

Resource Partitioning by Mangrove Bird Communities in North Australia

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ABSTRACT

Mangrove bird communities in north Australia comprise relatively few passerine species compared with other arboreal habitats in the region. Mangroves are dominated by a few tree species and there are potentially few resource axes available for partitioning by terrestrial birds. Competition for limited resources is predicted to cause strong niche differentiation and a highly structured, but low diversity, bird assemblage. Using multivariate and bipartite network analyses based on 1771 foraging observations (33% of 5320 behavioral observations), we examined resource partitioning by 20 terrestrial bird species in mangroves of north Australia. The mangrove bird community largely comprised generalist insectivores that partitioned insects by size with moderate-to-high interspecific overlap in diet. Gleaning for insects was the most common foraging mode. Few species specialized on nectar. Flowers of one or more mangrove species were available in every month of the year and insect abundance was correlated with flowering peaks. Niche differentiation by birds was determined by food type and foraging mode more than by broad spatial (mangrove zones) or temporal (seasonal) segregation of the use of resources. There was little evidence of bird species saturation or species sorting, suggesting loose species packing and a lesser role than expected for species interactions and interference competition in structuring the bird assemblage in mangroves.

Key words: avifauna; bipartite network analysis; community ecology; niche segregation; plant–animal interactions.

BIRD COMMUNITIES HAVE OFTEN BEEN USED AS MODEL SYSTEMS to understand the complex interactions among species that use similar resources (Wooller & Calver 1981, Ricklefs 2012). How species partition resources and differentiate their niches define how communities are structured (Schoener 1974, Greenberg & Olsen 2010). Studies of how sympatric species differ in their resource use can provide indirect inferences about how potential competitors manage to coexist (Robertson *et al.* 2013). Coexisting species in an assemblage separate their niches or ecological needs by partitioning resources along temporal, spatial and behavioral niche axes (Cody 1974, Schoener 1974). In most instances where resources are limiting, competitive interactions among species lead to non-random patterns of resource use among species (Cody 1974). Some studies of closely related coexisting bird species, particularly in ecosystems with low vegetation diversity, have shown that bird species partition food resources by using different foraging behaviors (Lefebvre & Poulin 1997, Kornan & Adamik 2007, Böhm & Kalko 2009, Greenberg & Olsen 2010), vertical strata (Recher & Davis 1998, Walther 2002, Styring & Zakaria 2004) or by the differential use of microhabitats (Cody 1974, Schoener 1974). In the tropics, bird species are often more specialized in the way they use resources, which enables communities to be more tightly ‘packed’, and species richness is thus associated with specialization (MacArthur *et al.* 1972, Belmaker *et al.* 2012).

However, one constraint on determining the role of species interactions on community assembly is obtaining sufficient information on all interactions in a species-rich assemblage, necessary to understand how resources are partitioned (Wheeler & Calver 1996, Lewinsohn *et al.* 2006). Mangroves are a particularly suitable model ecosystem for examining species interactions because they are structurally and floristically simple, and support relatively few species of terrestrial vertebrates, so that niche differentiation may be more easily identified than in complex ecosystems, such as rain forests. Although the diets of many bird species of Australian mangroves have been described semi-quantitatively (Johnstone 1990, Noske 2003), the relationship between food resource availability and niche partitioning has not been investigated (*cf.* neotropical mangrove bird communities—Lefebvre & Poulin 1997). The seasonal availability of food resources (*i.e.*, insects and nectar) in mangroves is thought to influence bird species distribution and abundance in mangroves (Noske 1996) and its associated habitats (Woinarski 1993). In addition, the mangrove bird communities of northern Australia are particularly diverse (Ford 1982, Noske 1996) and have more mangrove-specialized species than those of other parts of the world (Luther & Greenberg 2009, Nyári & Joseph 2013), increasing the expectation of resource partitioning among Australian mangrove bird species (Noske 1996).

In Australia, mangroves represent a larger proportion of the land area of the monsoon tropics than monsoon rain forest. The monsoon tropics of northern Australia contain some of the most diverse mangrove communities in the world, yet there have been few studies of the phenology of mangrove flowering and insect abundance (Noske 1996, McGuinness 1997, Coupland *et al.*

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2005). Noske (1996) and Metcalfe (2007) examined the foraging ecology of the mangrove bird communities near Darwin, and concluded that their assemblages were partitioned mainly by diet and associated foraging behavior among mangrove tree zones. Studies of bird foraging ecology in the monsoon tropics of Australia have mainly focused on birds of tropical savanna woodland (Brooker *et al.* 1990, Franklin & Noske 1999). Unlike the *Eucalyptus*-dominated savannas that dominate the region, mangroves have fewer nectarivores and no granivores, and as mangroves do not produce fleshy fruits, there are also very few frugivores. Mangroves are thus dominated by a rich assemblage of insectivores, which, unlike many nectarivores, are largely sedentary in mangroves (Noske 1996).

We have previously demonstrated that the avian assemblage structure in mangroves is determined, in part, by the type and diversity of mangrove zones, the timing of flowering and the nature of the matrix surrounding mangroves (Mohd-Azlan & Lawes 2011, Mohd-Azlan *et al.* 2012). Here, we explore the patterns of species association along food, and temporal, spatial and habitat niche dimensions of mangrove bird species in the Darwin region. We also examine the influence of flowering phenology and the seasonality of insect availability on the density and species composition of the bird community.

