Resource Partitioning in an Island Community of Insectivorous Birds During Winter

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Summary: Resource partitioning within an assemblage of seven species of insectivorous birds inhabiting remnant *Melaleuca* woodland on Rottnest Island off the coast of Western Australia was studied during May–July 1993. Foraging behaviour, foraging height, foraging substrate and foraging plant associations of all species (and of both sexes in two species) were recorded for each month. These data were used to calculate overlaps in each foraging dimension and for all foraging dimensions combined. The significance of total foraging overlap between species and sexes (defined as overlap > 0.6) was low in May (only 14% of all total forag-

ing overlaps) but increased slightly in June and July (25 and 29% of all total foraging overlaps respectively). Foraging habits were associated significantly both with bird species and month of observation, indicating that foraging partitioning occurred and that its pattern varied temporally. The diversity of foraging habits displayed by each bird species in each foraging dimension (determined by the Shannon-Wiener function) varied widely, although a species which was a generalist in one foraging dimension also tended to be a generalist in other foraging dimensions.

The presence of ecological guilds may be seen as a contradiction to competition theory, in that species with high resource overlap (as described by the definition of guilds) manage to coexist (Pontin 1982). Such coexistence may be facilitated by community structuring forces such as predation, so that competition has little effect on population dynamics (Sih et al. 1985) or the species in the guild may be partitioning the shared resources in some way so that competition is lessened (Wiens 1989). Resource partitioning has been demonstrated in a diverse range of taxa including aquatic invertebrates (Langton & Robinson 1990), insects (Niemelä 1993), fish (Penn et al. 1993) and mammals (Dickman 1988), but bird assemblages have been studied most frequently (e.g. Landmann & Winding 1993; Török 1993) because they are easily observable. However, a limitation of many of these studies is the difficulty of collecting data on all members of what are sometimes large and diverse groups. Island communities offer an attractive solution to this problem since their faunas are comparatively depauperate compared with those of mainland communities and the goal of a complete community survey is easier to attain. This paper reports resource partitioning in an island assemblage of insectivorous birds during winter.

Methods

Study site and bird community

Rottnest Island lies approximately 18 km west of Fre-

mantle, Western Australia (32°00′S, 115°30′E) and the study site was located in Bickley woodland. The dominant canopy species is *Melaleuca lanceolata* (height to 5 m with similar spread) with occasional *Acacia rostellifera* and *Callitris preissii* forming a clumped, patchy cover. An understorey of predominantly *Guichenotia ledifolia*, *Acanthocarpus preissii* and *Stipa flavescens* occurred where the canopy species were sparse or absent (Wheeler 1993).

Saunders & de Rebeira (1983) list 16 resident bird species of heath/woodland habitats on Rottnest Island, of which seven (Red-capped Robin *Petroica goodenovii*, Golden Whistler *Pachycephala pectoralis*, Spotted Scrubwren* *Sericornis frontalis*, Singing Honeyeater *Meliphaga virescens*, Silvereye *Zosterops lateralis*, Western Gerygone *Gerygone fusca* and Welcome Swallow *Hirundo neoxena* were included in this study. Although some are omnivorous, they all take insect prey. Species not included were the Nankeen Kestrel *Falco cenchroides*, Indian Peafowl *Pavo cristatus*, Common Pheasant *Phasianus colchicus*, Banded Plover *Vanellus tricolor*, Spotted Turtledove *Streptopelia chinensis*, Laughing Turtledove *Streptopelia senegalis*, Richard's Pipit *Anthus novaeseelandiae*, White-fronted Chat *Ephthianura albifrons*, Grey Fantail *Rhipidura fuliginosa* and the Australian Raven *Corvus coronoides*. Given that our aim was to determine the extent of resource partitioning amongst the common resident insectivores we did not consider the omitted species a

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* Western subspecies of White-browed Scrubwren

serious problem since they either do not take insect prey (e.g. the turtledoves) or they were uncommon in the woodland during our study (e.g. raven, chat, fantail and kestrel).

