

## Winter foraging patterns in the avifauna from south-western Australia with special reference to niche differentiation in the Acanthizidae and Meliphagidae

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**Abstract.** Winter foraging patterns of birds were documented at eight eucalypt-dominated sites along an aridity gradient, in south-western Australia, during 2004 and 2006. Trees were the dominant foraging stratum, accounting for 74% of all records. Gleaning comprised 69% of all foraging observations, and tended to increase with increasing aridity. Honeyeaters utilised both nectar and insects throughout the gradient. The Western Thornbill (*Acanthiza inornata*) and Weebill (*Smicrorhis brevirostris*) both favoured the tree stratum, the Chestnut-rumped (*A. uropygialis*) and Inland (*A. apicalis*) Thornbills favoured the shrub layer, and the Yellow-rumped Thornbill (*A. chrysorrhoa*) favoured the ground layer. Honeyeaters almost never foraged on the ground and 64% of species favoured the tree layer. Bird activity was highest in morning surveys. Spatial distribution patterns and measures of niche breadth and overlap in Acanthizidae and Meliphagidae are used to document possible patterns of competitive exclusion and niche differentiation.

**Keywords.** Acanthizidae, annual and diurnal variation, foraging ecology, Meliphagidae, niche breadth, niche overlap

### Introduction

The foraging ecology of bird communities can be described by various means, including vegetation/habitat strata utilised, types of foraging substrates, types of food resources taken and the mode of prey acquisition. In most bird assemblages, continuing coexistence of closely related species is due to the evolution of variation in utilisation of different resources (Cody 1974; Ford 1989). Closely related, co-existing species have been shown to differentially utilise available habitat (Bell 1985; Bell and Ford 1986; Recher 1989). Variations in avian assemblages and foraging patterns have previously been reported between times of the day (Craig and Roberts 2001; Timewell and Mac Nally 2004), seasons (Collins and Briffa 1982; Wilson and Recher 2001) and years (Maron *et al.* 2005). Inter-

specific relationships have also been shown to vary in time (Timewell and Mac Nally 2004), environmental conditions (Bell 1985) and vegetation structure (Crome 1978; Frith 1984). Foraging profiles of several individual communities in Western Australia have been described, highlighting niche differentiation among species within bird assemblages (Recher and Davis 1997, 1998, 2002). Large, closely related groups of species often show niche differentiation. The insectivorous thornbills (Acanthizidae) and the nectarivorous and insectivorous honeyeaters (Meliphagidae) have been studied in eastern Australia and have been shown to display segregation (Ford and Paton 1976, 1977; Bell 1985; Recher 1989). However, there has been only limited emphasis on niche differentiation in members of these groups in Western Australia. While Bell *et al.* (2007) described bird assemblages along a 625 km aridity gradient in south-western Australia, the present study documents aspects of bird foraging interactions over this same broad geographic gradient.

The objectives of this study were: 1) to determine stratum, foraging action, substrate and resource preferences in the foraging ecology of bird species along an



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aridity gradient in south-western Western Australia; 2) to determine whether changes exist in the foraging preferences of species over the gradient; 3) to measure niche breadth and overlap relationships within the Western Australian Acanthizidae and Meliphagidae; and 4) to assess differences in the diurnal foraging ecology of species in these two well-represented families.

## Methods

### Study Sites

Observations were made at eight sites (see Bell *et al.* 2007 for site details) along a straight-line distance of 625 km (825 km by road) and an annual mean precipitation gradient from 1050 mm at Mundaring in the west, to 230 mm at Leinster in the east (Table 1). Observations were made during 2004 and 2006 from mid-July to mid-August. Rainfall prior to the 2006 observations was significantly lower than that in 2004 (Bell *et al.* 2007).

### Sampling

At each sampling site, foraging data were collected over six separate two hour periods, consisting of three early morning and three late afternoon sessions. Foraging observations employed the feeding-observation methods of Morrison (1984), taking into account the precautions regarding sample completeness of Watson (2003). After a bird was identified, its location was recorded as from one of three vertical vegetation categories: tree/mallee  $\geq 3$  m, shrub  $< 3$  m, ground  $\leq 0.1$  m). The percentage utilisation of the three strata was recorded for each bird species from the cumulative observations for each site and year.

When a bird was also observed feeding or actively searching for a food resource, the first foraging action was allocated to one of the following classes:

- (1) Gleaning - where the bird picks prey off foliage, bark or the ground;
- (2) Probing - where the bird inserts its beak at least partly into the substrate;
- (3) Gathering - where the bird uses beak and occasionally also feet to collect and accumulate food resources;
- (4) Pouncing - where the bird flies from a perch down to prey on the ground;
- (5) Hawking - where the perched bird takes flight and captures flying prey in the air, then returns to perch; and
- (6) Sweeping - where airborne insects are caught on the wing by birds that forage in the air.

For each foraging action, the substrate type was recorded as foliage, bark, flowers, ground or air (Recher and Davis 2002). Each foraging action was also categorised as leading to the capture of invertebrates or carbohydrates associated with lerp, manna and honeydew (insectivory; Paton 1980), or the procurement of nectar from flowers or inflorescences, generally through probing for nectar or pollen, or insects present on flowers (nectarivory; Paton 1981). Only a single record of foraging stratum, action and substrate was made for each bird sighting and an attempt was made to avoid recording the same bird more than once during each observation period (Morrison 1984). Aerial hawkers observed between and above the trees were included in the tree foraging stratum records. Cumulative percentages for each foraging action were calculated for each site and year. Because initial analyses indicated that the birds did not alter their basic foraging ecology between sites or between years, the data for individual bird species' strata utilisation, foraging action and substrate use were combined for all sites and for both years. Relationships between foraging strata categories and mean annual site rainfall values were calculated by Spearman rank correlations. Two-factor repeated measures analysis of variance tests were performed on foraging habitat strata use and foraging action, with these factors as between-subjects factors within their respective tests and year (2004 and 2006)

**Table 1.** Site locations for avian foraging observations. Distance (km) by road from Mundaring, mean annual rainfall (mm) from nearest reporting weather station (Australian Bureau of Meteorology; <http://www.bom.gov.au/climate>) and subjective comparative index of flowering proliferation for each site for each year (- = no flowering to ++++ abundant flowering).