METHODS

STUDY SITE.—Data were collected from thirteen mangrove patches ranging from 1 to 595 ha (mean = 68.18 ha, SD = 113.33 ha) in the Darwin region (12°20′09.61″S; 130°54′26.81″E–12°28′18.33″S; 130°56′28.76″E), Northern Territory, between March 2008 and April 2009. Although the mangrove patches ranged in size by two orders of magnitude, bird species richness in a patch was independent of patch-size (Mohd-Azlan *et al.* 2012). Darwin is situated in the Australian monsoon tropics, which experience seasonal rainfall from late October through April, followed by a dry season of almost 6 mo.

FORAGING OBSERVATIONS.—Birds were observed along straight-line transects at each site, twice a month for a period of 14 mo (March 2008–April 2009). Transect lengths were proportional to patch area (transect length [km] = $0.14 + 0.27 \log_{10} A$ [ha]; $F_{1,10} = 21.86$, $P = 0.001$, $R^2 = 0.83$). At each site, transects were walked in random order (in areas with multiple transect lines) at low tide, and thus censuses were conducted throughout the day, although most were in the early morning and late afternoon (see operational protocols in Mohd-Azlan & Lawes 2011). The angle bearing (θ) from the path route to the observed bird was used to calculate the perpendicular distance. The calculated perpendicular sighting distances across all species within each mangrove patch were analyzed using DISTANCE 5.2 (Thomas *et al.* 2006) to estimate the density and abundance of mangrove bird species. The half-normal key function was fitted to the ungrouped, non-truncated data (distance w was at least as large as the largest recorded distance) with cosine series of expansion and found to fit well (Buckland *et al.* 2001).

Birds were observed for as long as possible during transect counts. Mangrove plants, but not monsoon vine-thicket plants, on which birds foraged were identified to species level. Only the initial foraging observation was used for analysis to avoid non-independence of data (Styring & Zakaria 2004). For each foraging bird encountered, the following niche dimensions (with categories) were recorded where possible: mangrove zone—based on the major mangrove zonation; feeding substrate—air, ground, prop-root, trunk, branch, foliage (leaves and twigs) and dead branch; food type—insect (by size class) or flower (by plant species); and foraging height, which was estimated to the nearest 0.1 m below 2 m and to the nearest 0.5 m above 2 m (Recher & Davis 1998), and grouped into four height classes (HC1: 0–0.2 m; HC2: 0.2–2 m; HC3: 2–4 m; HC4: >4 m). Foraging behavior was categorized as follows: (i) glean—foraging for stationary prey while perching; (ii) snatch—foraging for stationary prey during short flights from a perch; (iii) hover—feeding on stationary food resources including flowers; (iv) hawk—feeding on flying prey; (v) drill—repeated pecking at one location; (vi) probe—insertion of bill into flower or crevices; and (vii) pounce (Noske 1995, 1996).

Foraging observations with fewer than 10 observations per foraging category were excluded from the network and multivariate analyses to ensure statistical power, but all records of the size of insects captured by birds were included in analyses where appropriate (Recher & Davis 1998, Styring & Zakaria 2004). Where possible, invertebrates eaten by the birds were identified to order level, and their size estimated in relation to the bird's beak length. Mean values for avian body mass were sourced from the literature (Noske 1996, Higgins *et al.* 2006).

FLOWERING PHENOLOGY AND INSECT AVAILABILITY.—Flowering of mangrove plants was monitored from March 2008 to March 2009 to estimate the availability of nectar. The abundance of flowering phytophases (buds, open and senescent flowers) was scored each month. The abundance of open flowers was used as a surrogate estimate of nectar availability. The dominant flowering mangrove species were monitored, namely *Avicennia marina* (Grey Mangrove), *Aegiceras exaristata* (River Mangrove), *Bruguiera exaristata* (Rib-fruited Mangrove), *Ceriops australis* (Smooth-fruited Spur Mangrove), *Lumnitzera racemosa* (White-flowered Black Mangrove), *Rhizophora stylosa* (Stilt-root Mangrove) and *Sonneratia alba* (Star Mangrove). Ten mature individuals of each species were monitored at each site. Flowering peaks were defined as the period during which most of the reproductive trees at the sites bore open flowers. Vegetation density was assessed in sample plots using a stratified random sampling scheme. Because of the species homogeneity of mangrove zones (Noske 1996), only two 5 × 5 m plots were set at a site in each dominant mangrove zone. Within each of these plots, one 2.5 × 2.5 m subplot was established. In each 5 × 5 m plot, the diameter of all woody tree species, excluding dead trees, with a diameter at breast height (dbh) >10 cm was measured. In the 2.5 × 2.5 m subplot, all woody plant species with a dbh more than 2 cm and <10 cm were counted. These stem counts were used to estimate the stem density of flowering mangrove species.

A monthly flower availability index for each mangrove plant was derived as the sum of the availability indices for each species sampled during that month. The flower availability index was calculated using the formula (Lawes & Piper 1992):

$$FAI = D_{rel} \times F_{pot} \times F_{pi} \times N_{prop},$$

where, D_{rel} is the relative density based on the mean estimate of stem densities of a species at a site; F_{pi} is the mean proportion of open flowers of a species; and N_{prop} = the proportion of flowering individuals of a species out of 10 individuals. F_{pot} is the maximum flowering potential of the species, a constant that is based on the maximum proportion of the canopy volume given to a phytophase at the peak of the availability of that phytophase. Each plant species was ranked on a scale of 0.1–1, where 0.1 represents few flowers on a tree when flowers are at maximum availability and 1 represents a fully loaded canopy. In this study, the lower F_{pot} score was set by *Aegiceras corniculatum* = 0.4 and the upper limit by *Bruguiera exaristata* and *Rhizophora stylosa* both scoring 0.8.

