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The Invertebrate Diets of Small Birds in *Banksia* Woodland near Perth, W.A., during Winter

K. J. Tullis, M. C. Calver and R. D. Wooller

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

Abstract

Honeyeaters were the most abundant birds in *Banksia* woodland in winter, and all species ate insects. Short-billed honeyeaters and non-nectarivores took mostly beetles, ants and bugs by gleaning, whereas long-billed honeyeaters fed more on nectar and caught mostly flies and wasps by hawking. Short-billed species segregated in their foraging heights, prey types and sizes. Long-billed species, however, overlapped considerably in these respects and all took similar small insects whose capture they may have had to subsidize with energy from nectar.

Introduction

In a recent review of foraging by honeyeaters (Meliphagidae), Pyke (1980) noted that all species were known to eat insects, but that some genera were more insectivorous than others. Quantitative information on the diets of honeyeaters has been collected almost entirely by observation. Some stomach contents have been analysed, but this work has either been opportunistic (Lea and Gray 1935) or directed towards a specific prey type taken by one species (Matthiessen and Springett 1973).

This paper presents some information on the diets of honeyeaters and other small passerines in *Banksia* woodland near Perth in Western Australia, during late autumn and winter. In addition to observations of the heights and methods by which insects were captured, the types and sizes of invertebrates eaten were determined from the faeces of birds caught. The diets of different honeyeaters were compared not only with other honeyeaters but also with the diets of wholly insectivorous birds in the area.

Study Area and Methods

The study area was that used by Davidge (1979) and is described in detail by Milewski and Davidge (1981). It was an extensive area of relatively homogeneous and undisturbed mature *Banksia* woodland on a Bassendean dune at Jandakot, near Perth. The community was co-dominated by trees of *Banksia menziesii* and *B. attenuata*, 4–5 m high, over a floristically diverse heath layer (0·5–1 m), consisting mainly of plants in the Proteaceae, Myrtaceae and Epacridaceae. Bushes of *Adenanthos cygnorum* up to 3 m high were widespread throughout the area, together with occasional trees of *Banksia littoralis*, *B. ilicifolia* and *Eucalyptus* spp. Total projected foliage cover was 60%.

The climate was mediterranean with a warm to hot dry season from October to April. Observations of feeding birds were made from April to July in 1980, so as to minimize any effects on behaviour or diet occasioned by breeding or climatic changes. Although honeyeaters, especially, sometimes breed in autumn in mediterranean areas, there was no evidence of this in our study. During this period

Adenanthos, Banksia menziesii and *B. littoralis* were in flower and produced substantial amounts of nectar.

Birds were mist-netted at the same time as observations were made, and faecal samples obtained from them. The method of faecal analysis and the possible biases associated with it are discussed in Wooller and Calver (1981). Most birds were caught in the morning when birds fed most actively. All birds caught were weighed, and measurements taken of their bill lengths (to the base of the skull) and bill depths (at the feathering).

Results

Although the relative numbers of birds varied considerably from day to day and during the study period, the most common birds in the area were the honeyeaters and the silvereye (Table 1). All nectarivores, including the silvereye, will henceforth be called honeyeaters, and the other species will be termed insectivores. All the common species were caught in reasonable numbers except for red and little wattlebirds, which flew too high for the nets. Hooded robins and rainbow bee-eaters were only transient members of the community.

Table 1. The birds seen and caught in the *Banksia* woodland study area near Murdoch, W.A., from March to June

Species are ranked from 5 (most abundant) to 1 (least abundant)