Bird observations

Bird observations were made within 30 m each side of a north-south 900 m transect, four times each day (two morning and two afternoon transects) for four days each in May, June and July. The first transect each day was at sunrise (around 0600 h) in a north-south direction; the following three transects alternated in direction (second south-north, third north-south, last south-north). Generally the first two transects were completed by late morning (1100-1200), while the afternoon transects were from early afternoon (1230-1300) until sunset (around 1745). Repeating the same transect was unlikely to alter bird behaviour since observations were taken as unobtrusively as possible and birds are not easily disturbed by human presence (Tingay & Tingay 1984; Hutto & Mosconi 1990), even on repetitive transects (Frith 1984). Foraging height, foraging behaviour, foraging substrate and foraging plant associations (hereafter called the foraging dimensions) of all species were recorded. Separate observations were made for males and females of the sexually dimorphic Red-capped Robin and Golden Whistler. Hereafter we refer to 'bird categories' to indicate these separate observations for the males and females of these species; nine bird categories based on species and sex were recognised in all months.

The foraging height at which a bird captured its prey was recorded as: on the ground, at 0-1.5 m (above the ground but less than observer height), at 1.5-3.0 m (observer eye-level to twice observer height), at 3.0-4.5 m (above twice observer height but less than the tallest *Melaleuca* trees), or above 4.5 m (the height of the tallest *Melaleuca* trees, by reference to a nearby telephone pole). Eight foraging behaviour categories were adapted from Crome (1978), Ford et al. (1986) and Recher et al. (1985) and were defined as follows. Hawk: a flying bird captures a flying invertebrate from the air; Sally: a bird leaves a perch, captures an invertebrate from the air, and returns to the perch or one nearby; Snatch: a flying bird captures an invertebrate from a substrate other than air; Hover: a bird hovers in the air just before, or while, capturing invertebrate prey in any way; Glean: a perched bird captures an invertebrate from a nearby substrate; Pounce: a bird jumps or drops from its perch to capture an invertebrate prey from a

nearby substrate, and (generally) returns to its perch; Probe/tear: a bird inserts its beak into the substrate, or tears off pieces of the substrate, to capture an invertebrate prey; and Fruit/nectar: a bird uses a plant resource such as fruit, seed or nectar as a food source.

The Fruit/nectar classification was used to record all frugivorous behaviour since the use of plants by omnivorous birds was only of relevance in comparison to their insectivorous behaviour. Probe and Tear categories were grouped (as in Recher et al. 1985), since neither had enough observations to be considered separately.

Seven foraging substrates were recognised for each feeding episode: Ground, Trunk, Branch, Branch/Bark (branches with loose bark on their surface), Foliage, Air and Nectar/Fruit. The substrate recorded was that which the invertebrate prey was captured on (in) rather than that which the bird was on (in), e.g. a bird hawking an insect from the air used the air substrate, while one snatching an invertebrate from foliage used the foliage substrate. Plants upon which prey was captured were classified as: *Melaleuca lanceolata*, *Acacia rostellifera*, *Acanthocarpus preissii*, *Rhagodia baccata*, Others or No Plant, depending on the most abundant plant species; uncommon plants were combined in 'Others' and 'No Plant' covered foraging records in which prey was captured from a substrate other than plant. All successful and unsuccessful attempts to capture invertebrate prey were recorded in these categories.

Where possible each individual bird was recorded for five successive feeding events so that rare behaviours were more likely to be recorded (Morrison 1984), although such successive observations may be dependent (Gravatt 1970; Bell 1982). Thirty independent observations are recommended to represent the behaviour of a bird accurately (Morrison 1984). Birds that left the transect while still being studied were followed until five feeding observations were completed or until they were lost from sight; in all cases one of these events occurred within 20 m of the transect. A conscious attempt was made to scan all areas of the habitat so that intensity of observation was equal and inconspicuous behaviours as well as conspicuous ones were detected.