Insect abundance at all sites (13 sites) was sampled on the low tide using the 'sweep-net' technique once a month (over 14 mo). A sample unit comprised 20 consecutive sweeps of mangrove tree foliage up to 3.5 m height, every 20–50 m depending on the size of the mangrove patch, alongside the transects that were used for bird counts. Insects were sorted and then grouped into seven size classes (IC1 = <0.5 cm; IC2 = 0.5–0.99 cm; IC3 = 1.0–1.49 cm; IC4 = 1.5–1.99 cm; IC5 = 2.0–2.49 cm; IC6 = 2.5–2.99 cm; and IC7 = >3 cm).

ANALYSIS.—A combination of ordination plots, specialization metrics and species interaction networks analysis (Lewinsohn *et al.* 2006, Blüthgen *et al.* 2007) was used to investigate whether non-random patterns of resource partitioning exist among mangrove birds, in terms of: (i) foraging behaviors (behavioral partitioning); (ii) foraging height (vertical spatial partitioning); (iii) foraging substrates (microhabitat partitioning) (iv) diet (food partitioning— insects and nectar); and (v) mangrove zone use (horizontal spatial partitioning).

Insect abundance in the mangroves was compared among months and between seasons. Initial observations made in February 2008 were excluded from the analyses and data from March 2008 through February 2009 were analyzed. Mean insect abundance was compared between the wet and dry seasons using a *t*-test paired by site, while the variability of insect species richness and abundance was compared among months using repeated measures ANOVA.

ORDINATION.—Principal components analysis (PCA) and correspondence analysis (CA) were used to explore patterns of species co-occurrence in each resource partitioning category (Styring & Zakaria 2004). PCA was used to reduce the 40 resource partitioning variables to an orthogonal set of twelve variables (branch, foliage, hover, probe, HC2, HC3, *Bruguiera* and *Rhizophora* zones,

IC1, IC2, *B. exaristata* and *R. stylosa* flowers) that captured most of the variance (McCune & Mefford 1999). Because the original variables were not measured on the same scale, the analysis was performed on standardized variables using a correlation matrix. The resource variables selected in PCA were plotted using CA because correspondence analysis accounts for more variation in foraging data than other multivariate techniques (Miles 1990, Styring & Zakaria 2004, Lewinsohn *et al.* 2006). Multivariate analyses were performed using PCORD v.4.34 (McCune & Mefford 1999) and MVSP 3.131 (Kovach 2004).

BIPARTITE 'NETWORK' ANALYSIS.—It is difficult to demonstrate interspecific competition for resources in ecology (Connell 1983), particularly at the community level (Mac Nally 1995), without experimental manipulation (Clarke & Schedvin 1999) or where special circumstances present a natural experiment (*e.g.*, Kemmerer *et al.* 2008, Robertson *et al.* 2013). Here, we use network analyses to estimate interspecific overlap in resource use. Bipartite network analysis provides mathematical functions to visualize and describe pattern in ecological webs (Blüthgen *et al.* 2007). We tested the networks of interactions between mangrove bird species and five resource dimensions, namely zone, food (flower and insects), behavior, height and substrate. Ten indices derived from network analysis were used in this study. (i) *Connectance* (C), a widely used measure of community-wide specialization, indicating the proportion of the observed interactions to all possible links (Dunne *et al.* 2002). (ii) *Links per species* (L_s) is the mean number of categories of a resource or niche dimension (groups) used by a species (Dormann *et al.* 2008). (iii) *Mean number of shared groups* (S_g) in a resource axis that is used by the bird species (Stone & Roberts 1992). (iv) *Togetherness*, or *T-score*, describes the level of similarity in the use of resources by two species (Stone & Roberts 1992). (v) The *C-score* is the mean (normalized) number of checkerboard combinations across all species along a resource axis, with values close to 1.0 indicating disaggregation (through species interactions) within the network, and values close to 0 indicating aggregation of species (no resisting forces between species) (Stone & Roberts 1990). (vi) *Niche overlap* is the mean similarity in interaction pattern between species of the same trophic level, based on Horn's index (R_o) (Horn 1966); values approaching zero indicate no common use of niches, while one indicates perfect niche overlap. (vii) *Evenness* is the web interaction evenness, based on Shannon's evenness for the web links, treating zeros as no data (Dormann *et al.* 2009). (viii) *Shannon diversity* index was used to represent the diversity of interactions in a network (*i.e.*, network entries) (Dormann *et al.* 2009). (ix) The *network-level measure of species specialization* index (H_2'), following Blüthgen *et al.* (2006), ranges between 0 (no specialization) and 1 (complete specialization) (Dormann *et al.* 2009). (x) *Individual species specialization* index (d'), also ranging from 0 (no specialization) to 1 (perfect specialist) (Dormann *et al.* 2009), expresses how specialized a given species is in relation to the resources available.

All tests were computed using R v.2.11 statistical programming language (R Core Team 2010). The 'bipartite' 1.10

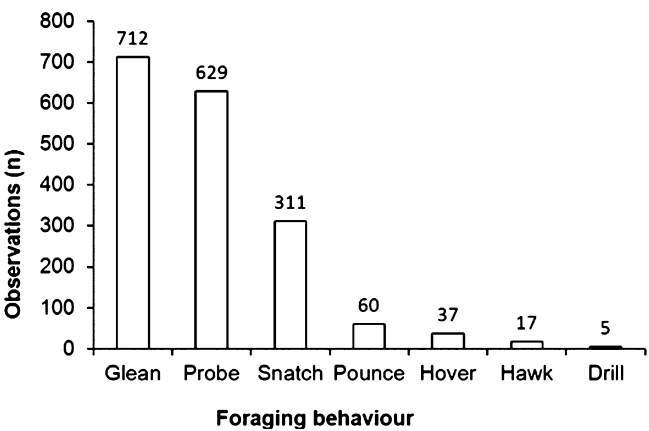


FIGURE 1. Frequency distribution of all observed foraging behaviors (43 species, $N = 1771$ observations), including species for which there were fewer than 10 observations of foraging behavior.