Site name	Latitude	Longitude	Distance	Rainfall	Flower 2004	Flower 2006
Mundaring	31° 55'S	116° 11'E	0	1050	++++	+++
Mt. Observation	31° 53'S	116° 31'E	45	460	+++	++
Durokoppin	31° 25'S	117° 31'E	180	330	+	-
Westonia	31° 15'S	118° 41'E	270	310	++	-
Yellowdine	31° 17'S	119° 39'E	320	290	+	++
Kurrawang	30° 45'S	120° 25'E	495	260	+++	+
Goongarrie	29° 55'S	121° 10'E	605	250	+	-
Leinster	27° 45'S	121° 45'E	825	230	-	++

as the within-subject (repeated) factor. Percentage values of each category (calculated from summation across all species) at each site were ranked before testing, thus approximating a non-parametric equivalent of a two-way repeated measures ANOVA. Chi-square analyses of foraging habitat strata and substrate use were performed on individual species to test which species exhibited preferential foraging strata and substrate use. All chi-square analyses were undertaken on count data rather than percentage data, and as such, only those species with at least 15 and 30 records of habitat strata and substrate use (respectively) were considered for chi-square analysis in order to avoid the breaching of assumptions of minimum expected values. Avian nomenclature follows Christidis and Boles (2008).

Niche breadths and species overlaps were determined for species within the Acanthizidae and the Meliphagidae. These measures were calculated from the percentage incidence of eight foraging strata/substrate/action categories: tree foliage gleaning, tree bark gleaning, tree flower probing, shrub foliage gleaning, shrub bark gleaning, shrub flower probing, ground layer feeding and hawking. Niche breadth was calculated using the Shannon index of diversity. Niche overlap was calculated using the formula:

$$D = 1 - 0.5 \sum |p_{i,j} - p_{i,k}|$$

where  $p_{i,j}$  and  $p_{i,k}$  are the proportions of observations species  $j$  and  $k$  in the  $i$ th foraging action/substrate category (Schoener 1968). Average overlap between species was used to construct a dendrogram of niche similarity (Cody 1974).

## Results

### *Strata-use comparisons*

Foraging birds most commonly utilised the tree stratum (75% of all foraging observations in both years), followed by the shrub stratum (19%) and the ground stratum (6%) ( $F_{2,21} = 106.7$ ,  $P < 0.001$ ; Table 2). There was no significant difference between sampling years ( $F_{1,21} = 0.16$ ,  $P = 0.690$ ), although there was a significant interaction effect ( $F_{2,21} = 4.53$ ,  $P = 0.023$ ), on account of a higher utilisation of shrubs in 2006. Along the aridity gradient in both 2004 and 2006, there was no significant pattern between the rainfall gradient and stratum use of trees ( $r_s = 0.14$ ,  $P = 0.74$ ) or shrubs ( $r_s = 0.24$ ,  $P = 0.96$ ). In 2004, however, there was a significant decrease in the extent of use of the ground as rainfall decreased ( $r_s = -0.83$ ,  $P = 0.01$ ).

Members of the Columbidae, Cacatuidae and Artamidae divided their activities mainly between the tree and ground layers, making little use of the shrub layer (Table 3). The members of the Psittacidae, Climacteridae, Pardalotidae, Neosittidae, Campephagidae, Corvi-

dae and Hirundinidae were almost exclusively found feeding in or around the tree layer. Birds found by chi-square analysis to equally exploit all three layers of the vegetation (Chi-square  $< 5.99$ ,  $P > 0.05$ ) included the Red-capped Robin (*Petroica goodenovii*) and the Magpie-lark (*Grallina cyanoleuca*), although taking into account an adjusted Bonferroni correction added the Grey Shrike-thrush (*Colluricincla harmonica*), Major Mitchell's Cockatoo (*Lophochroa leadbeateri*), Carnaby's Black-Cockatoo (*Calyptorhynchus latirostris*), Splendid Fairy-wren (*Malurus splendens*), and White-browed Babbler (*Pomatostomus superciliosus*) as other species not favouring any particular strata (Table 3).

Among the Acanthizidae, the Weebill (*Smicrorhynchus brevirostris*) and Western Thornbill (*Acanthiza inornata*) were mostly observed in the trees, the Chestnut-rumped (*A. uropygialis*) and Inland (*A. apicalis*) Thornbills occurred mostly in the shrub layer and the Yellow-rumped Thornbill (*A. chrysorrhoa*) favoured the ground layer. The Western Gerygone (*Gerygone fusca*) was found in limited numbers and there was no statistically significant difference in its use of any particular vegetation strata.

Among the Acanthizidae, the Weebill (*Smicrorhynchus brevirostris*) and Western Thornbill (*Acanthiza inornata*) were mostly observed in the trees, the Chestnut-

**Table 2.** Number of bird foraging observations ( $n$ ) and percentages of foraging observations for each stratum for each study site, each sampling year and overall.

Location	Stratum			
	$n$	% Tree	% Shrub	% Ground
<b>2004</b>				
Mundaring	270	55	34	11
Mt. Observation	199	66	25	9
Durokoppin	432	76	16	8
Westonia	403	82	11	7
Yellowdine	336	78	15	7
Kurrawang	495	89	9	2
Goongarrie	364	85	9	6
Leinster	164	72	21	7
<b>Total</b>	<b>2663</b>	<b>78</b>	<b>16</b>	<b>6</b>
<b>2006</b>				
Mundaring	398	58	36	6
Mt. Observation	476	70	24	6
Durokoppin	518	81	12	7
Westonia	333	80	17	3
Yellowdine	516	69	22	9
Kurrawang	341	83	14	3
Goongarrie	344	73	26	1
Leinster	313	63	34	3
<b>Total</b>	<b>3139</b>	<b>72</b>	<b>23</b>	<b>5</b>
<b>Overall total</b>	<b>5802</b>	<b>75</b>	<b>19</b>	<b>6</b>

**Table 3.** Number of bird foraging observations (*n*) and percentages of foraging observations for each stratum for each species. Data for 2004 and 2006 are combined for individual species, with chi-square analysis undertaken on counts of three habitat strata categories for the 49 bird species with at least 15 records (*n*) across both years. All species exhibited significant (Chi-square  $P < 0.05$ ) inequality of strata use, except for the Magpie-lark and Red-capped Robin. At a Bonferroni adjusted *P*-value ( $0.05/49 = 0.00102$ ), species exhibited inequality of strata use included all except those mentioned above as well as the Grey Shrike-thrush, Major Mitchell's Cockatoo, Carnaby's Black-Cockatoo, Splendid Fairy-wren, Western Gerygone and White-browed Babbler.

