

Feeding Segregation within an Assemblage of Small Birds in the Karri Forest Understorey

R. D. Wooller and M. C. Calver

School of Environmental and Life Sciences, Murdoch University, W.A. 6150.

Abstract

The feeding habits of small birds in the understorey of a wet sclerophyll forest near Pemberton, W.A., were studied in May of 1979 and 1980. Observations were made of the height and substrate at which birds fed, and the sizes and types of invertebrates eaten were determined by faecal analysis. None of the seven most common species showed more than 55% overlap with each other in all four of these feeding dimensions. It is suggested that the inference of diets from purely observational data may give misleading results. An attempt to estimate foraging overlap between birds from their morphological similarity was unsuccessful.

Introduction

Bird communities have proved to be useful systems for investigating the coexistence of species which utilize similar resources. Several studies have recently been made of resource partitioning within such communities in Australia, particularly those of honeyeaters (Recher and Abbott 1970; Recher 1971, 1977; Ford and Paton 1976; Halse 1978) and rainforest birds (Crome 1978). This paper deals with differences in the feeding habits of some small birds in the understorey of a wet sclerophyll forest during the non-breeding season.

Methods

This study site was an area of wet sclerophyll forest in the Big Brook State Forest near Pemberton, W.A., which has remained free from logging and fire for over 50 y. The dominant trees were karri *Eucalyptus diversicolor* and occasional marri *E. calophylla*, with an understorey of *Casuarina decussata*, *Bossiaea laidlawiana* and *Trymalium spathulatum*. The heights and densities of these plants are indicated in Table 3. Only the small, diurnal birds of the understorey were studied and observations were confined to the period 7-17 May in both 1979 and 1980.

Birds were caught in 20 mist nets, each 13 m long, placed along an overgrown track and operated for 6 days in each year. Each bird that was caught was kept in a box for at least 1 h to obtain a faecal sample. Before release a series of those measurements thought to be most relevant to the foraging habits of birds (Hespenheide 1973) were made on each individual: these were wing length, tarsus length, bill length, bill width and bill depth.

Observations of foraging birds were made at all times of day. No more than three observations were recorded for the same individual on any one occasion. The heights at which birds were seen foraging were recorded in terms of nine height categories. Birds were also allocated to five categories on the basis of the substrate upon which they were seen feeding: the ground, air, foliage, large branches and tree trunks. The information from both years proved to be essentially similar and was combined in all subsequent analysis.

Representative samples of the invertebrates present on the ground were obtained by hand sorting six 0.25-m² litter samples and from 40 pitfall traps operated for 8 days in 1980. Twenty plants each of *Bossiaea*, *Trymalium* and *Casuarina* were sampled with beating trays and sweep nets, and the bark of 20 *E. diversicolor* and *Casuarina* was sampled up to 5 m from the ground with a heavy-duty vacuum cleaner and also by hand. Flying insects were collected with a Malaise trap (Southwood 1978) but the sample was too small for further analysis.

The invertebrate remains within each faecal sample were identified to the level of order, or occasionally family, under a binocular microscope. This has been found to give a reasonable estimate of diet items for all except soft-bodied invertebrates (Bryant 1973). The sizes of invertebrates present in the faeces were assessed by reference to the invertebrate samples taken from the area.

Each of the four sets of data (foraging height and substrate; prey type and size) provided indices of overlap between each pair of the seven most common species in the area, calculated in the manner described by Ricklefs and Cox (1977). A single index of foraging overlap between each pair of species was constructed by taking the arithmetic mean of each set of four indices. The arithmetic, rather than the geometric mean was preferred because the four foraging parameters were not completely independent (Crome 1978). An index of morphological similarity between each pair of species was calculated in terms of bill dimensions and wing : tarsus ratio (Ricklefs and Cox 1977).