(Dormann *et al.* 2008) and ‘Social Network Analysis’ (Butts 2008) packages were used to calculate the indices listed above.

RESULTS

FORAGING ECOLOGY.—Of 5320 observations of bird behavior from 70 bird species, 1771 (33%) were foraging behaviors (Fig. 1). For nine bird species, 50 or more foraging observations were obtained; 30–49 observations were obtained for four species; 10–29 observations were recorded for seven species while 23 species were observed foraging fewer than 10 times. Gleaning was the most common foraging behavior by 31 bird species (Fig. 1), and was almost the exclusive foraging mode used by gerygones and the Yellow White-eye *Zosterops luteus*. Snatching was the most common foraging technique used by

fantails and flycatchers. Red-headed *Myzomela erythrocephala* and Brown Honeyeaters *Lichmera indistincta* were probers and seldom gleaned prey (Table S1—Online Supplementary Material). Several insectivores employed a ‘sit-and-wait’ strategy, hawking or snatching prey from leaves or bark. The only species that almost exclusively hawked prey was the Rainbow Bee-eater *Merops ornatus*. Most of the insectivores foraged over a wide range of substrates, but foliage was the most frequently used substrate in the mangroves ($N = 1166$ observations, 28 species). Honeyeaters used foliage to glean insects and probe flowers.

Most species foraged in the tree canopy on insects and nectar with the 2–4 m stratum used most by honeyeaters, while flycatchers used the sparse understory or snatched prey from above the canopy. Except for the Rainbow Bee-eater, the foraging height of mangrove bird species ranged from 0 to 18 m. Red-headed Honeyeaters probed flowers mainly on *B. exaristata* and *R. stylosa*, while Brown Honeyeaters obtained most of their nectar from *B. exaristata* and *S. alba* (Table S2). Generalizing across the foraging activities among mangrove plant species, *A. marina* was mainly used by birds as a source of insects, while *B. exaristata* was used more frequently for its nectar (Fig. 2). The body mass of mangrove bird species was significantly correlated with the size of the insects captured ($F_{1,19} = 29.9$, $R^2 = 0.62$, $P < 0.0001$) and larger birds captured larger insect prey as expected (Fig. 3). Helmeted Friarbirds (HFB) *Philemon buceroides* the largest omnivore, and Rainbow Bee-eaters, consumed larger insects than those eaten by other species, the latter frequently feeding on dragonflies. The gerygones, Yellow White-eye, Red-headed Honeyeater and Rufous-banded Honeyeater *Conopophila albogularis* fed largely on small insects (< 0.5 cm), while the Brown Honeyeater, flycatchers and the Grey Whistler *Pachycephala simplex* fed mostly on larger insects (0.5–1.0 cm), suggesting niche partitioning by prey size (Table S2).

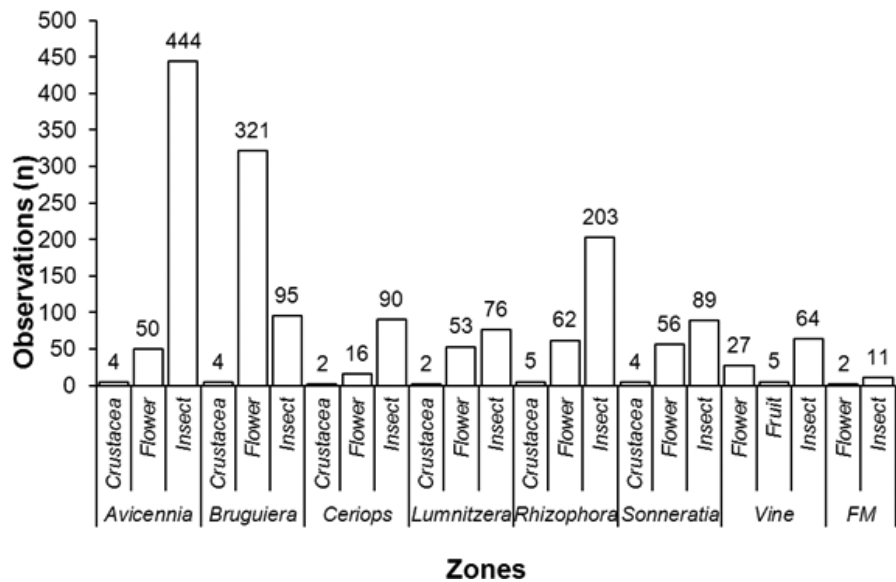


FIGURE 2. Types of food resources acquired by birds in mangrove zones, vine thickets (Vine), and mangrove fringe (FM).

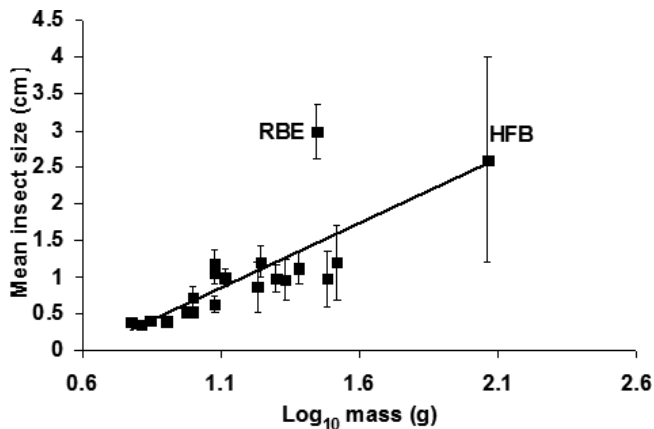


FIGURE 3. Relationship between body mass of mangrove birds and insects captured by mangrove birds, based on estimates obtained in the field. Acronyms: RBE, rainbow bee-eater; HFB, helmeted friarbird.