Species	Abundance
White-cheeked honeyeater, *Phylidonyris nigra*	5
Silvereye, *Zosterops lateralis*	4
Brown honeyeater, *Lichmera indistincta*	4
Western spinebill, *Acanthorhynchus superciliosus*	4
Singing honeyeater, *Meliphaga virescens*	3
Little wattlebird, *Anthochaera chrysoptera*	3
Red wattlebird, *Anthochaera carunculata*	3
Splendid fairy-wren, *Malurus splendens*	3
Tawny-crowned honeyeater, *Phylidonyris melanops*	2
Rufous whistler, *Pachycephala rufiventris*	2
Yellow-rumped thornbill, *Acanthiza chrysorrhoa*	2
New Holland honeyeater, *Phylidonyris novaehollandiae*	2
Western thornbill, *Acanthiza inornata*	2
Inland thornbill, *Acanthiza apicalis*	2
Grey fantail, *Rhipidura fuliginosa*	2
Varied sittella, *Daphoenositta chrysoptera*	2
Black-faced woodswallow, *Artamus cinereus*	2
Western gerygone, *Gerygone fusca*	1
Grey shrike-thrush, *Colluricincla harmonica*	1
Scarlet robin, *Petroica multicolor*	1
Red-capped robin, *Petroica goodenovii*	1
Hooded robin, *Melanodryas cucullata*	1
Rainbow bee-eater, *Merops ornatus*	1
Shining bronze-cuckoo, *Chrysococcyx lucidus*	1
Painted button-quail, *Turnix varia*	1
Yellow-plumed honeyeater, *Lichenostomus ornatus*	1

The honeyeaters that fed furthest from the ground (the white-cheeked and New Holland honeyeaters) caught most of their insects in the air, by hawking (Table 2). Silvereyes and singing honeyeaters fed closer to the ground and spent more time gleaning. The western spinebill and the brown honeyeater, which fed in the intermediate zones, were the least insectivorous honeyeaters. Apart from the grey fantail, a specialist aerial flycatcher, the insectivores took more insects by gleaning.

Table 2. The percentage frequency distributions of heights at which the most common birds were observed feeding, the percentage taking insects and percentage which did so by hawking
N, number of observations

Species	*N*	Foraging height (m)					Percentage	
		Ground	1	2–3	4–6	>6	Insect feeding	Hawking
Silvereye	406	34	23	9	30	4	60	20
Singing honeyeater	103	22	28	21	27	2	52	32
Western spinebill	137	20	27	35	17	1	20	39
Brown honeyeater	252	14	40	20	25	1	30	27
White-cheeked honeyeater	204	7	15	22	41	15	49	72
New Holland honeyeater	270	5	24	20	33	18	66	75
Splendid fairy-wren	415	56	20	8	14	2	100	17
Western thornbill	179	12	32	27	29	0	100	6
Yellow-rumped thornbill	171	36	6	25	33	0	100	9
Rufous whistler	33	6	27	33	34	0	100	30
Grey fantail	141	3	20	46	31	0	100	86
Varied sittella	25	0	4	52	44	0	100	4
Inland thornbill	97	4	4	17	63	12	100	53

Table 3. The percentage frequency distributions of invertebrate taxa identified in the faeces of the most common birds
C, Coleoptera; D, Diptera; F, Formicoidea; Hy, other Hymenoptera; He, Hemiptera; O, others

Species	Birds caught	Invertebrates identified	Percentage of invertebrates					
			C	D	F	Hy	H	O
White-cheeked honeyeater	46	107	10	28	11	49	1	1
New Holland honeyeater	4	15	13	27	40	7	13	0
Western spinebill	30	80	6	20	34	36	3	1
Brown honeyeater	22	54	6	11	57	26	0	0
Tawny-crowned honeyeater	4	37	0	5	46	46	3	0
Singing honeyeater	9	88	2	2	81	12	2	1
Little wattlebird	3	20	0	0	85	10	5	0
Silvereye	40	236	22	9	37	5	1	26
Varied sittella	4	100	81	0	12	1	4	2
Splendid fairy-wren	19	494	7	1	84	4	2	2
Grey fantail	11	49	27	69	0	2	2	0
Western thornbill	2	19	16	0	11	0	73	0
Yellow-rumped thornbill	5	44	26	12	6	9	38	9
Rufous whistler	8	67	40	3	7	7	28	15

The types of invertebrates identified in the faeces of birds caught are given in Table 3. The silvereye had a more diverse insect diet than any of the honeyeaters. All the nectarivores ate many ants as well as substantial numbers of flies and wasps, except for the two largest species, which ate mainly ants. The greater sizes of singing honeyeaters and little wattlebirds may make them inefficient at hawking for insects. Apart from the grey fantail, a specialist hawker, the insectivores had far fewer wasps and flies in their faeces than the honeyeaters. This would be expected from the observational data which showed that insectivores gleaned for insects more than did honeyeaters.