Family	Common name	Species name	<i>n</i>	Stratum		
				% Tree	% Shrub	% Ground
Columbidae	Common Bronzewing	<i>Phaps chalcoptera</i>	41	44	0	56
	Crested Pigeon	<i>Ocyphaps lophotes</i>	110	77	0	23
Cacatuidae	Carnaby's Black-Cockatoo	<i>Calyptorhynchus latirostris</i>	18	56	0	44
	Galah	<i>Eolophus roseicapillus</i>	340	91	0	9
	Major Mitchell's Cockatoo	<i>Lophochroa leadbeateri</i>	24	58	0	42
Psittacidae	Australian Ringneck	<i>Barnardius zonarius</i>	383	91	6	3
	Elegant Parrot	<i>Neophema elegans</i>	43	100	0	0
	Purple-crowned Lorikeet	<i>Glossopsitta porphyrocephala</i>	43	100	0	0
	Red-capped Parrot	<i>Purpureicephalus spurius</i>	59	85	8	7
Climacteridae	Rufous Treecreeper	<i>Climacteris rufa</i>	18	100	0	0
Maluridae	Splendid Fairy-wren	<i>Malurus splendens</i>	31	10	29	61
Acanthizidae	Chestnut-rumped Thornbill	<i>Acanthiza uropygialis</i>	220	18	72	10
	Inland Thornbill	<i>Acanthiza apicalis</i>	74	34	62	4
	Weebill	<i>Smicrornis brevirostris</i>	869	86	13	1
	Western Gerygone	<i>Gerygone fusca</i>	18	67	33	0
	Western Thornbill	<i>Acanthiza inornata</i>	101	79	19	2
	Yellow-rumped Thornbill	<i>Acanthiza chrysorrhoa</i>	76	13	32	55
Pardalotidae	Striated Pardalote	<i>Pardalotus striatus</i>	198	96	0	4
Meliphagidae	Brown Honeyeater	<i>Lichmera indistincta</i>	218	43	57	0
	Brown-headed Honeyeater	<i>Melithreptus brevirostris</i>	93	92	8	0
	New Holland Honeyeater	<i>Phylidonyris novaehollandiae</i>	178	28	71	1
	Red Wattlebird	<i>Anthochaera carunculata</i>	408	92	7	1
	Singing Honeyeater	<i>Lichenostomus virescens</i>	61	57	43	0
	Spiny-cheeked Honeyeater	<i>Acanthagenys rufogularis</i>	58	74	26	0
	Western Spinebill	<i>Acanthorhynchus superciliosus</i>	67	57	43	0
	Western Wattlebird	<i>Anthochaera lunulata</i>	26	23	77	0
	White-cheeked Honeyeater	<i>Phylidonyris niger</i>	50	22	78	0
	White-eared Honeyeater	<i>Lichenostomus leucotis</i>	179	67	32	0
	White-fronted Honeyeater	<i>Purnella albifrons</i>	35	40	60	0
	White-naped Honeyeater	<i>Melithreptus lunatus</i>	31	87	13	0
Yellow-plumed Honeyeater	<i>Lichenostomus ornatus</i>	312	93	6	1	
Yellow-throated Miner	<i>Manorina flavigula</i>	275	72	26	2	
Pomatostomidae	White-browed Babbler	<i>Pomatostomus superciliosus</i>	38	11	55	34
Neosittidae	Varied Sitella	<i>Daphoenositta chrysoptera</i>	50	100	0	0
Campephagidae	Black-faced Cuckoo-shrike	<i>Coracina novaehollandiae</i>	25	100	0	0
Pachycephalidae	Grey Shrike-thrush	<i>Colluricincla harmonica</i>	48	56	27	17
	Rufous Whistler	<i>Pachycephala rufiventris</i>	16	88	12	0
Artamidae	Australian Magpie	<i>Cracticus tibicen</i>	44	82	0	18
	Dusky Woodswallow	<i>Artamus cyanopterus</i>	44	93	5	2
	Grey Butcherbird	<i>Cracticus torquatus</i>	36	83	3	14
	Grey Currawong	<i>Strepera versicolor</i>	39	74	3	23
	Pied Butcherbird	<i>Cracticus nigrogularis</i>	62	92	0	8
Rhipiduridae	Grey Fantail	<i>Rhipidura albiscapa</i>	128	76	23	2
Corvidae	Australian Raven	<i>Corvus coronoides</i>	141	96	1	3

**Table 3.** Continued.

Family	Common name	Species name	n	Stratum		
				% Tree	% Shrub	% Ground
	Little Crow	<i>Corvus bennetti</i>	76	97	0	3
Monarchidae	Magpie-lark	<i>Grallina cyanoleuca</i>	17	59	12	29
Petroicidae	Red-capped Robin	<i>Petroica goodenovii</i>	35	20	46	34
	Scarlet Robin	<i>Petroica boodang</i>	40	10	5	85
Hirundinidae	Tree Martin	<i>Petrochelidon nigricans</i>	111	100	0	0

rumped (*A. uropygialis*) and Inland (*A. apicalis*) Thornbills occurred mostly in the shrub layer and the Yellow-rumped Thornbill (*A. chrysorrhoa*) favoured the ground layer. The Western Gerygone (*Gerygone fusca*) was found in limited numbers and there was no statistically significant difference in its use of any particular vegetation strata.

The members of the family Meliphagidae were rarely found on the ground, but differentially utilised the tree and shrub strata. Species predominantly observed in the tree stratum were the Brown-headed (*Meliphaga brevirostris*), Spiny-cheeked (*Acanthopneuste rufogularis*), White-naped (*M. lunatus*), White-eared (*Lichenostomus leucotis*) and Yellow-plumed (*L. ornatus*) Honeyeaters, the Red Wattlebird (*Anthochaera carunculata*) and the Yellow-throated Miner (*Manorina flavigula*). Honeyeaters favouring the shrub stratum were the Brown (*Lichmera indistincta*), New Holland (*Phylidonyris novaehollandiae*),

White-cheeked (*P. niger*) and White-fronted (*Purnella albifrons*) Honeyeaters and the Western Wattlebird (*Anthochaera lunulata*).

#### Community foraging

Of the 3516 foraging observations recorded, there was a significant difference in incidence of particular foraging actions ( $F_{5,42} = 12.34$ ,  $P < 0.001$ ; Table 4), with a greater number of foliage gleaning actions recorded (69%) than all other foraging actions (Dunnett's T3,  $P < 0.01$ ). Gathering, pouncing, hawking and sweeping were each minor contributors. There was no significant difference between sampling years across all species ( $F_{5,42} = 0.16$ ,  $P = 0.690$ ), despite the more limited rainfall of 2006, although there was a significant interaction effect ( $F_{5,42} = 2.67$ ,  $P = 0.035$ ), due in large part to a decrease in incidence of gathering from 2004 to 2006.