SEASONALITY OF FOOD RESOURCES.—The dominant mangrove species flowered at discrete, predictable times of the year. *Lumnitzera racemosa* flowered during the wet season, while *R. stylosa* flowered throughout the year with peak flowering toward the early wet season (Fig. 4). Except for *S. alba*, all the mangrove plants had a single flowering peak. *Bruguiera exaristata* flowered during the dry season with the longest flowering period over 6 mo from May to October. A total of 3749 arthropods were collected and measured from sweep samples at 13 mangrove patches. They included Arachnida (spiders) and 13 orders of insects. The mean size of arthropods was 4.5 ± 0.1 mm (mean \pm SE, $N = 3749$). The most abundant taxon was the order Hemiptera ($N = 2059$), followed by spiders ($N = 476$). Insects were present year-round, but mean insect abundance differed significantly between the wet and dry seasons ($t = 3.62$; $df = 11$; $P = 0.005$) with insects more abundant in the dry (mean = 129.4 ind./site/sample survey; SE = 39.0) than in the wet season (mean = 90.45; SE = 16.65). Insect abundance varied significantly among months (repeated measures ANOVA; $F_{13,130} = 4.88$, $P < 0.001$) with the highest abundance occurring in the mid and late dry seasons. The FAI and mean monthly insect abundance were correlated (linear regression: $F_{1,12} = 5.5$; $P = 0.04$; $R^2 = 0.33$) (Fig. 4). The first peak of insect abundance during the early dry season coincided with the flowering peak of *B. exaristata* while the second peak in insect abundance during the late dry coincided with the flowering peak of *Cerriops australis*.

Overall bird density at a mangrove site was correlated with mean insect abundance ($F_{1,12} = 7.3$, $P = 0.02$, $R^2 = 0.4$) (Fig. S1). Bird density increased significantly with insect abundance among mangrove sites during the wet season ($F_{1,12} = 7.2$, $P = 0.009$, $R^2 = 0.6$), but not during the dry season ($F_{1,12} = 3.4$, $P = 0.09$, $R^2 = 0.3$), suggesting that dry season insect abundance may limit bird density in the mangroves (but not species richness). Nectarivore and overall bird species richness was not influenced by FAI or insect availability ($P > 0.05$).

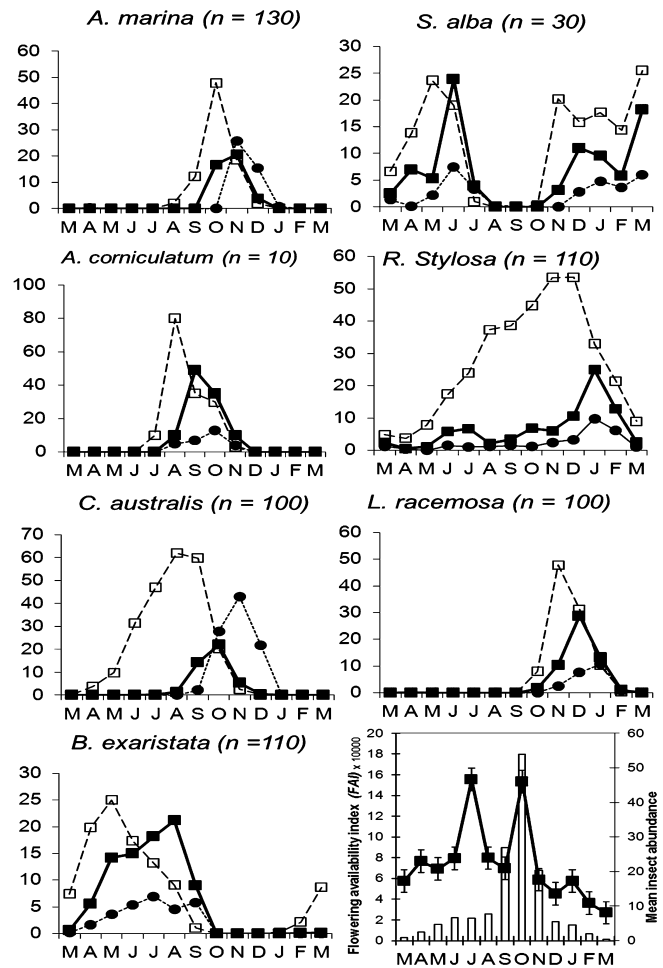


FIGURE 4. Flowering phenology of seven species of mangrove from 13 sites (10 individuals per site) in the Darwin region between March 2008 and March 2009. Bud (—); fresh flowers (■); old flowers (●). Also relationship between flowering availability index (FAI = bars) and mean insect abundance (■). SE is denoted by vertical whiskers.