Table 1. The birds most commonly observed in the Big Brook study area and the total number of different individuals of each species captured in mist nets during 1979 and 1980

Species	No. of individuals caught
Inland thornbill, <i>Acanthiza apicalis</i>	38
White-browed scrubwren, <i>Sericornis frontalis</i>	35
White-breasted robin, <i>Eopsaltria georgiana</i>	26
Golden whistler, <i>Pachycephala pectoralis</i>	23
Red-winged fairy-wren, <i>Malurus elegans</i>	21
White-naped honeyeater, <i>Melithreptus lunatus</i>	17
Silvereye, <i>Zosterops lateralis</i>	15
New Holland honeyeater, <i>Phylidonyris novaehollandiae</i>	4
White-browed babbler, <i>Pomatostomus superciliosus</i>	4
Red-eared firetail, <i>Emblema oculata</i>	3
Red wattlebird, <i>Anthochaera carunculata</i>	3
Grey fantail, <i>Rhipidura fuliginosa</i>	2
Grey shrike-thrush, <i>Colluricincla harmonica</i>	2
Scarlet robin, <i>Petroica multicolor</i>	2
Collared sparrowhawk, <i>Accipiter cirrhocephalus</i>	1
Western rosella, <i>Platycercus icterotis</i>	0
Fan-tailed cuckoo, <i>Cuculus pyrrhophanus</i>	0
Laughing kookaburra, <i>Dacelo novaeguineae</i>	0
Rufous tree creeper, <i>Climacteris rufa</i>	0
Grey currawong, <i>Sirepera versicolor</i>	0

Results

Composition of the Community

The birds most frequently seen and caught in the study area are listed in Table 1. Recaptures within and between the two periods of study suggest that these species make up a relatively sedentary community within the understorey (Wooller and Milewski 1981). However, the agility of the grey fantail and the foraging heights of New Holland honeyeaters and red wattlebirds probably led to them being under-represented in the numbers caught. All silvereyes were caught as a single itinerant flock.

The most common birds in the community were either insectivores or honeyeaters, which are partly insectivorous. Most of the insectivores fed by searching substrates, but the grey fantail specialized in the pursuit of flying insects and the white-breasted robin pounced on ground-dwelling invertebrates.

Analysis of Faeces

Similar numbers of the common species were caught in both years, and the relative proportions of different types of invertebrates determined in their faeces were also very similar in both years (Table 2), except that spiders figured more prominently as diet items in 1980. Not surprisingly, the grey fantail ate many flies and wasps. The red-winged fairy-wren took relatively large numbers of ants and the white-browed scrubwren substantial numbers of spiders. The thornbill, fairy-wren, scrubwren, robin and whistler all showed extensive overlap in the types of invertebrates they consumed (see Table 6), resulting largely from the many beetles which they all eat. Of 22 samples from the white-naped honeyeater, only 13 contained any identifiable invertebrate remains, while most samples contained pollen grains.

Table 2. Percentage frequency distributions of invertebrate taxa found in the faeces of seven species of birds caught in the Big Brook study area during 1979 and 1980

Values are those for 1979 + 1980. Note that the taxon Hymenoptera includes all hymenopterans other than ants, which are shown separately

Taxon	<i>A. apicalis</i>	<i>M. elegans</i>	<i>S. frontalis</i>	<i>E. georgiana</i>	<i>P. pectoralis</i>	<i>M. lunatus</i>	<i>R. fuliginosa</i>
Coleoptera	72+51	41+18	55+44	49+32	31+50	40+17	21+25
Araneidae	2+7	0+7	31+37	2+20	0+25	0+33	0+0
Hymenoptera	7+15	8+7	4+8	5+11	11+8	0+0	26+42
Formicoidea	7+14	40+59	3+7	19+29	20+13	0+0	0+0
Diptera	2+3	0+7	0+4	9+3	19+0	20+17	53+33
Orthoptera	2+1	11+2	7+0	6+2	19+4	20+33	0+0
Hemiptera	2+5	0+0	0+0	0+1	0+0	20+0	0+0
Other	6+3	0+0	0+0	10+3	0+0	0+0	0+0
No. of birds	16+23	11+12	16+17	20+24	8+9	7+15	2+2
No. of insect samples	76+98	34+44	21+27	84+152	32+24	7+6	11+12