Many honeyeaters showed a wide range of insect types in their faeces, but the insectivores showed a tendency to specialize on one prey type. Thus sittellas took mainly beetles, fairy-wrens mostly ants, fantails specialized on flies and the western thornbill on bugs. Those honeyeaters which observations showed to be most insectivorous also had a high arthropod content in their faeces (Table 3).

The silvereye and the singing honeyeater took larger prey than the other honeyeaters (Table 4). These two species were among the most insectivorous members of this group (Table 2) and are known to take substantial numbers of

Table 4. The percentage frequency distributions of prey sizes in the faeces of some birds in *Banksia* woodland, and the mean masses, bill length and bill depths of these birds

Species	Percentage items of prey length 0–2 mm	2–4 mm	4–6 mm	>6 mm	Mass (g)	Bill length (mm)	Bill depth (mm)
New Holland honeyeater	47	40	12	1	19·3	21·5	4·6
White-cheeked honeyeater	37	49	11	3	18·2	24·8	4·5
Brown honeyeater	41	51	4	4	10·6	17·7	3·6
Western spinebill	41	52	7	0	9·7	22·2	3·0
Silvereye	32	41	17	10	8·9	11·3	3·7
Singing honeyeater	3	62	10	25	25·2	18·7	4·8
Western thornbill	42	41	9	8	6·2	10·3	2·7
Inland thornbill	31	47	9	13	7·0	10·7	3·0
Yellow-rumped thornbill	37	37	11	15	8·8	11·2	3·4
Splendid fairy-wren	10	33	40	17	9·3	9·9	3·0
Grey fantail	7	39	26	28	9·8	11·6	2·7
Varied sittella	47	36	6	11	14·7	14·9	4·1
Hooded robin	0	21	29	50	20·9	12·7	4·4
Rufous whistler	0	0	17	83	24·7	13·9	5·6

berries at some times of the year (Pyke 1980; personal observations). Their bills were only about three or four times longer than they were deep, similar to the bills of the insectivores, whereas the other honeyeaters had bills from five to seven times longer than their depth. These long-billed honeyeaters all took insects of similar small size (Table 4). If the hawking grey fantail is excluded, the insectivores showed a clear correlation between the size of a bird and the size of its prey ($r_4 = +0 \cdot 949$; $P < 0 \cdot 01$). This trend was not apparent in honeyeaters.

Values for the overlap between pairs of honeyeaters and insectivores were calculated for foraging height, prey type and prey size, by the method outlined in Ricklefs and Cox (1977). These values are shown in Table 5. The insectivores overlapped less (65%) than the honeyeaters (75%) in their foraging heights ($t_{28} = 6 \cdot 75$ after angular transformation of percentages; $P < 0 \cdot 001$). Insectivores also overlapped less (58%) than honeyeaters (79%) in the sizes of prey they ate ($t_{28} = 5 \cdot 75$; $P < 0 \cdot 001$). Although the honeyeaters showed more overlap in types of prey eaten (58%) than insectivores (36%), this difference was not statistically significant ($t_{28} = 0 \cdot 49$).