To prevent the same individual being observed twice on one transect, only birds ahead of the observer were recorded. Where ambiguity was present, only the initial sighting was recorded and five minutes were left before recording any further birds of that species. Where birds were feeding in flocks records were taken for as many individual birds as it was possible to identi-

fy. Where birds could no longer be identified as pre-recorded, observations ceased.

Statistical analyses

For each bird category the proportion of observations in each subset of each foraging dimension was recorded. To determine the similarity of overall foraging behaviour, overlap values were calculated for each pairwise combination of bird categories for each foraging dimension and each month using the formula $O_{ij} = \sum p$ min $(p_i$ or $p_j)$, where O_{ij} is the degree of overlap between species i and j, and p min is the smaller of the two proportions under comparison (Ricklefs & Cox

1977). Total foraging overlaps between each pair of bird categories for each month were calculated as the arithmetic mean of the overlaps for each dimension, as values were not completely independent (Wooller & Calver 1981). Overlap values greater than 0.6 were regarded as biologically significant (Schoener 1986).

Possible dependence of the observed frequencies of behaviours in each foraging dimension on the factors of bird category and month was determined with three-way G tests (Sokal & Rohlf 1969). The foraging specialisation of each bird category for each foraging dimension and each ▢h was further analysed using the Shannon-Wiener ▢ex $H' = \sum p_i \ln p_i$ (where $H' = $ di-

Table 1 The foraging height distribution by percentage and the foraging behaviour distribution by percentage for each bird category in May, June and July. N_1 = number of independent observations in each bird category and N_2 = number of dependent observations in each bird category. Dependent and independent observations were combined to calculate the values shown in Tables 1-4. Key to bird species: RCRM = Red-capped Robin (male); RCRF = Red-capped Robin (female); GWM = Golden Whistler (male); GWF = Golden Whistler (female); WG = Western Gerygone; SSW = Spotted Scrubwren; SHE = Singing Honeyeater; SE = Silvereye; and WS = Welcome Swallow.

Bird	Month	Foraging height (%)							Behaviour (%)							
		1	2	3	4	5	N_1	N_2	A	B	C	D	E	F	G	H
RCRM	May	77	12	10	0	1	40	123	13	41	43	1	0	2	0	1
	June	85	12	2	0	0	43	155	9	55	30	1	1	1	0	1
	July	92	6	1	1	0	46	186	4	46	46	0	0	1	0	2
RCRF	May	76	10	7	7	0	45	136	14	38	46	2	0	0	0	0
	June	85	11	4	1	0	40	121	6	70	15	2	0	0	0	7
	July	92	4	4	1	0	44	137	4	50	42	1	0	3	0	1
GWM	May	24	45	18	13	0	15	38	34	10	53	3	0	0	0	0
	June	9	24	43	24	0	21	46	13	11	35	11	0	32	0	0
	July	6	11	45	38	0	17	47	8	2	66	4	0	19	0	0
GWF	May	15	38	46	0	0	15	26	46	4	38	0	0	12	0	0
	June	12	42	21	25	0	13	24	29	8	38	4	0	21	0	0
	July	15	28	36	21	0	33	72	7	1	57	1	1	32	0	0
WG	May	0	14	51	35	0	32	124	6	0	33	2	0	2	0	56
	June	2	48	27	23	0	45	143	8	1	26	1	0	5	0	59
	July	0	22	58	20	0	41	156	2	0	31	0	0	9	0	58
SSW	May	21	29	29	21	0	34	140	1	0	90	0	9	0	0	0
	June	16	16	32	37	0	8	9	0	0	84	0	10	5	0	0
	July	49	33	15	2	0	25	85	0	0	92	0	8	0	0	0
SHE	May	4	30	21	44	0	31	92	37	1	23	12	0	1	26	0
	June	4	29	50	17	0	10	24	8	12	42	0	21	17	0	0
	July	8	40	11	40	0	12	37	3	0	89	3	0	5	0	0
SE	May	44	44	6	1	5	39	169	7	1	44	1	6	2	38	0
	June	18	56	5	21	0	40	159	2	1	67	0	3	0	26	1
	July	69	20	6	6	0	38	177	0	0	98	0	1	1	0	0
WS	May	0	33	17	50	0	10	8	100	0	0	0	0	0	0	0
	June	0	60	20	10	10	10	0								
	July	0	65	12	23	0	17	7								