The range and proportions of invertebrate types present in samples taken from a variety of substrates are shown in Table 3. Very few flying insects were seen or caught. Many taxa appeared to be taken by the birds in approximately the proportions in which they occurred in our samples, although millipedes, centipedes, isopods and spiders did not occur in birds' faeces as often as might have been expected. However, the secretive habits of these invertebrates may make them less accessible to birds than other taxa, and some of them may be distasteful.

The lengths of diet items determined in the faeces of different species are given in Table 4. Not surprisingly the smaller birds took a higher proportion of small items, and there was substantial overlap in prey size between the thornbill, fairy-

wren and scrubwren, but the scrubwren took more small prey than the fairy-wren. Similarly, the robin and the whistler took prey of equivalent sizes but the whistler took rather more small items.

Table 3. Heights and densities of the most common plants in the Big Brook study area, and percentage frequency distributions of invertebrate taxa in samples from the substrates shown

	Ground litter	<i>Bossiaea</i>	<i>Trymalium</i>	<i>Casuarina</i> Foliage	Bark	Karri bark
Height (m)	—	2-5	2-5	10		25-40
Plants per 10 ³ sq m	—	239	90	49		9
Frequency distribution of:						
Coleoptera	12	34	27	24	26	14
Araneida	25	41	29	5	12	15
Formicoidea	6	—	11	27	48	3
Diplopoda	31	—	1	5	8	39
Chilopoda	4	—	—	—	1	10
Isopoda	7	2	4	—	1	4
Blattodea	2	1	—	7	3	4
Amphipoda	6	—	—	—	—	7
Hemiptera	1	5	—	32	—	—
Orthoptera	2	1	—	—	—	—
Diptera	—	5	6	—	—	—
Scorpionidea	1	—	—	—	1	4
Larvae	3	11	22	—	—	—
Invertebrate sample size	280	112	81	65	149	73

Table 4. Percentage frequency distribution of the lengths of the invertebrate prey items identified from the faeces of the seven most common birds in the Big Brook study area, and mean weights of these birds

Sample sizes as in Table 2

Species	Mean weight (g)	Length of prey item (mm)		
		<3	3-8	>8
<i>A. apicalis</i>	6.9	88	6	6
<i>M. elegans</i>	9.7	79	14	7
<i>S. frontalis</i>	11.3	92	8	0
<i>E. georgiana</i>	17.5	27	38	35
<i>P. pectoralis</i>	23.3	42	21	37
<i>M. lunatus</i>	16.2	100	0	0
<i>R. fuliginosa</i>	8.7	20	60	20

Observations on Foraging

The proportions of occasions on which birds were seen feeding at different heights and on different substrates are given in Table 5, and show that several species differed markedly in these dimensions. The robin fed mainly on the ground, the thornbill on the understorey foliage and branches, and the fairy-wren and scrubwren foraged at both locations. The fantail caught much of its food in the air but also on the ground, but the whistler and the babbler fed at higher levels.

Table 5. Percentage frequency distributions of the heights at which birds were observed foraging in the Big Brook study area, and of the substrates upon which they were foraging

Species	N	N, number of observations										Frequency of substrate (%)			
		0	0-1	1-2	2-5	5-10	10-15	15-20	20-25	>25	Ground	Air	Foliage	Branch	Trunk
<i>M. apicalis</i>	156	3	9	13	47	10	18	0	0	0	3	0	62	29	6
<i>M. elegans</i>	219	39	22	22	17	0	0	0	0	0	39	3	52	6	0
<i>S. frontalis</i>	98	31	10	29	27	2	1	0	0	0	31	0	39	25	5
<i>E. georgiana</i>	174	76	15	9	0	0	0	0	0	0	76	3	16	4	1
<i>P. pectoralis</i>	70	6	0	7	45	17	8	15	2	0	6	17	39	32	6
<i>M. lunatus</i>	140	1	1	6	11	16	25	23	14	3	1	3	37	28	31
<i>R. fuliginosa</i>	108	24	11	17	35	5	4	4	0	0	24	49	23	3	1
<i>P. superciliosus</i>	48	0	0	8	54	17	13	8	0	0	0	0	33	65	2
<i>P. novaehollandiae</i>	122	0	0	3	3	4	14	61	12	13	0	5	53	39	3
All species	1135	25	10	13	22	6	9	11	3	2	25	8	41	20	6