Table 5. Percentage overlap between pairs of honeyeaters and insectivores in their foraging heights (FH), prey types (PT) and prey sizes (PS)

(*a*) Honeyeaters

		Silvereye	Singing honey-eater	Western spinebill	Brown honeyeater	White-cheeked honeyeater
Singing honeyeater	FH	83				
	PT	48				
	PS	64				
Western spinebill	FH	70	86			
	PT	56	53			
	PS	80	62			
Brown honeyeater	FH	72	88	79		
	PT	57	73	77		
	PS	87	62	96		
White-cheeked honeyeater	FH	65	72	62	68	
	PT	37	30	75	54	
	PS	87	65	93	93	
New Holland honeyeater	FH	71	78	67	75	88
	PT	65	53	70	64	56
	PS	85	54	88	86	89

(*b*) Insectivores

		Splendid fairy-wren	Western thornbill	Yellow-rumped thornbill	Rufous whistler	Grey fantail
Western thornbill	FH	56				
	PT	20				
	PS	60				
Yellow-rumped thornbill	FH	66	72			
	PT	22	60			
	PS	69	91			
Rufous whistler	FH	48	89	70		
	PT	23	51	79		
	PS	34	17	26		
Grey fantail	FH	45	79	65	87	
	PT	12	18	42	34	
	PS	83	63	70	45	
Varied sittella	FH	26	60	62	71	84
	PT	24	31	39	54	30
	PS	60	92	90	17	60

Discussion

In common with those of other studies (Collins 1980; Pike 1980) our results showed that all honeyeater species in the area took insects, although nectar was available from several plant species during the study period. Estimates of the degree of insectivory and the types of insects present in the faeces were very similar to those obtained by observation, suggesting that any bias in observational data is slight.

Ford and Paton (1977) and Pyke (1980) have suggested that honeyeaters may be divided into two different types. Long-billed species in the genera *Acanthorhynchus*, *Lichmera* and *Phylidonyris* feed on nectar more than insects, and catch mostly small flies and wasps by hawking. Shorter-billed species in the genera *Lichenostomus* and *Meliphaga* feed more on insects than nectar, and glean beetles and bugs from leaves and bark. The results of our study agreed very closely with this scheme. On this basis, the silvereye, a non-meliphagid nectarivore, was clearly a member of the second group. The substantial number of ants eaten by honeyeaters may be taken at nectar sources, where many ants also feed.

The short-billed honeyeaters were closer to the insectivores than to other honeyeaters in their foraging behaviour and the types and sizes of insects eaten. They showed less overlap with each other in their foraging behaviour and diet than did other honeyeaters, possibly a result of competition for a limited resource. In contrast, the long-billed honeyeaters all ate similarly small insects taken in a similar manner.

Recher and Abbott (1970) and Ford and Paton (1976) have suggested that long-billed honeyeaters take insects as a source of protein and that they subsidize the energetically expensive capture of these insects with energy obtained from nectar. This model probably applies to the four smallest long-billed honeyeaters in our study (and perhaps the wattlebirds also) since the energetic returns from the small insects eaten would be unlikely to justify the cost of hawking for them.

There are at least three possible ways in which this situation may have been produced. The long-billed honeyeaters may take insects in proportion to their relative abundances. Since small insects are much more common than larger ones this is reflected in their diet. However, small insects require an energy subsidy and can therefore be taken only by honeyeaters, other insectivores being forced to take larger insects whose energy return justifies their capture.

Secondly, honeyeaters may be less efficient than other insectivores at catching insects and be forced to take the energetically expensive, but abundant, small insects whose capture they subsidize with nectar. Thirdly, the long bills of honeyeaters, which allow them to exploit nectar so efficiently, may not enable them to handle larger insects very effectively, resulting in a preference for smaller insects. Further work may reveal that all of these factors are involved.

Short-billed honeyeaters are sometimes found in areas where there is little obvious nectar, which suggests that they can live largely on insects and fruit if necessary. Alternative sources of carbohydrates, such as manna and honeydew (Paton 1980) may also be used. It would be interesting to know whether short-billed honeyeaters always require an energy subsidy from some carbohydrate food, or whether they are able to obtain all their energetic needs from the larger insects they eat.

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