**Table 4.** Number of foraging observations (*n*) and percentages for each foraging action for each study site, each sampling year and overall.

Location	n	Foraging action					
		% Gleaning	% Probing	% Gathering	% Pouncing	% Hawking	% Sweeping
<b>2004</b>							
Mundaring	266	48	33	12	7	0	0
Mt. Observation	183	60	9	4	1	22	3
Durokoppin	217	64	6	2	1	13	14
Westonia	220	76	5	14	1	1	4
Yellowdine	210	91	2	3	1	2	1
Kurrawang	314	50	45	1	1	0	0
Goongarrie	284	90	8	0	1	1	0
Leinster	72	93	0	3	4	0	0
<b>Total</b>	<b>1766</b>	<b>69</b>	<b>17</b>	<b>5</b>	<b>2</b>	<b>4</b>	<b>2</b>
<b>2006</b>							
Mundaring	219	34	46	3	7	6	3
Mt. Observation	332	51	21	1	3	8	16
Durokoppin	254	80	1	0	3	8	8
Westonia	135	88	0	0	1	2	10
Yellowdine	294	79	18	2	0	1	0
Kurrawang	210	83	6	0	1	3	7
Goongarrie	174	98	0	0	2	1	0
Leinster	132	58	41	0	1	0	0
<b>Total</b>	<b>1750</b>	<b>70</b>	<b>17</b>	<b>1</b>	<b>2</b>	<b>4</b>	<b>6</b>
<b>Overall total</b>	<b>3516</b>	<b>69</b>	<b>17</b>	<b>3</b>	<b>2</b>	<b>4</b>	<b>4</b>

**Table 5.** Avian community guild structure, number of foraging observations (*n*) and percentages by foraging substrate/action: Insectivory (FoGl=Foliage gleaning, BaFe=Bark feeding, GrFe=Ground feeding, Poun=pounce, HwSw=hawking or sweeping), Nect (Nectarivory by probing) and Gra/Herb (Granivory and herbivory by probing, gathering and gleaning combined). Data for 2004 and 2006 are combined for individual species with Chi-square analysis undertaken on counts of six foraging substrate/action categories (ground and pounce records combined) for the 25 bird species with at least 30 foraging records across both years. All species exhibited significant (Chi-square  $P < 0.05$ ) inequality of foraging substrate/action incidence, and this still held true at a Bonferroni adjusted  $P$ -value ( $0.05/25 = 0.002$ ).

Guild Type/species	%Insectivory							
	<i>n</i>	%FoGl	%BaFe	%GrFe	%Poun	%HwSw	%Nect	%Gra/Herb
All species – 2004	1766	51	14	4	2	7	17	5
All species – 2006	1750	48	17	6	2	10	16	1
All species – both years	3516	50	16	5	2	8	17	3
<b>Insectivores</b>								
<b>Foliage &gt; Bark</b>								
Striated Pardalote	185	89	7	4	0	0	0	0
Weebill	835	97	3	0	0	0	0	0
Western Thornbill	97	95	3	2	0	0	0	0
<b>Bark &gt; Leaves or ground</b>								
Chestnut-rumped Thornbill	212	42	48	10	0	0	0	0
Inland Thornbill	73	47	49	4	0	0	0	0
Varied Sittella	46	0	100	0	0	0	0	0
White-browed Babbler	38	0	76	26	0	0	0	0
<b>Ground &gt; Leaves or bark</b>								
Scarlet Robin	35	9	0	0	91	0	0	0
Yellow-rumped Thornbill	74	24	19	57	0	0	0	0
<b>Air &gt; Foliage or bark</b>								
Dusky Woodswallow	38	3	5	3	0	89	0	0
Grey Fantail	125	1	1	0	0	98	0	0
Tree Martin	111	0	0	0	0	100	0	0
<b>Insectivore &gt; Nectarivore</b>								
Brown-headed Honeyeater	82	68	25	1	0	0	6	0
Western Spinebill	59	54	3	0	0	0	43	0
White-eared Honeyeater	92	28	52	0	0	0	14	0
Yellow-plumed Honeyeater	207	41	31	1	0	1	26	0
Yellow-throated Miner	188	37	23	2	0	0	39	0
<b>Nectarivore &gt; Insectivore</b>								
Brown Honeyeater	148	31	3	0	0	1	65	0
New Holland Honeyeater	129	23	5	0	0	5	70	0
Red Wattlebird	172	32	7	1	0	0	60	0
Singing Honeyeater	40	8	15	0	0	0	77	0
Spiny-cheeked Honeyeater	33	33	15	0	0	0	52	0
<b>Granivore &gt; Nectarivore</b>								
Australian Ringneck	47	38	13	0	0	0	11	38
Galah	30	7	0	0	0	0	0	93
Red-capped Parrot	32	0	3	3	0	0	10	84

There were site-specific patterns of change evident such as the influence of greater flower proliferation in some sites associated with a higher incidence of flower probing (e.g. Mundaring and Mt. Observation in both years, Kurrawang in 2004, and Yellowdine and Lein-

ster in 2006; Table 1 and 4). There were also species-specific patterns of foraging behaviours consistent across sites such as gathering at Mundaring and Westonia by Australian Ringnecks (*Barnardius zonarius*) and aerial hawking at Mt. Observation and Durokoppin by

Grey Fantails (*Rhipidura albiscapa*) and Dusky Woodswallows (*Artamus cyanopterus*).