Table 6. Percentage overlap in foraging and morphology between each pair of the most common bird species

Overlap calculated separately for: FH, foraging height; FS, foraging substrate; PT, prey type; PS, prey size; FO, overall foraging overlap; MS, morphological similarity. All values for overlap were calculated by the method of Ricklefs and Cox (1977)

		<i>A. apicalis</i>	<i>M. elegans</i>	<i>S. frontalis</i>	<i>E. georgiana</i>	<i>P. pectoralis</i>	<i>M. lunatus</i>
<i>M. elegans</i>	FH	42					
	FS	61					
	PT	55					
	PS	91					
	FO	62					
	MS	56					
<i>S. frontalis</i>	FH	55	80				
	FS	72	76				
	PT	69	49				
	PS	94	87				
	FO	72	73				
	MS	62	44				
<i>E. georgiana</i>	FH	21	63	50			
	FS	24	62	52			
	PT	73	72	68			
	PS	39	48	35			
	FO	39	61	51			
	MS	27	38	47			
<i>P. pectoralis</i>	FH	73	30	43	13		
	FS	77	54	75	30		
	PT	71	66	70	85		
	PS	54	63	50	83		
	FO	69	53	59	53		
	MS	5	5	13	42		
<i>M. lunatus</i>	FH	47	19	22	8	59	
	FS	72	47	68	25	75	
	PT	37	38	52	46	57	
	PS	88	79	92	27	42	
	FO	61	46	58	26	58	
	MS	9	0	36	48	42	
<i>R. fuliginosus</i>	FH	69	69	81	44	61	32
	FS	30	54	51	47	50	31
	PT	38	34	31	36	42	41
	PS	32	41	28	78	61	20
	FO	42	49	48	51	53	31
	MS	33	29	27	28	17	23

Both honeyeaters foraged mainly in the understorey canopy, but the New Holland honeyeater fed at a higher level and concentrated more on foliage than the white-naped honeyeater.

Overall, foraging heights reflected the vertical stratification of vegetation in the forest, with peaks at the level of the ground and the understorey foliage. Observations of foraging in the higher strata may be slightly under-represented because of difficulty of observations.

Foraging Overlap

Indices of overlap for each of the four parameters measured are shown for each pair of the seven most common species in Table 6. Some species overlapped greatly in one dimension but not in others. Thus the whistler and the robin showed substantial overlap in the type and size of food taken (85 and 83%) but far less overlap in foraging height (13%) or substrate (30%). The fantail and the scrubwren foraged at similar heights (81%) but on different substrates (51%) and took different prey (31%) of different sizes (28%). However, some pairs of species were very similar in all aspects. The thornbill showed more than 50% overlap in all four dimensions with both the scrubwren and the whistler.

For the 21 pairs of species compared, foraging substrate overlap was significantly correlated with overlap in prey size ($r_{19} = +0.46$; $P < 0.05$) but not with overlap in prey type ($r_{19} = +0.12$). Foraging height overlap was not correlated with overlap in either prey size or prey type.

Morphological Similarity

The similarity between each pair of species, in terms of their bill, wing and leg dimensions, is shown in Table 6. Not surprisingly, the thornbill, scrubwren and fairy-wren were morphologically similar; these species also showed considerable foraging overlap. However, the thornbill was also very similar to the whistler and the honeyeater in its feeding habits, but was morphologically very dissimilar to these two species. There was no significant relationship between morphological similarity and overall foraging overlap ($r_{19} = +0.16$). None of the four indices of foraging overlap showed a significant relationship with overlap in either bill dimensions or wing : tarsus ratios.