Key to foraging heights: 1 = ground; 2 = 0-1.5 m; 3 = 1.5-3.0 m; 4 = 3.0-4.5 m; and 5 = > 4.5 m. Key to foraging behaviours: A = hawk; B = pounce; C = glean; D = sally; E = probe/tear; F = snatch; G = nectar/fruit; and H = hover.

versity in foraging and p_i = the proportion of observations in subset i). These values were then converted to a standardised range using the formula $J' = H' / H$ max (where J' = specialisation and H max = the H' value obtained when the observations are distributed equally across all subsets of the foraging dimension) (Crome 1978). J' values range between one and zero, with foraging specialisation increasing as J' falls. Kendall's rank coefficient of concordance test incorporating a correction for ties (Zar 1984) was then used to determine if the bird categories showed a similar rank order of specialisation in all foraging dimensions and across all months.

Results

Foraging sample sizes and foraging relationships

The number of independent observations (initial obser-

vations) and dependent observations (sequential observations) for each bird category and each month are shown as N_1 and N_2 respectively in Table 1. Although overall sample sizes were large, the minimum of 30 independent observations recommended by Morrison (1984) was not achieved in 12 of the 27 bird categories recorded. While this problem could have been overcome by combining data across all three months this might mask changes in bird behaviour with time, so we present the monthly data. This may mean that rare behaviour has not been recorded and conspicuous behaviour could have been over represented. All our analyses referred to below are based on total observations, both initial and sequential.

Table 1 shows the foraging height observations for each bird category during each month and observations of foraging behaviour for each bird category in each month. For the foraging height data, G tests (Sokal and

Table 2 The foraging substrate distributions by percentage and the foraging plant distribution by percentage for each bird category in May, June and July. Sample sizes and the key to bird species are given in Table 1.

Bird	Month	Substrate							Foraging plant (%)					
		A	B	C	D	E	F	G	1	2	3	4	5	6
RCRM	May	13	1	78	2	4	2	0	10	0	0	0	0	90
	June	10	2	85	1	2	0	0	2	0	2	0	0	95
	July	4	2	92	0	1	1	0	1	0	1	0	1	97
RCRF	May	15	6	75	1	3	0	0	10	0	1	0	0	90
	June	7	2	85	2	1	2	0	5	0	1	0	0	92
	July	5	1	92	1	0	1	0	4	0	3	0	1	96
GWM	May	37	3	24	7	21	7	0	39	0	0	0	0	60
	June	22	43	11	0	17	6	0	67	4	0	0	0	28
	July	13	34	6	2	32	13	0	81	0	0	0	0	19
GWF	May	46	4	19	12	0	19	0	35	0	0	0	0	65
	June	29	29	17	0	17	8	0	50	0	4	0	0	46
	July	8	25	15	4	35	12	0	74	0	1	0	1	24
WG	May	9	87	0	0	4	0	0	89	2	0	0	0	9
	June	8	87	3	0	2	0	0	76	1	10	0	1	12
	July	2	86	0	0	12	0	0	95	3	0	0	0	2
SSW	May	1	10	21	26	21	21	0	77	0	0	0	0	23
	June	0	0	5	11	26	58	0	95	0	0	0	0	5
	July	0	14	26	10	23	13	13	72	0	0	0	2	24
SH	May	48	11	4	3	4	2	26	18	0	1	26	0	54
	June	17	38	4	0	8	33	0	75	4	0	0	0	21
	July	3	42	6	0	0	49	0	60	0	11	11	3	16
SE	May	8	4	39	1	10	0	38	13	0	0	38	0	49
	June	2	38	18	1	4	11	26	31	0	14	26	9	19
	July	0	28	63	0	8	0	0	30	0	1	0	5	63
WS	May–July	100	0	0	0	0	0	0	0	0	0	0	0	100

Key to foraging substrates: A = air; B = foliage; C = ground; D = trunk; E = branch with bark; and F = fruit/flower. Key to foraging plants: 1 = *Melaleuca* sp.; 2 = *Acacia* sp.; 3 = *Acanthocarpus* sp.; 4 = *Rhagodia* sp.; 5 = Others; and 6 = No plants.