#### Foraging guild structure

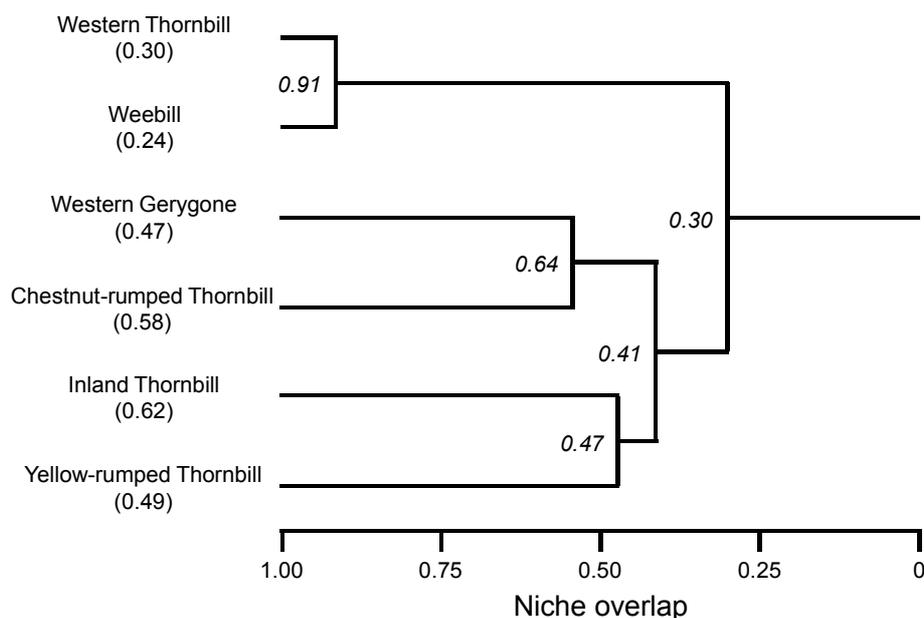
Foliage-gleaning insectivory was the most common combination of foraging action, substrate and resource type, totaling about half of all foraging observations (Table 5). The Weebill, Western Thornbill and Striated Pardalote (*Pardalotus striatus*) were almost exclusively foliage-gleaning insectivores during the winter surveys. Nectarivory (17%) and the gleaning of bark for insects (16%) were also reasonably common community foraging methods. The most common bark gleaners were the Chestnut-rumped and Inland Thornbills, Varied Sittella (*Daphoenositta chrysoptera*), White-browed Babbler and White-eared Honeyeater. Species that tended to either pounce to the ground or feed by probing or gleaning litter on the ground included the Scarlet Robin (*Petroica boodang*) and the Yellow-rumped Thornbill. The Dusky Woodswallow, Grey Fantail and Tree Martin (*Petrochelidon nigricans*) tended to use sweeping or hawking to capture insects on the wing. Overall, hawking accounted for 8% of all foraging observations.

Among the species foraging both for the capture of insects and the acquisition of nectar were several members of the Meliphagidae. The Brown-headed, White-eared and Yellow-plumed Honeyeaters, the Western Spinebill (*Acanthorhynchus superciliosus*) and the Yellow-throated Miner were more insectivorous than nectarivorous. The Red Wattlebird and the Brown, New Holland, Singing (*Lichenostomus virescens*) and Spiny-cheeked Honeyeater were more nectarivorous than insectivorous (Table 5).

Granivorous activity was uncommon, totaling only 3% of all foraging observations. The Red-capped Parrot (*Purpureicephalus spurius*) was observed gathering and cracking eucalypt fruits for the seeds and probing or eating flowers. The Galah (*Eolophus roseicapillus*) tended to gather and crack eucalypt fruits for seeds, to consume leafy herbs on the ground or to dig up bulbs and tubers. The Australian Ringneck gathered eucalypt fruits for the enclosed seeds, gleaned leaves and bark for lerp and insects and probed or ate flowers.

#### Interspecies niche relationships

Within the family Acanthizidae, the predominately tree stratum foliage gleaners, the Western Thornbill and the Weebill had the smallest niche breadth values at 0.30 and 0.24, respectively, and the greatest niche overlap at 0.91 (Fig. 1). Geographically, the Western Thornbill was recorded at Mundaring (the western-most location) for 8.9% of all foraging observations of all species in 2004 and 3.5% in 2006, but the Weebill was not seen in 2004 and only for 1.3% in 2006 at this most western location. The Western Thornbill accounted for 18.1% and 5.7% of records for 2004 and 2006 (respectively) at Mt. Observation, but was absent from sites further to the east. The Weebill co-occurred with the Western Thornbill at Mt. Observation and represented 14.6% and 13.0% of all 2004 and 2006 (respectively) foraging observations of all species observed at this site. The Weebill was then the predominant tree foliage gleaning species in all sites to the east. The other members of the Acanthizidae had wider niche breadths (0.47-0.62) and lower niche overlap values with the other species. These four species occurred more often in the shrub and ground layers than the Western Thornbill and



**Figure 1.** Niche overlap dendrogram of species of the Acanthizidae. Niche breadth value for species shown in parentheses.

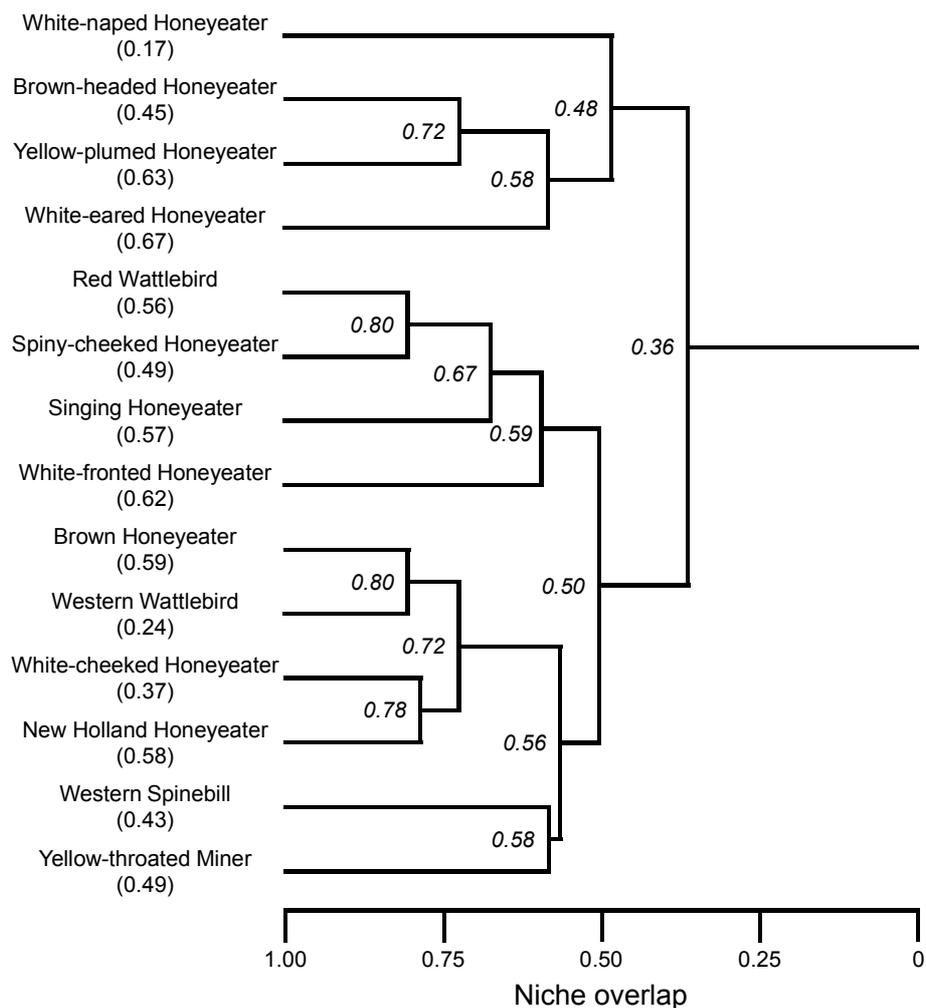
Weebill. The Chestnut-rumped Thornbill and the Western Gerygone fed more in the shrub foliage, and the Inland Thornbill and the Yellow-rumped Thornbill fed more on shrub bark substrates or on the ground. Geographically, the Western Gerygone had a scattered and uncommon occurrence, while the other three species were found in many of the sites of the Wheatbelt and arid north-east, and in higher percentages than the Western Gerygone.