Discussion

The composition of the bird community studied was very similar to that detailed by Kikkawa (1968) for a wet sclerophyll forest in New South Wales during the non-breeding season. In both cases, most species were insectivores with relatively few nectarivores, frugivores and granivores, and this probably reflects the food resources available. Even the resident honeyeaters had fairly short bills and fed extensively on insects.

Since this study was restricted to the non-breeding season the results obtained may not apply to other times of year. Analysis of the invertebrates eaten showed selective feeding by certain birds and some attempt to partition the food resources. It is not surprising that beetles formed a large part of the diet of many birds, because they made up at least 12% by number of the invertebrates sampled from each substrate. Indeed, birds may actively favour beetles because they are not difficult to detect or catch, and they yield more energy per unit ash-free dry weight

than other insect orders (Beaver and Baldwin 1975), which is a measure of the energy return from digestible material. This may explain why thornbills, which foraged intensively on foliage where bugs are numerous, nonetheless ate many beetles but few bugs.

In contrast, spiders were not eaten in the proportions in which they occurred, which probably reflects their secretive habits; only the scrubwren fed extensively on spiders. Ants were extensively utilized, particularly by fairy-wrens, probably because ants have an aggregated distribution and an exposed life-style. Only the fantail specialized in taking flying insects such as flies and wasps.

The birds differed not only in their diets but also in their use of foraging space. Although all species considered restricted their feeding to the understorey, many showed preferences for particular heights and substrates within that zone. The robin, fairy-wren and scrubwren frequently foraged on the ground, but other species particularly the honeyeaters, preferred higher levels. This separation by height sometimes, but not always, led to birds taking different types of prey. The extent of segregation is revealed by the values for foraging overlap.

No pair of species showed an overlap of more than 55% in all four dimensions measured, and only three pairs of species had an overall foraging overlap of more than 65%. The scrubwren showed considerable overlap with both the thornbill and the fairy-wren, and the thornbill also had a high overlap with the whistler. However, although this last pair overlapped greatly in height, substrate, and prey type, they showed only moderate overlap in prey size. The scrubwren and the fairy-wren fed on prey of similar size and at a similar height, but the scrubwren specialized on spiders and the fairy-wren on ants.

The overlap between the scrubwren and the thornbill is harder to explain. Although they foraged at slightly different heights (55% overlap), they were very similar in the other aspects considered. Such situations have often been interpreted to mean that the birds are minimizing competition for food by foraging at different heights. Cody (1974) argued that where species differed in preferred foraging height but had similar diets, the diet overlap was spurious and had no real relationship to the foraging overlap of the birds. This view assumes that insects are also distributed in vertical zones and that these zones exactly parallel those of the birds. However, if insects were distributed in a pattern overlapping the different foraging zones of bird species, then it would be possible for two species of birds, apparently segregated by foraging height, to feed on the same type of prey. Since each species would influence the number of insects available to the other, there would still be competition for food between them.

The robin and the whistler also overlapped greatly in the type and size of food eaten but not in foraging height or site. Although these two species are segregated in terms of foraging space, they are still eating the same food. The problem of avoiding competition for food by feeding in different places is further complicated by the life histories of many insects. Although the larvae and the adults of the same species of insect may be taken by different birds from different substrates, the birds will still be in competition. The same species of insect may be taken by one bird while flying but another bird may glean it from bark. The apparent separation on the basis of foraging behaviour and site disguises competition for food in such cases.