ORDINATION.—Twelve relatively independent resource variables (branch, foliage, hover, probe, HC2, HC3, *Bruguiera* and *Rhizophora* zones, IC1, IC2, *B. exaristata* and *R. stylosa* flowers) were identified using PCA. These variables, when plotted using CA, indicate resource partitioning between the nectarivores and insectivores, as expected, but less partitioning of resources within the insectivores (Fig. 5). Most of the insectivores partitioned their use of insect size classes, but foraged opportunistically at the spatial scale. The Green-backed Gerygone (GBG), *Gerygone chloronotus*, was found mostly in the *Lumnitzera* zone, foraged in the higher canopy and showed more spatial segregation than most other insectivorous species (Fig. 5). In addition, substrate preference was important in subdividing height classes based on the size of insects preyed upon.

STRUCTURE OF INTERACTION NETWORK.—Network analysis suggested that mangrove birds partitioned food resources mainly by

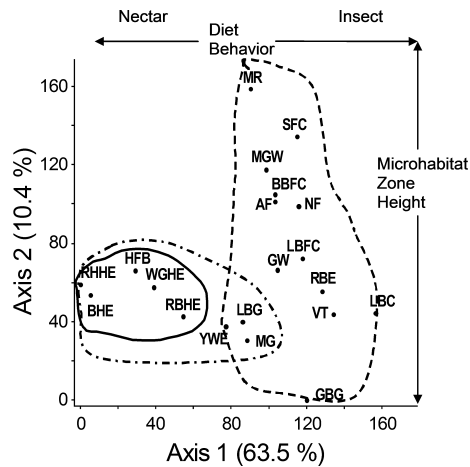


FIGURE 5. Correspondence Analysis plot showing that the mangrove bird assemblage is structured more on its food and behavioral partitioning (63.5%) compared with spatial partitioning (10.4%). Bold line (—) encompasses nectarivores, (---) encompasses snatchers at mid to high canopy; (· · ·) encompasses gleaners at lower canopy. Species acronyms are explained in Table 2.

food type (and prey size in the case of insectivores) and foraging mode, but overlapped substantially in their use of foraging height strata (Table 1; see both R_o and S_g). There were low levels of specialization among species along most resource axes and it appears that within the context of the available food resources that most species are generalist foragers.

Connectance ranged from 0.51 to 0.83 for all resource axes, illustrating that most species were generalists and used a variety of resources, resulting in broad overlap in resource use (Table 1). The mean number of links (L_x) per bird species ranged from 2.17 in bird–flower interactions (on average, one bird species uses 30% of the available flowering plants) to 4.5 in bird–zone interactions (on average, one bird species uses 60% of the available zones) (Table 1). There was greater similarity (S_g) in spatial

partitioning by the bird assemblage compared with similarity in their use of food resources (Table 1). Togetherness (T) ranged from 0.09 (zonation) to 0.44 (foraging behavior), implying that birds showed flexibility in the use of mangrove zones, but were relatively specialized in foraging behavior (Table 1). The C -score values ranged from 0.14 to 0.35, indicating aggregation and low levels of competition among species in the mangrove bird assemblage. Relatively high niche overlap (R_o) was observed for all the foraging dimensions ranging from 0.5 to 0.79 (Table 1). The behavioral dimension consistently showed the lowest overlap confirming that mangrove birds specialized in their foraging behavior while displaying general use of space. These trends are consistent with the findings of the CA (Fig. 5).

Web evenness ($E5$) was relatively high and ranged between 0.69 and 0.84, demonstrating broad overlap between species and guild dimensions (Table 1). The network-level measure of specialization (H_2') indicated a high level of specialization on prey size among insectivores (Fig. S2). At the species level, specialization (d') was low with most species being generalists, especially in their use of space (*i.e.*, height and mangrove zones) (Table 2).

DISCUSSION

Most mangrove bird species exhibited broad patterns of use of space (foraging height and substrates, and mangrove zones) and mainly partitioned food resources, either through differences in their foraging behavior or diet. Even then, there were few true dietary specialists and food resources were largely exploited in an opportunistic fashion. The broad interspecific overlap along most resource axes is expected as mangrove birds have to cope with significant diurnal variation in substrate accessibility, due to tidal movements, as well as seasonal fluctuations in food availability (Noske 1995). In addition, even though mangrove and bird species richness in northwestern Australia is high by global standards, and there are more mangrove specialists (Luther & Greenberg 2009), there was little or no evidence of competitive exclusion (*i.e.*, no checkerboard pattern of distribution of potentially competing species among sites), or indeed strong interfer-

TABLE 1. Number of resource partitioning categories and the indices used in network analysis of the interaction structure within the mangrove bird assemblages.

Interaction categories	No. of dimensions	No. of birds	Matrix size	C	L_x	S_g	T	C_s	R_o	$E5$	H'	H_2'
Food partitioning												
Insect size	7	20	140	0.53	2.74	5.52	0.34	0.22	0.52	0.84	3.63	0.31
Nectar	7	4	28	0.74	2.17	2.90	0.11	0.17	0.60	0.70	2.30	0.16
Spatial partitioning												
Foraging substrate	7	20	140	0.64	3.30	8.00	0.30	0.35	0.59	0.69	3.10	0.30
Foraging height	4	20	80	0.83	2.80	13.00	0.41	0.14	0.79	0.83	3.50	0.07
Horizontal distribution (zone)	8	20	160	0.79	4.50	12.78	0.10	0.47	0.57	0.82	4.00	0.15
Behavioral partitioning												
Foraging techniques	7	20	140	0.51	2.60	4.90	0.44	0.14	0.50	0.72	3.10	0.44

C , connectance; L_x , linkage level of bird species; S_g , Mean number of shared groups; T = togetherness, C_s = C -score, R_o = niche overlap, $E5$ evenness, H' = evenness, H_2' = specialization on network level.

TABLE 2. Level of specialization (d') of bird species on different resources. The values in bold font indicate the most specialized species on a resource axis.