The niche breadth and overlap calculations for the family Meliphagidae reinforced the information attained from the foraging action and substrate observations; separating the predominately nectarivorous honeyeaters from the predominately insectivorous honeyeaters (Fig. 2). The White-naped Honeyeater had the lowest niche breadth value of all species (0.17) with nearly 90% of the foraging observations in the tree foliage-gleaning category. The White-eared Honeyeater had the largest niche breadth (0.67), utilising foliage, bark and flowers, both in trees and in shrubs. The major division within the predominately nectarivorous honeyeaters was between the four species (Red Wattlebird and the Spiny-cheeked, Singing

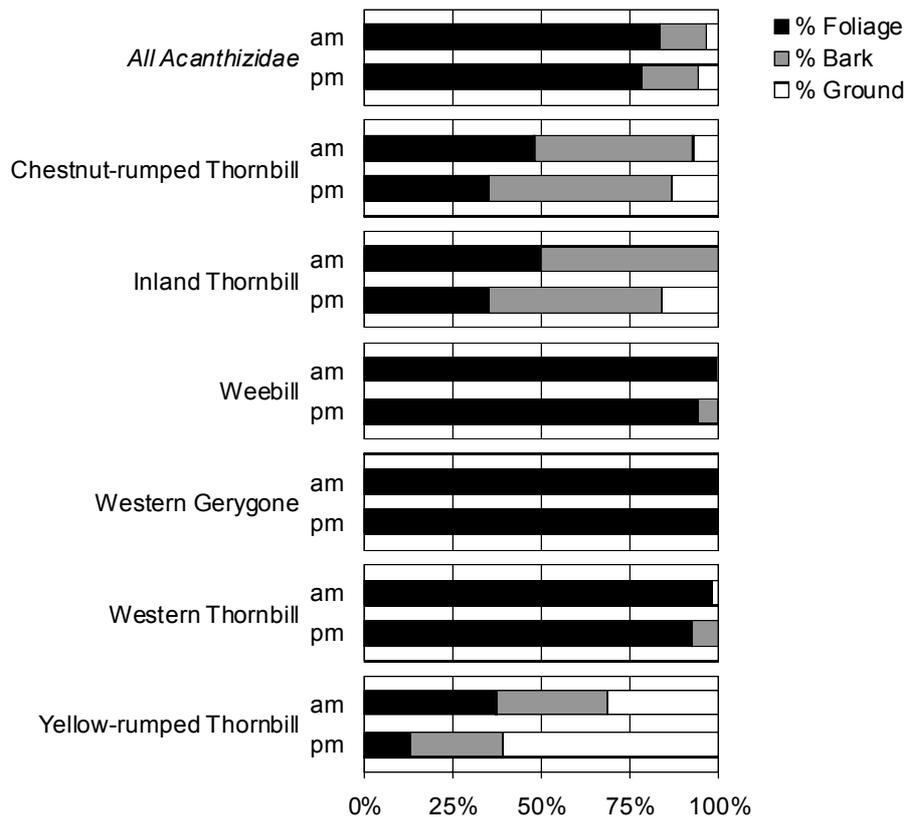
and White-fronted Honeyeaters) that favoured the flowers of the canopy eucalypts and the remaining species that favoured shrub-layer flowers. Within the latter group, the New Holland and White-cheeked Honeyeaters had a niche overlap of 0.78, as both had more than 70% of observations in the shrub flower-probing category. These two species, however, were geographically separated, with the New Holland Honeyeater occurring only at Mundaring and the White-cheeked Honeyeater occurring only at Mt. Observation.

#### *Diurnal foraging variations*

There were 1159 foraging observations of Acanthizids recorded during morning surveys, and 857 recorded during afternoon surveys. Overall, these predominantly insectivorous species utilised foliage as the foraging substrate in 83% of the morning observations (Fig. 3). Morning bark and ground foraging accounted for 13% and 4% of observations respectively. In the afternoon, observations of foraging on foliage substrates fell to 78%, while bark and ground foraging increased to 16% and 6%, respectively. This trend of increasing use of



**Figure 2.** Niche overlap dendrogram for species of the Meliphagidae. Niche breadth values for species shown in parentheses.



**Figure 3.** Morning (am) and afternoon (pm) percentage contribution of foliage, bark and ground substrate foraging by members of the Acanthizidae.

bark and ground in the afternoon at the expense of foliage utilisation was consistent for all individual species of the Acanthizidae.