Spatial segregation may result, in part, from the need to avoid interference from other foraging birds. Charnov *et al.* (1976) have suggested that birds feeding in an area cause invertebrates to hide or escape, so that other birds attempting to feed in the area soon afterwards are poorly rewarded. This is the phenomenon of resource depression, and can be avoided by species either segregating spatially or forming mixed-species flocks. Resource depression may underlie the spatial separation of the whistler and the robin or that of the thornbill and the scrubwren. The problem is minimized in the case of the fairy-wren and the scrubwren by differences in their major prey. Spiders are secretive and cannot hide further while birds forage nearby, whereas ants are forced to expose themselves. Thus fairy-wrens and scrubwrens can forage in the same area. Resource depression by conspecifics would be largely avoided by the evident territoriality of the species studied (Wooller and Milewski 1981).

It is evident, therefore, that there are problems involved in inferring the diets of birds from observational data, and that it may be better to infer feeding behaviour and site from diet analysis, as was done by Orians and Horn (1969). However, it is important that workers distinguish the same insect types as the birds. Hespeneide (1971) has shown that the behaviour of the prey was the crucial factor in prey selection by flycatchers, and further suggested that the characteristics of a species' preferred invertebrate prey may influence its niche width (Hespeneide 1975).

The attempt to estimate foraging overlap between birds from their morphological similarity was largely unsuccessful. Although morphology would undoubtedly separate such disparate forms as finches, parrots, honeyeaters and flycatchers, it was not a reliable predictor of foraging overlap for the group of insectivores studied. This may be because species with similar morphologies can still exhibit great plasticity in foraging behaviour.

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References

- Beaver, D. L., and Baldwin, P. H. (1975). Ecological overlap and the problem of competition and sympatry in Western and Hammond's flycatchers. *Condor* 77, 1-17.
- Bryant, D. M. (1973). The factors influencing the selection of food by the House Martin (*Delichon urbica* (L.)). *J. Anim. Ecol.* 42, 539-64.
- Charnov, E. L., Orians, G. H., and Hyatt, K. (1976). Ecological implications of resource depression. *Am. Nat.* 110, 247-59.
- Cody, M. L. (1974). 'Competition and the Structure of Bird Communities.' (Princeton University Press.)
- Crome, F. H. J. (1978). Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. *Aust. J. Ecol.* 3, 195-212.
- Ford, H. A., and Paton, D. C. (1976). Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Aust. J. Ecol.* 1, 281-7.

- Halse, S. A. (1978). Feeding habits of six species of honeyeater in south-western Australia. *Emu* **78**, 145-8.
- Hespenheide, H. A. (1971). Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. *Ibis* **113**, 59-72.
- Hespenheide, H. A. (1973). Ecological inferences from morphological data. *Annu. Rev. Ecol. Syst.* **4**, 213-29.
- Hespenheide, H. A. (1975). Prey characteristics and predator niche width. In 'Ecology and Evolution of Communities'. (Eds M. L. Cody and J. R. Diamond.) pp 158-80. (Belknap Press: Harvard.)
- Kikkawa, J. (1968). Ecological association of bird species and habitats in eastern Australia: similarity analysis. *J. Anim. Ecol.* **37**, 143-65.
- Orians, G. H., and Horn, H. S. (1969). Overlap in foods and foraging of four species of blackbirds in the potholes of Washington. *Ecology* **50**, 930-8.
- Recher, H. J. (1971). Sharing of habitat by three congeneric honeyeaters. *Emu* **71**, 147-52.
- Recher, H. J. (1977). Ecology of co-existing White-cheeked and New Holland Honeyeaters. *Emu* **77**, 136-42.
- Recher, H. J., and Abbott, I. J. (1970). Some differences in use of habitat by White-eared and White-cheeked Honeyeaters. *Emu* **70**, 117-25.
- Ricklefs, R. E., and Cox, G. W. (1977). Morphological similarity and ecological overlap among passerine birds on St Kitts, British West Indies. *Oikos* **29**, 60-6.
- Southwood, T. R. E. (1978). 'Ecological Methods.' (Chapman and Hall: London.)
- Wooller, R. D., and Milewski, A. V. (1981). Site fidelity in some birds of the understorey in karri forest. *Emu* **81**, in press.