Species	Substrates	Height	Behavior	Zones	Insect	Flower
Arafura Fantail (AF) <i>Rhipidura dryas</i>	0.08	0.06	0.30	0.14	0.05	N/A
Broad-billed Flycatcher (BBFC) <i>Myiagra ruficollis</i>	0.17	0.01	0.40	0.10	0.28	N/A
Brown Honeyeater (BHE) <i>Lichmera indistincta</i>	0.06	0.00	0.16	0.04	0.02	0.04
Green-backed Gerygone (GBG) <i>Gerygone chloronotus</i>	0.01	0.02	0.11	0.21	0.08	N/A
Grey Whistler (GW) <i>Pachycephala simplex</i>	0.06	0.06	0.19	0.05	0.14	N/A
Helmeted Friarbird (HFB) <i>Philemon buceroides</i>	0.15	0.02	0.07	0.11	0.31	0.15
Large-billed Gerygone (LBG) <i>Gerygone magnirostris</i>	0.03	0.01	0.23	0.04	0.14	N/A
Lemon-bellied Flycatcher (LBFC) <i>Microeca flavigaster</i>	0.18	0.01	0.31	0.16	0.09	N/A
Little Bronze-cuckoo (LBC) <i>Chrysococcyx minutillus</i>	0.18	0.02	0.16	0.11	0.04	N/A
Mangrove Gerygone (MG) <i>Gerygone levigaster</i>	0.05	0.06	0.25	0.25	0.14	N/A

(continued)

Table 2 (continued)

Species	Substrates	Height	Behavior	Zones	Insect	Flower
Mangrove Golden Whistler (MGW) <i>Pachycephala melanura</i>	0.13	0.03	0.11	0.14	0.25	N/A
Mangrove Robin (MR) <i>Peneoenanthe pulverulenta</i>	0.42	0.17	0.37	0.18	0.29	N/A
Northern Fantail (NF) <i>Rhipidura rufiventris</i>	0.21	0.05	0.39	0.02	0.23	N/A
Rainbow Bee-eater (RBE) <i>Merops ornatus</i>	0.44	0.11	0.35	0.17	0.65	N/A
Red-headed Honeyeater (RHHE) <i>Myzomela erythrocephala</i>	0.09	0.02	0.25	0.17	0.08	0.12
Rufous-banded Honeyeater (RBHE) <i>Conopophila albogularis</i>	0.02	0.01	0.06	0.11	0.02	0.52
Shining Flycatcher (SFC) <i>Myiagra alecto</i>	0.61	0.21	0.41	0.04	0.04	N/A
Varied Triller (VT) <i>Lalage leucomela</i>	0.17	0.05	0.10	0.25	0.48	N/A
White-gaped Honeyeater (WGHE) <i>Lichenostomus unicolor</i>	0.06	0.01	0.03	0.05	0.05	0.08
Yellow White-eye (YWE) <i>Zosterops luteus</i>	0.03	0.01	0.22	0.07	0.05	N/A
MEDIAN	0.11	0.02	0.23	0.11	0.12	0.12

ence competition (overt aggression between species), structuring the mangrove bird assemblage (Mohd-Azlan & Lawes 2011, Mohd-Azlan *et al.* 2012). The latter findings provide some support for the notion that the prevalence of the generalist strategy among mangrove bird species may be historically contingent on the ecological filtering of the high-diversity rain forest (Ford 1982, Schodde *et al.* 1982, Nyári & Joseph 2012, 2013) and savanna woodland (Noske 1996) assemblages from which mangrove birds have originated, rather than by contemporary processes of community assembly (*cf.* Mac Nally & Timewell 2005, Belmaker *et al.* 2012).

Mangrove birds were more specialized in their foraging behaviors ($H^2 = 0.44$) than in other resource dimensions, and least specialized in their use of foraging heights ($H^2 = 0.07$). A shift toward larger bill size among mangrove bird species has been noted (Schodde *et al.* 1982) (potentially increasing the range of food items that can be taken) and presumably relates to reduced interspecific and increased intraspecific competition (Luther & Greenberg 2011). These findings of niche differentiation based on mainly foraging behavior are consistent with several other studies of the foraging ecology of mangrove birds in the tropics (Noske 1996, Noske & Franklin 1999, Mulyani 2004, Metcalfe 2007, Luther & Greenberg 2011) and in simplified (dominated by a few tree species) temperate and/or high-altitude forest systems (*e.g.*, Wheeler & Calver 1996, Adamik *et al.* 2003, Kornan & Adamik 2007, Böhm & Kalko 2009). However, this is not the case in tropical rain forest where bird biomass is dominated by frugivores, insectivores and omnivores, proportionately fewer seasonally transient species, greater spatial segregation (as opposed to temporal segregation) of individuals, and species are tightly packed so that interspecific niche differentiation involves several resource dimensions (food type, food item size, foraging height and mode) (Wong 1986, Johnson *et al.* 2011). In this study, and corroborated by Noske (1996), mangrove bird species overlapped in at least one resource dimension, with niche overlap ranging from 50 to 80 percent in foraging behavior and height. In comparison, rain forest bird assemblages in northern Queensland had a 38 percent overlap among species in foraging behavior and 90 percent overlap in habitat use (Crome 1978), suggesting more dense species packing in rain forest than in mangroves. Consistent with patterns of high niche overlap among bird species in the mangroves, there was little evidence in our study of interference competition or dominance by generalist species and/or the loss of specialist species as observed in some fragmented woodlands in Australia (Robertson *et al.* 2013).