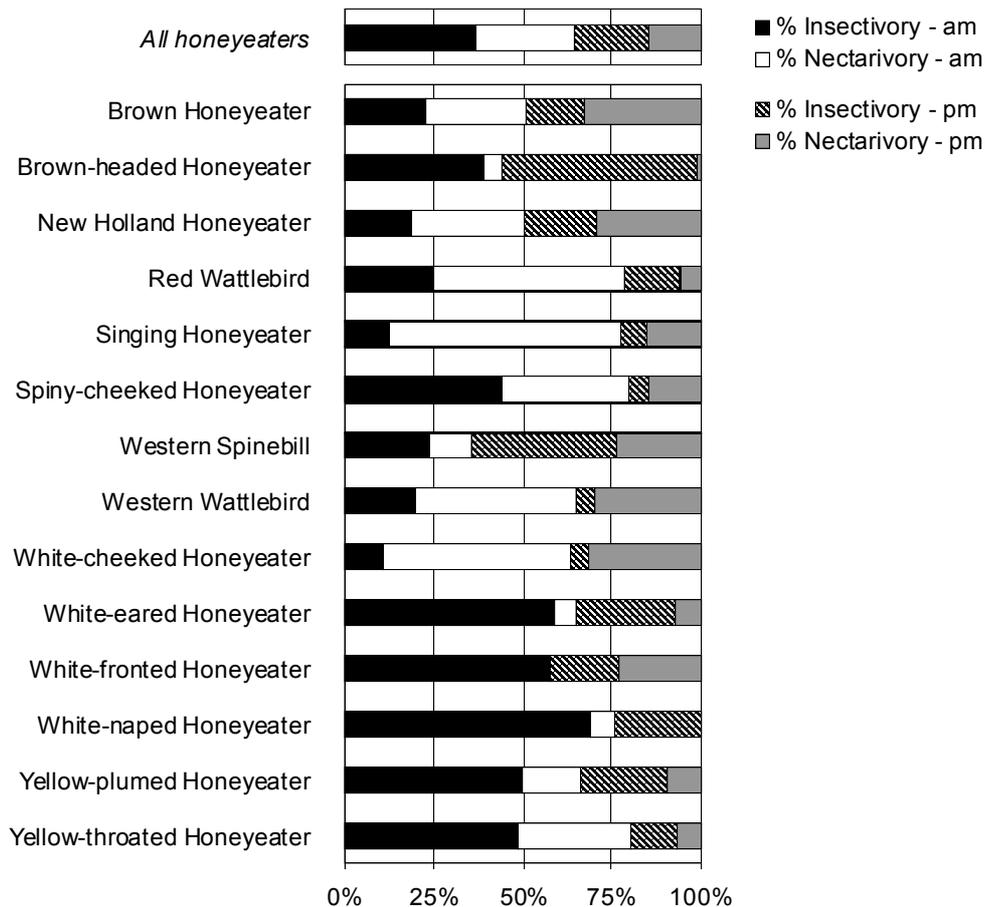
Foraging observations for species of the Meliphagidae recorded in this study totaled 811 records during morning surveys and 444 records during afternoon surveys. Overall, the morning percentages of 57% insectivory and 43% nectarivory were almost identical with the afternoon percentages of 59% insectivory and 41% nectarivory (Fig. 4). Most of the predominantly insectivorous honeyeaters (White-naped, Brown-headed and Yellow-plumed Honeyeater, Yellow-throated Miner, and Western Spinebill) were consistently more insectivorous in the morning and afternoon. Most of the largely nectarivorous honeyeaters, (New Holland, Brown, Singing and White-cheeked Honeyeaters, Western Wattlebird) were consistently more nectarivorous in both the morning and the afternoon, with the exception of the Red Wattlebird, for which the incidence of nectarivory decreased from 69% in the morning to only 27% in the afternoon.

## Discussion

### *Strata utilisation*

The structural diversity of vegetation has been shown to be the major determinant of avian diversity in a

number of countries (MacArthur and MacArthur 1961; Willson 1974; James and Wamer 1982). Foraging heights have also been reported as the major determinant in separating feeding niches in Australian rainforest communities in Queensland (Crome 1978; Frith 1984). However, studies in south-eastern Australian eucalypt forests and woodlands have indicated that height, per se, appears to be less important than substrate or behaviour in determining niche specialisation among birds (Loyn 1985; Woinarski *et al.* 1997). In Western Australia, studies have shown that floristic diversity is also a major determinant in avifaunal niche diversity (Abbott and Van Heurck 1985; Arnold 1988). Our study found that while most birds utilised the tree stratum, certain species were more commonly found in particular habitat strata. This is most likely due to preferred resources dictating foraging stratum preferences. Wooller and Calver (1981) reported that such preferential relationships explained niche overlaps for foraging heights and foraging substrates. The stratum preference of most species determined over the entire gradient were similar to those reported earlier for individual vegetation communities in Mulga woodland (Recher and Davis 1997), Wandoo woodland (Recher and Davis 1998) and Salmon Gum woodland (Recher and Davis 2002).



**Figure 4.** Percentage contribution of foraging observations by members of the Meliphagidae recorded in the morning (am) and afternoon (pm), and whether they represented insectivory or nectarivory.

### Foraging methods

Characteristic differences between strata such as floristic composition, associated invertebrate populations and particular leaf, bark and flower-types, can have greater influences on the avifauna than merely strata height and foliage density differences (Woinarski *et al.* 1997). In turn, these differences influence the foraging behaviour of birds, and such behaviours usually reduce competition for foraging resources, foraging substrates and foraging actions (Ford 1989). Gleaning for invertebrates has been the most common method of resource acquisition reported for birds in a wide range of Australian eucalypt habitats (e.g., Recher *et al.* 1985; Arnold 1988; Recher and Davis 1998; Morris and Wooller 2001). In the present study, gleaning was the most common technique used to forage for resources. Seasonal differences could be expected to influence the higher overall value gleaning reported in this study, compared to that from secondary eucalypt forests of New South Wales (Recher and Holmes 1985; Recher *et al.* 1985). Foliage gleaning was more common than bark gleaning. Common gleaning species that favoured foliage included the Striated Pardalote, Weebill and the Western Thornbill. Species that gleaned from bark in-

cluded the Chestnut-rumped and Inland Thornbills, Varied Sittella, Rufous Treecreeper (*Climacteris rufa*), White-eared Honeyeater and the White-browed Babbler. Comparisons of our data on foliage and bark gleaning with data from the southern tablelands of New South Wales (Recher and Holmes 1985) indicate that bark was a much more widely used substrate in NSW, although again seasonal differences in sampling times could be a major factor for this substrate preference.

Overall, probing for nectar was the second most common foraging method, and was a characteristic feature of honeyeaters. The influence of the major flowering episodes at Kurrawang in 2004 and Leinster in 2006 greatly increased flower probing as a foraging action. Flowering in the eucalypt canopy has been previously reported to greatly increase numbers of the honeyeaters in woodlands of the Western Australian Goldfields (Morris and Wooller 2001; Recher and Davis 2002).