Rohlf 1969) showed that three factors — bird category, month and foraging height distribution — were strongly associated $\chi^2_{135} = 2163.9$, $P < 0.001$), as were two-way combinations foraging height distribution x bird category ($\chi^2_{32} = 2192.1$, $P < 0.001$), foraging height distribution x month ($\chi^2_8 = 80.0$, $P < 0.001$) and bird category x month ($\chi^2_{16} = 178.4$, $P < 0.005$). Foraging height distributions depended both on the bird category and the month when observations were taken; the relative abundance of different bird categories varied across months. Generalising across the three field months, Red-capped Robins foraged mainly on the ground; Golden Whistlers had a variable height range, with a slightly greater presence above the ground; Western Gerygones were prominent from 0-4.5 m above ground; Scrubwrens were widely spread over the whole height range up to 4.5 m, as were Singing Honeyeaters; Silvereyes were mostly on the ground to 1.5 m; Welcome Swallows did not forage on the ground and were spread mainly from 0-4.5 m.

For the foraging behaviour observations (Table 1), G tests showed that three factors — bird category, month and foraging behaviour distribution — were strongly associated ($\chi^2_{198} = 3294.0$, $P < 0.001$), as were the two-way combinations foraging behaviour distribution x bird category ($\chi^2_{56} = 2642.2$, $P < 0.001$), foraging behaviour distribution x month ($\chi^2_{14} = 324.1$, $P < 0.005$) and bird category x month ($\chi^2_{16} = 178.4$, $P < 0.005$). Foraging behaviour distributions therefore depended both on the bird category and the month when observations were made. Generalising across the three months, Red-capped Robins mainly pounced and gleaned; Golden Whistlers gleaned most of the time while snatching and hawking occurred slightly less often; Western Gerygones hovered for the majority of their foraging but also gleaned a lot; Scrubwrens gleaned mainly and probed a little, virtually to the exclusion of all other behaviours; Singing Honeyeaters predominantly gleaned, but hawked and ate fruit during May; Silvereyes also gleaned predominantly and ate large amounts of fruit in May and June; and Welcome Swallows hawked in all foraging observations.

Foraging substrate observations and foraging plant observations for each bird category during each month are shown in Table 2. Within the foraging substrate observations, G tests showed that three factors — bird category, month and foraging substrate distribution — were strongly associated ($\chi^2_{172} = 3435.3$, $P < 0.001$), as were the two-way combinations foraging substrate distribution x bird category ($\chi^2_{48} = 2701.1$, $P < 0.001$), for-

aging substrate distribution x month ($\chi^2_{12} = 171.4$, $P < 0.005$) and bird category x month ($\chi^2_{16} = 178.4$, $P < 0.005$). Thus the foraging substrate distributions observed depended on both the bird category and the month in which the observations were made. Generalising across the three months, Red-capped Robins pounced and gleaned mainly on the ground; Golden Whistlers foraged over a wide range of substrates, mostly on foliage and branches; Western Gerygones foraged mainly from foliage, Scrubwrens foraged on most substrates except air and fruit/flowers; Singing Honeyeaters foraged largely in the air and off foliage in May; Silvereyes foraged mainly off the foliage and the ground, with fruit/flowers observations important in May and June; Welcome Swallows foraged exclusively in the air.

