' being so habitat- and zone-specific in the Darwin region and further west, yet among the most ecologically flexible on islands to the east.

Inter-continental Comparisons

Although mangals in other parts of the world are used by numbers of bird species similar to those using mangals in northern Australia, no other region has so many specialists (Table 12). Saenger *et al.* (1977) listed 186 bird species for Queensland mangals, and 104 for north-western Australia (including the Northern Territory), although this includes many waders and aerial

species not considered in the present study. Most of the 125 bird species recorded in or above mangals in Guinea-Bissau in West Africa (Altenburg and Spanje 1989) were commoner in adjoining forests and ricefields, and many used mangal only for roosting purposes. Only one species, an insectivorous sunbird, is confined to mangal in Africa (Cawkell 1964; Field 1968; Altenburg and Spanje 1989). In the neotropics, Haverschmidt (1965) and Ffrench (1966) listed 84 and 94 species living and/or nesting in mangals in Surinam and Trinidad, respectively. In both countries only one species, a crab-eating hawk, was considered endemic to mangal. Both Africa and South America have smaller areas of mangals than those of Asia and Australia, with few species of mangroves, which could partly explain the lack of mangal-specialists.

In Peninsular Malaysia, where mangrove diversity is comparable to that in north-eastern Australia, Nisbet (1968) listed 125 bird species in mangals, although Noske (1995) recorded only 47 species (excluding waders and aerial species) from four sites in the state of Selangor. Only seven species are restricted to mangals in Peninsular Malaysia, and three of these extend into inland forests elsewhere in South-east Asia (Nisbet 1968; Medway and Wells 1976; Wells 1985). One explanation for the lack of mangal-endemic birds in South-east Asia is that, until relatively recently, mangals broadly retained their connection with inland rainforests, and were rarely isolated sufficiently long enough to prevent genetic exchange between mangal and rainforest populations. Many of the species listed by Nisbet (1968) are typical of rainforests, but are now apparently rare or extinct in mangals of Peninsular Malaysia, owing to large-scale destruction of mangals and of 'back mangals' (*sensu* Tomlinson 1986) and swamp forests linking mangals to rainforests.

In contrast to rainforests, mangals have contributed many species to rural and urban habitats in Peninsular Malaysia and Singapore. The avifaunal similarity between anthropogenic habitats and mangals has been attributed to the simple habitat structure and flora of both habitats, and, at the proximate level, to relatively broad niches and/or physiological tolerances among mangal-dwelling bird species (Nisbet 1968; Ward 1968; Medway and Wells 1976; Hails and Jarvis 1987; van Balen 1989; Noske 1995). Noske (1995) related broad niches of several common mangal-dwelling species to fluctuations in food availability driven by tidal cycles, and the dynamic physiography of mangals, in which 'new' habitat is regularly formed by deposition of sediment and rapid colonisation by mangroves in estuaries, while 'old' habitat is gradually colonised by terrestrial plant species. Except for the opportunistic nectarivores, mangal-specialised birds have not yet colonised urban Darwin, in contrast to several rainforest-specialised species, such as the frugivorous figbird, *Sphecotheres viridis*, and pied imperial pigeon, *Ducula bicolor*, which are very common in the suburbs. Urban colonisation by these frugivores was probably facilitated by the abundant availability of fruiting figs and palms. The ecological inflexibility of many mangal-specialist bird species, and hence their inability to colonise urban habitats, in mainland coastal north-western Australia could well be due to the lack of any suitable ecotone between the relatively stable, evergreen and fire-protected mangal environment and the highly seasonal, deciduous, and very fire-prone savannas abutting them.

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Appendix. Species recorded at the Palmerston mangal site

Except for species that are mangal-dependent (*) or that were encountered on censuses (#), wading and aerial species have been excluded, as well as species recorded only once. Scientific names follow Christidis and Boles (1994). *n*, number of months recorded (max. 54); does not include records within each month

Common name	Scientific name	<i>n</i>
Great-billed heron*	<i>Ardea sumatrana</i>	1
Striated heron*	<i>Butorides striatus</i>	1
White ibis#	<i>Threskiornis molucca</i>	12
Royal spoonbill#	<i>Platalea regia</i>	2
Brown goshawk	<i>Accipiter fasciatus</i>	3
Grey goshawk	<i>Accipiter novaehollandiae</i>	3
Chestnut rail	<i>Eulabeornis castaneiventris</i>	37
Common sandpiper#	<i>Actitis hypoleucos</i>	3
Bar-shouldered dove#	<i>Geopelia humeralis</i>	39
Peaceful dove#	<i>Geopelia placida</i>	40
Little bronze-cuckoo#	<i>Chrysococcyx malayanus</i>	35
Large-tailed nightjar	<i>Caprimulgus macrurus</i>	3
Australian owl-nightjar	<i>Aegotheles cristatus</i>	3
Azure kingfisher	<i>Alcedo azurea</i>	2
Little kingfisher#	<i>Alcedo pusilla</i>	25
Sacred kingfisher#	<i>Todirhamphus sancta</i>	33
Collared kingfisher*	<i>Todirhamphus chloris</i>	2
Rainbow bee-eater#	<i>Merops ornatus</i>	31
Mangrove gerygone**	<i>Gerygone laevigaster</i>	42
Large-billed gerygone#	<i>Gerygone magnirostris</i>	53
Green-backed gerygone#	<i>Gerygone chloronata</i>	39
Helmeted friarbird#	<i>Philemon buceroides</i>	11
Silver-crowned friarbird#	<i>Philemon argenticeps</i>	20
Little friarbird#	<i>Philemon citreogularis</i>	11
Brown honeyeater#	<i>Lichmera indistincta</i>	50
Rufous-banded honeyeater	<i>Conopophila albogularis</i>	2
Dusky honeyeater#	<i>Myzomela obscura</i>	14
Red-headed honeyeater**	<i>Myzomela erythrocephala</i>	54
Lemon-bellied flycatcher#	<i>Microeca flavigaster</i>	28
Mangrove robin**	<i>Eopsaltria pulverulenta</i>	49
Grey whistler#	<i>Pachycephala simplex</i>	42
Mangrove golden whistler*	<i>Pachycephala melanura</i>	4
White-breasted whistler*	<i>Pachycephala lanioides</i>	1
Rufous whistler	<i>Pachycephala rufiventris</i>	10
Little shrike-thrush#	<i>Colluricincla megarhyncha</i>	11
Broad-billed flycatcher**	<i>Myiagra ruficollis</i>	26
Leaden flycatcher#	<i>Myiagra rubecula</i>	25
Shining flycatcher #	<i>Myiagra alecto</i>	36
Northern fantail#	<i>Rhipidura setosa</i>	28
Mangrove fantail**	<i>Rhipidura phasiana</i>	20
Rufous fantail#	<i>Rhipidura rufifrons</i>	2
Spangled drongo	<i>Ducurus bracteatus</i>	5
White-bellied cuckoo-shrike#	<i>Coracina papuensis</i>	25
Cicadabird#	<i>Coracina tenuirostris</i>	25
Varied triller#	<i>Lalage leucomela</i>	35
Black butcherbird**	<i>Cracticus quoyi</i>	41
Yellow white-eye**	<i>Zosterops lutea</i>	51
Total No. of species and months	50	54