Partitioning of insect prey through different foraging techniques has been reported in several Australian bird communities (Crome 1978, Wooller & Calver 1981, Wheeler & Calver 1996) and the mangrove bird assemblage is no exception (Noske 1996). In general, the mangrove bird community comprised generalist insectivores that partition weakly to moderately along the prey size and foraging height dimensions of the food resource niche axes. For example, small foliage-gleaning insectivores, like the Mangrove Gerygone (*Gerygone levigaster*, 6 g), preferred small insects (<0.5 cm), while the Varied Triller (*Lalage leucomela*, 33 g)

consumed larger insects. Not surprisingly, small insects (<0.5 cm) formed a large part of the diet of many mangrove bird species, especially the foliage gleaners, and this size class comprised 74 percent of invertebrates sampled by sweep net from the mangrove foliage. The Red-headed Honeyeater fed more frequently on spiders than other insectivores, and was occasionally seen picking insects or spiders from spider webs. Only a few species of ground foragers are represented in the mangroves, because of tidal flooding, which greatly restricts foraging time for ground foragers, and the anoxic, waterlogged and probably toxic condition of soils, which limit the kinds of invertebrates that can survive in it. Consequently, some generalist insectivores (*e.g.*, Shining Flycatcher, *Myiagra alecto*; Mangrove Robin, *Peneoenanthe pulverulenta*) are known to feed on crustaceans during low tides and on insects during high tides.

The seasonal flowering phenology of mangroves may cause seasonal increases in insect abundance. The flowering phenology described in this study is consistent with that reported by Noske (1996) and McGuinness (1997). Peak flowering in mangroves occurred between the late dry and early wet season except for *S. alba* and *B. exaristata*. Similar to mangrove birds in South America, bird density in this study underwent seasonal change in response to fluctuations in food abundance, with an increase in insect abundance during the dry season possibly explaining why some smaller mangrove birds (*e.g.*, Red-headed Honeyeater, Mangrove Gerygone, Large-billed Gerygone, *Gerygone magnirostris*, Yellow White-eye and Lemon-bellied Flycatcher, *Microeca flavigaster*) have breeding peaks during the dry season (Noske 1996, Lefebvre & Poulin 1997). In addition, given the high frequency of fire in adjacent savanna woodland, north Australian mangroves may provide temporary refugia from fire and maintain avian biodiversity by providing feeding sites and shelter for terrestrial insectivores that visit during critical periods (Noske 2003, Metcalfe 2007). On the other hand, the tropical savanna woodlands comprising the matrix are dominated by eucalypt species that support a diversity of nectarivorous and insectivorous bird species, some of which also use the mangroves (Woinarski *et al.* 1988).

In conclusion, contemporary mangrove bird assemblages in the Darwin region are dominated by generalists and owe their structure and composition mainly to how food resources and the associated foraging behaviors are partitioned, rather than to partitioning along other resource dimensions (microhabitat, zone and height). Even though these north Australian mangrove bird communities are species-rich compared with mangrove bird assemblages globally (Luther & Greenberg 2009, Nyári & Joseph 2013), they comprised relatively loosely packed species assemblages. These relatively species-rich mangrove bird assemblages in north Australia appear not to be strongly deterministic assemblages structured by local ecological processes, but are probably an evolutionary consequence of the lack of alternative evergreen habitats for many species when the continent was drying out during the Pleistocene, causing these species to become more dependent on mangroves (Ford 1982, Schodde *et al.* 1982, Nyári & Joseph 2012, 2013). We have argued that the loosely packed mangrove-dependent bird species assemblage in these mangroves

has resulted in many species being shared with, and derived from, the species pool in the savanna matrix (Mohd-Azlan & Lawes 2011). The strong effect of the species pool on mangrove bird assemblage composition indicates that local ecological processes, such as resource partitioning among species, the diversity of mangrove plant species at a site (and in the matrix; Mohd-Azlan & Lawes 2011) and the phenology of foods (arthropods and nectar), are all less influential and very local determinants of contemporary mangrove bird assemblage structure and composition.

However, there are contrasting gradients of mangrove plant and bird diversity across northern Australia. For example, the floristically rich mangroves of northeastern Australia have fewer mangrove specialist bird species than the floristically poorer mangroves of northwestern Australia, which are especially rich in birds specialized to mangroves (Ford 1982, Noske 1996, Kutt 2007). Further comparisons of mangrove bird assemblage structure across north Australia may determine whether these assemblages are contingent on vegetation changes in the past (Lessard *et al.* 2012). The role of past vegetation changes in the evolution of mangrove bird assemblages might be expected to be strong in northwestern Australia, where rain forest fragmentation and vicariance events were severe during the Pleistocene (Ford 1982, Nyári & Joseph 2013). In contrast, in northeastern Australia, large tracts of rain forest remained contiguous with mangroves throughout the Pleistocene (Ford 1982, Nyári & Joseph 2013). Mangrove bird assemblages there should reflect a stronger rain forest element and fewer mangrove-dependent species, as indeed they do (Kutt 2007). An increase in mangrove bird species richness from east to west across north Australia with no appreciable increase in the resource base, floristic diversity, or an increase in interspecific interactions may be evidence of the important influence of historical contingency in the evolution of mangrove bird assemblages in north Australia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Foraging substrates, techniques and heights used by the most abundant bird species in mangroves of Darwin region.*

TABLE S2. *The observed frequency of use by mangrove birds of the size classes of insects/arthropods, and the use of mangrove flowers by five species of honeyeaters.*

FIGURE S1. The relationship between bird density and mean insect abundance at 13 mangrove sites.

FIGURE S2. Interaction network of bird species versus insect size class showing that nearly all mangrove bird species feed mainly on the smaller insects.

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