Within the foraging plant observations (Table 2), G tests showed that three factors — bird category, month and foraging plant distribution — were strongly associated ($\chi^2_{146} = 2409.4$, $P < 0.001$), as were the two-way combinations foraging plant distribution x bird category ($\chi^2_{40} = 1819.1$, $P < 0.001$), foraging plant distribution x month ($\chi^2_{10} = 210.5$, $P < 0.001$) and bird category x month ($\chi^2_{16} = 178.4$, $P < 0.005$). Foraging plant distributions observed depended both on bird category and the month in which the observations were made. Generalising across the three field months, Red-capped robins pounced and gleaned mainly in the No Plant category; Golden Whistlers foraged mainly on *Melaleuca* but also in the No Plant category; Western Gerygones foraged on *Melaleuca*, with minor uses of several of the other plant categories; Scrubwrens foraged mainly on *Melaleuca*, with fewer records on the No Plant category; Singing Honeyeaters mostly foraged in the *Melaleuca* and No Plant categories for the majority of observations, but also in *Rhagodia* during May; Silvereyes were mainly in *Melaleuca* and No Plant, but also in *Rhagodia*, *Acanthocarpus* and Other in particular field months; Welcome Swallows were recorded exclusively in No Plant.

Foraging overlap

Table 3 displays overall foraging overlaps for each month, and values of biological significance (greater than 0.6, Schoener 1986), are in bold type. Although we do not present the overlap values in each foraging dimension, these may be calculated from Tables 1 and 2.

In May five of the total 36 possible overlap combinations (approximately 14%) were biologically significant; two of these were intraspecific overlaps (between

Table 3 Total foraging overlap for each month of the study. Total foraging overlaps > 0.6 are in bold type. The key to bird species is given in Table 1.

		RCRM	RCRF	GWM	GWF	WG	SSW	SHE	SE
RCRF	May	**0.951**							
	June	**0.931**							
	July	**0.640**							
GWM	May	0.572	0.589						
	June	0.329	0.283						
	July	0.254	0.258						
GWF	May	0.516	0.507	**0.796**					
	June	0.406	0.360	**0.826**					
	July	0.314	0.313	**0.846**					
WG	May	0.243	0.254	0.422	0.395				
	June	0.218	0.200	**0.636**	**0.608**				
	July	0.128	0.131	**0.618**	0.584				
SSW	May	0.374	0.388	**0.644**	0.562	0.498			
	June	0.196	0.165	0.553	0.525	0.462			
	July	0.406	0.400	**0.644**	**0.732**	0.433			
SHE	May	0.378	0.404	**0.633**	**0.625**	0.395	0.411		
	June	0.292	0.245	**0.842**	**0.743**	**0.656**	**0.671**		
	July	0.258	0.254	**0.681**	**0.654**	0.574	**0.642**		
SE	May	0.569	0.571	0.587	0.504	0.250	0.440	0.588	
	June	0.292	0.261	0.514	**0.606**	0.512	0.464	0.555	
	July	**0.649**	**0.636**	0.468	0.524	0.328	**0.704**	0.545	
WS	May	0.346	0.355	0.487	0.520	0.225	0.227	0.580	0.257
	June	0.321	0.302	0.292	0.455	0.264	0.128	0.280	0.236
	July	0.281	0.282	0.216	0.248	0.148	0.180	0.248	0.236

male and female Red-capped Robins and male and female Golden Whistlers), while three were interspecific. Nine overall foraging overlap values (25% of total) were of biological significance in June, of which two were intraspecific (male and female Red-capped Robins and Golden Whistlers) and seven interspecific. In July there were 11 biologically significant overall overlap values (30% of total); two of these values were intraspecific (male and female Red-capped Robins and Golden Whistlers), while the others were between different species.

However, in all months, several bird categories that did not overlap significantly in overall foraging did overlap significantly for particular foraging dimensions. For example, in May male Golden Whistlers and female Red-capped Robins overlapped significantly in foraging behaviour and foraging plant dimensions but did not overlap significantly overall. In June the Scrubwren and the Western Gerygone overlapped significantly in the foraging plant and foraging height dimensions but did not overlap significantly overall. In July the West-

ern Gerygone and female Golden Whistler overlapped significantly in the foraging plant and foraging height dimensions but not in overall foraging.

Foraging specialisation

The J' values of foraging specialisation for each bird category in each foraging dimension during each month, as well as an overall value for each bird category in each foraging dimension combining all months, are shown in Table 4. Values range from 0-1, with J' values close to zero indicating specialists and those close to one generalists.