Gathering, hawking, sweeping and pouncing were foraging techniques used only sparingly by species in our study. These foraging techniques have also been reported to be only of minor significance in eastern

Australian eucalypt communities (Recher and Holmes 1985). Gathering of eucalypt fruits to obtain the enclosed seeds was a common foraging action observed in our study by Australian Ringnecks, Red-capped Parrots, Carnaby's Black-Cockatoo and Galahs. Eucalypt communities throughout Australia have species of parrots that specialise in the gathering and consumption of eucalypt seeds (Woinarski *et al.* 1997), although members of this group also glean foliage for lerp and insects, utilise flowers for nectar and forage on the ground (Wyndham and Cannon 1985). Hawking and sweeping were techniques used only by Grey Fantails, Dusky Woodswallows and Tree Martins in this study. The density and spacing of trees has been shown to influence the proportion of hawkers and sweepers in eucalypt communities (Woinarski *et al.* 1997). Open eucalypt woodlands have more aerial insectivores than forests (Mac Nally 1994). In this study, Grey Fantails and Tree Martins did not occur in the Mundaring Jarrah (*Eucalyptus marginata*) forest site, but were among the avifauna of the more open Mt. Observation Wandoo (*E. wandoo*) woodland and the Durokoppin Salmon Gum (*E. salmonophloia*)/York Gum (*E. loxophleba*) woodland sites. Aerial foraging by these two species was also recorded in Wandoo woodlands near Bakers Hill (Arnold 1988). However, towards the more arid end of the gradient, birds which employed hawking and sweeping were uncommon despite the more open habitats. Tree Martins were also recorded at Westonia and Welcome Swallows (*Hirundo neoxena*) were recorded at Yellowdine, but no hawkers or sweepers were recorded at Kurrawang in 2004 or Goongarrie and Leinster in either year. Morris and Wooller (2001) recorded no sweepers among the birds of their 18 months of records in the Western Australian Goldfields Blackbutt (*E. lesouefii*) woodland at Kambalda, just south of our Kurrawang site. The reported presence of Tree Martins at Yellowdine in the spring sample of Recher and Davis (2002) might have been related to swarms of flying termites present at that time. A lack of sweepers could, therefore, be in response to limitations in the numbers of flying insects available in the more arid regions of the gradient during the cool winter period of the sample. Pouncing was a seldom used foraging action recorded in our study, with species using this action including Scarlet, Red-capped, Hooded (*Melanodryas cucullata*) and Western Yellow (*Eopsaltria griseogularis*) Robins, the Australian Magpie (*Cracticus tibicen*), Laughing Kookaburra (*Dacelo novaeguineae*) and the Grey (*Cracticus torquatus*) and Pied (*C. nigrogularis*) Butcherbirds. Robins commonly use pouncing to obtain invertebrates (Cousin 2004), but are rarely abundant species in Australian eucalypt communities (Woinarski *et al.* 1997; Recher and Davis 1998, 2002; Recher *et al.* 2002).

#### *Niche breadth, overlap and competitive exclusion*

Niche differentiation as documented for the Acanthizidae in our study, can be compared to studies of this family from Eastern Australia. Eastern Australian canopy foliage gleaning species in this taxonomic group include the Weebill, White-throated Gerygone (*Gerygone albogularis*), Yellow Thornbill (*Acanthiza nana*) and Striated Thornbill (*A. lineata*) (Bell 1985; Recher 1989). The western counterparts seem to be the Weebill, Western Gerygone and Western Thornbill. The Brown Thornbill (*A. pusilla*) of eastern Australia utilises more of the lower strata and bark substrates, possibly comparable to the Western Australian Chestnut-rumped and Inland Thornbills. The eastern Australian Buff-rumped Thornbill (*A. reguloides*) seems to be ecologically similar to the Yellow-rumped Thornbill, spending considerable time on the ground. Bell (1985) claims that the eastern species of Acanthizidae retreat into their specialised niche when food becomes scarce. Limited invertebrate activity due to the cool morning temperatures during our winter sampling could also have intensified resource competition within the species of this family in Western Australia.

Woinarski (1985) noted that niche overlap of coexisting eastern Spotted (*Pardalotus punctatus*) and Striated (*P. punctatus*) Pardalotes could be extraordinarily high. In our study, we only observed the Spotted Pardalote at Mundaring in 2004 and this species was replaced in 2006 at this site by the Striated Pardalote. Possible competitive exclusion was also noted in the honeyeaters of the genus *Phylidonyris* with the New Holland Honeyeater restricted to Mundaring, the White-cheeked Honeyeater restricted to Mt. Observation and the White-fronted Honeyeater (previously considered *Phylidonyris*) restricted to Kurrawang. The Tawny-crowned Honeyeater (*Glyciphila melanops*, previously also considered a member of *Phylidonyris*), found only at Mt. Observation, occurred in the small-stature shrub areas compared to the White-cheeked Honeyeaters, which occurred in the taller, *Dryandra*-shrub patches. Somewhat contradictory was the pattern of coexistence and niche overlap observed in the three species of honeyeaters of the genus *Lichenostomus*. These three species had the broadest niche values of all the species recorded. The White-eared, Yellow-plumed and Singing Honeyeaters were also geographically widespread. The fourth species, the Purple-gaped Honeyeater (*Lichenostomus cratitius*), was found only rarely, but occurred in three different sites. Flexibility in foraging ecology may allow the coexistence of these closely-related species.

#### *Diurnal variations*

As was recorded in our study, most previous studies have found significant decreases in bird density between morning surveys to afternoon surveys (Robbins

1981; Slater 1994; Craig and Roberts 2001). The Meliphagidae have been the most commonly studied family in relation to diurnal patterns of resource acquisition. Previous Western Australian studies have shown that nectarivory by Brown Honeyeaters (Collins and Cary 1981), Singing Honeyeaters (Collins and Morellini 1979) and Brown-headed Honeyeaters (Collins and Briffa 1983a) declined throughout the day; however, another study found no change (Collins and Briffa 1983b). Diurnal change in the foraging activity patterns of five honeyeaters in a central Victorian forest was recorded by Timewell and Mac Nally (2004), who found early morning nectarivory was much greater than insectivory, but by late morning and early afternoon nectarivory reduced and insectivory increased. Measures of the diurnal variation in the food resources and local climatic factors (ambient temperature, windiness and cloud cover) were consistent with the change from nectarivory in the early morning to insectivory in the afternoon, when insect activity increased. In our study, most of the honeyeaters split their foraging between insects and nectar in approximately similar percentages between morning and afternoon, with the exception of the Red Wattlebird, which greatly reduced nectar foraging in the afternoon. This species may be taking advantage of greater insect activity during the higher temperatures of the late afternoon during winter surveys. Higher afternoon insectivory may also be due to a depletion of nectar availability. The increased utilisation of bark and ground in the afternoon by Acanthizids may also be due to increased availability of bark- and litter-dwelling invertebrates as temperatures rise and insect activity increases. Direct measures of resource availability would be required to lend support to either of these possible explanations.

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