Kendall's rank coefficient of concordance (Zar 1984) was used to test the hypothesis that the ranking of the J' values for the bird categories was the same in all four foraging dimensions, treating each month separately. Significant concordance was found for each month (May: $(\chi^2_r)_{4,9} = 17.6$, $P < 0.01$; June: $(\chi^2_r)_{4,9} = 18.2$, $P < 0.01$; July: $(\chi^2_r)_{4,12} = 33.0$, $P < 0.01$). These results show that for all three months, a bird which generalised in one foraging dimension, as shown by high J'

Table 4 Extent of specialisation by birds in each of four foraging dimensions in May, June and July, as shown by J' values. J' values range from 0-1, and specialisation increases as J' falls. The original data for each foraging dimension are shown in Tables 1 and 2, and a key to bird species is given in Table 1.

Dimension	Month	Bird species								
		RCRM	RCRF	GWM	GWF	WW	SSW	SHE	SE	WS
Behaviour	May	0.547	0.521	0.498	0.528	0.490	0.168	0.678	0.602	0.000
	June	0.537	0.460	0.698	0.677	0.528	0.258	0.719	0.217	0.000
	July	0.480	0.492	0.488	0.504	0.466	0.136	0.217	0.047	0.000
	All	0.530	0.531	0.630	0.508	0.503	0.169	0.737	0.445	0.000
Plant	May	0.179	0.199	0.373	0.360	0.229	0.300	0.583	0.548	0.000
	June	0.134	0.175	0.423	0.462	0.445	0.116	0.357	0.856	0.000
	July	0.101	0.110	0.273	0.383	0.131	0.371	0.660	0.481	0.000
	All	0.145	0.168	0.399	0.433	0.299	0.320	0.680	0.743	0.000
Substrate	May	0.403	0.426	0.787	0.700	0.238	0.821	0.724	0.685	0.000
	June	0.293	0.318	0.728	0.794	0.264	0.544	0.720	0.782	0.000
	July	0.177	0.184	0.778	0.822	0.231	0.796	0.417	0.428	0.000
	All	0.288	0.327	0.835	0.876	0.260	0.823	0.822	0.766	0.000
Height	May	0.450	0.496	0.795	0.629	0.615	0.852	0.735	0.548	0.628
	June	0.303	0.315	0.782	0.814	0.700	0.818	0.711	0.690	0.676
	July	0.187	0.218	0.709	0.831	0.601	0.678	0.731	0.559	0.543
	All	0.315	0.363	0.821	0.819	0.682	0.843	0.760	0.686	0.671

values, was also likely to generalise in the other foraging dimensions. For example, Singing Honeyeaters, generalists in the behaviour dimension throughout all three months, were also generalist in the plant, substrate and height dimensions. Conversely, male and female Red-capped Robins were specialists in the plant dimension (J' less than 0.2 in all months) but also tended to have low J' values in other foraging dimensions, indicating specialisation there as well.

Discussion

Resource partitioning reduces the effect of competition by decreasing the amount of overlap between the competing species (Wiens 1989), so the incidence of overlap amongst potential competitors may be used to assess whether resource partitioning is occurring. All bird categories in this study overlapped significantly with others in at least one foraging dimension for at least one month, and there was high intraspecific overlap in all foraging dimensions for male and female Red-capped Robins and Golden Whistlers. However, the pairings of Singing Honeyeaters with Golden Whistler males and Singing Honeyeaters with Golden Whistler females were the only interspecific combinations with significant overall foraging overlap for all months of the study, and significant associations occurred between

bird category and the distribution of foraging activities in all four foraging dimensions studied in each month. Thus, we consider that partitioning of foraging dimensions occurred. Most species were partitioning the insect food resource, assuming that the kinds of insects encountered by different foraging activities varied (Wiens 1989).

The changes in all foraging dimensions shown by many bird categories and the differences in the nature and extent of overlap within the bird assemblage from month to month throughout the study indicated that all aspects of foraging habits were plastic, probably varying in response to environmental conditions affecting bird behaviour and/or physiology (Osborne & Green 1992) or climatic changes affecting insect abundances (Wolda 1988, 1990). Given the changes which occurred in these factors over three winter months, it is likely that different seasons would also show different resource partitioning patterns.

Partitioning of an insect resource through different foraging habits has been reported in many Australian bird communities (e.g. Crome 1978; Noske 1979; Tullis et al. 1982; Recher et al. 1985; Ford et al. 1986; Recher et al. 1987) and seasonal variation is also known (Calver & Wooller 1981), so the Rottnest situation is no exception. However, the highest incidence of significant overall foraging overlap on Rottnest was 28% of

all overlaps, equal to the result reported by Wooller & Calver (1981) for a bird assemblage from wet sclerophyll forest and less than the results of 90% for overlap in overall habitat use and 38% for overlap in foraging behaviour reported by Crome (1978) for a rainforest bird assemblage. Although such comparisons must be made with caution because of differences in habitat and methods between the studies, they do suggest that the incidence of significant overlap between the island birds may be less than that for mainland assemblages, which are part of larger communities.

In general, the behaviour of the bird categories on Rottnest was consistent with other studies on the island or elsewhere on the mainland. Red-capped Robins were most likely to pounce and/or glean on the ground, agreeing with the observations of Saunders & de Rebeira (1985) for the Red-capped Robin on Rottnest Island and Stewart (1982) for the Australian mainland. Western Gerygones mainly hovered and gleaned in the foliage of *Melaleuca* trees, supporting observations of Saunders & de Rebeira (1985) on Rottnest Island and by Schodde (1982) on the mainland. Spotted Scrubwrens gleaned off nearly all substrates, at a range of heights on *Melaleuca* trees and on the ground. White-browed Scrubwrens on mainland Australia are thought to forage more often on the ground (Keast 1978), although gleaning is still its dominant foraging behaviour (Recher et al. 1985).

Singing Honeyeaters were found to be generalists, largely gleaning off the *Melaleuca* foliage and hawking at a range of heights, in common with many nectarivores/frugivores that use insects as a partial food resource (Paton 1980; Thomas 1980; Krebs 1985). Silvereyes mainly gleaned insects and foraged nectar/fruit at heights from the ground up to 1.5 m and Recher et al. (1985) also observed Silvereyes gleaning off the foliage on the Australian mainland. Welcome Swallows were specific insect hawkers at a range of heights, as found previously on Rottnest Island (Saunders & de Rebeira 1985) and on the Australian mainland (Ford et al. 1986).

Golden Whistlers have been recorded foraging on foliage and branches at Rottnest (Saunders & de Rebeira 1985) and on the mainland (Bell 1986), as they did in our study. However, the exact proportion of these behaviours varies in different environments, with Recher et al. (1985) reporting a large proportion of snatching from the foliage, while Ford et al. (1986) recorded both snatching and gleaning from the foliage. That Golden Whistlers were generalists in the Rottnest community is

evidence that their foraging habits can be modified in accordance with the environment and that generalists can adapt to environmental changes much more quickly than specialists (Thompson 1988). Slight changes in the proportions of different foraging behaviours by Golden Whistlers, presumably to suit changes in environmental conditions during different months, may also explain why the number of bird categories showing overall overlap with them changed between months.

We also found a high degree of overlap between male and female Golden Whistlers in all foraging dimensions in all months, contrary to the results of Bell (1986) who found sexual differences in their foraging behaviour in Eastern Australia. Bell suggested that these may have occurred to reduce intraspecific competition, and could have been facilitated by the lack of a bird with similar foraging habits in the community. On Rottnest Singing Honeyeaters had significant overall overlap with both Golden Whistler sexes for all three months. Intraspecific overlaps in Red-capped Robins were also high because sexual foraging differences in bird species are widespread (Hanowski & Niemi 1990), the lack of evidence for it on Rottnest suggests that intraspecific competition was not a significant factor for those island species that we studied.

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