

## Seasonal Variation of Abundance and Foraging of Three Species of Australian Honeyeaters

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### Abstract

Seasonal changes in the abundance and food preferences of three species of honeyeater, *Lichmera indistincta*, *Phylidonyris nigra* and *Melithreptus brevirostris*, at Wongamine Reserve, W.A., were investigated between 1977 and 1981. It has been demonstrated that these birds exhibited movements that were related to the abundance of flowers and associated nectar. None of the honeyeater species relied on a single plant species for nectar in any given season. An estimate of the degree to which honeyeaters relied on arthropods has also been made.

### Introduction

In recent years, several comprehensive studies of foraging and food selection by nectarivorous birds have been reported. The majority have involved American hummingbirds (e.g. Wolf 1970; Wolf *et al.* 1976). Others have related to African sunbirds (e.g. Wolf 1975; Frost and Frost 1980) and some have concerned Australian honeyeaters (e.g. Recher and Abbott 1970; Ford and Paton 1976; Paton and Ford 1977; Halse 1978; Collins 1980; Pyke 1980; Hopper 1981). Most of these investigations have been of relatively short duration, with few focussing on seasonal variations in the abundance of the birds concerned or their food sources (e.g. Ford and Paton 1977; Crome 1978). The present study was designed to investigate such parameters in relation to three species of Australian meliphagid birds at Wongamine Nature Reserve, W.A., over approximately 4 years.

### Materials and Methods

#### Study Area

Investigations were carried out at the Wongamine Nature Reserve, in Western Australia 125 km north-east of Perth. The reserve comprises approximately 259 ha of relatively undisturbed vegetation, and is surrounded by agricultural land. As reported by Collins (1980), the major study area was approximately 5 ha in size, and located near the northern boundary of the reserve. Another study area, of approximately 1 ha, was situated near the south-west corner of the reserve. Three observation sites were established in the study areas: one in the heath section of the major area; another approximately 500 m away in the neighbouring woodland; the third in the south-west corner of the reserve, roughly 4 km from the major area. At the first site, dominant plants associated with honeyeater foraging are *Banksia attenuata*, *Calothamnus quadrifidus* and *Eucalyptus macrocarpa*; at the second site, *Adenanthes argyrea*, *Adenanthes cygnorum*, *Anigozanthos humilis*, *Calothamnus sangineus*, *Dryandra sessilis*, *Eucalyptus drummondii* and *E. wandoo* are most abundant; in the south-west corner, plants similar to those at site 2 are found, except that *Banksia prionotes* is present and some *Dryandra carduacea* co-exist with *D. sessilis*. Characteristics of most of these plants have been described elsewhere (Collins 1980).

Several species of honeyeater are found in the study areas, the most abundant being the brown honeyeater *Lichenmera indistincta*, the white-cheeked honeyeater *Phylidonyris nigra* and the brown-headed honeyeater *Melithreptus brevirostris*. Morphological characteristics of these birds have been described previously (Collins 1980).

#### *Experimental Design*

This study extended over 4 years, commencing in March 1977. The major objectives were to document seasonal changes in honeyeater population densities and to relate these to variations in the availability and utilization of food resources such as nectar and arthropods. In general, observations were made during March, June, September and December of each year.

#### *Bird Population Density Estimates and Movements*

Estimates of population densities for *L. indistincta*, *P. nigra* and *M. brevirostris* were made during each visit to the two major study sites between 1977 and 1981; densities were measured at the third site only during the last two years. Conventional methods of censusing birds along strip transects were not used. Instead, the mean numbers of birds trapped per hour in two 10 by 3-m mist nets placed amongst the vegetation at each site were used to indicate relative changes in population density from season to season.

On most occasions when birds were trapped, unbanded honeyeaters were marked with numbered aluminium leg bands. All recaptures of banded birds were recorded.

#### *Flowering Phenology and Nectar Standing Crops*

From 1977 to 1980, estimates of flower density on 20 marked members of each of the plant species visited by honeyeaters at sites 1 and 2 were made at regular intervals; the plants studied were initially selected at random. Estimates of plant abundance for each species were made by a plotless point-centred quarter method (Mueller-Dombois and Ellenberg 1974). Similar measurements were made at site 3 from 1979 to 1981. During each visit to the study sites, standing crops of nectar were measured in unbagged flowers during approximately the first and third hours after dawn, with 5- $\mu$ l capillary tubes; flowers tested were on the plants used for estimates of flower density. The equivalent sucrose concentrations of nectar samples were measured with a direct-reading National temperature-compensated refractometer (Collins *et al.* 1980). Nectar volume and percentage sucrose concentration (w:w adjusted to w:v) data were converted to energy equivalents, assuming that 1 mg sucrose was equivalent to 16.74 J.

#### *Phenology of Arthropod Availability*

The abundance of honeyeaters at each of the three sites varied considerably from season to season. At the site attracting most honeyeaters in any given season, 12 glass pitfall traps, 7 by 10 cm, containing 70% ethyl alcohol, were placed 1 m apart in the soil beneath plants visited by honeyeaters. These were used to sample the soil and litter arthropod fauna between dawn and dusk for several days. Sweep nets were used to sample airborne arthropods and those associated with leaves, bark or flowers of representative members of each plant species visited by honeyeaters (Southwood 1966); the technique used involved making eight sweeps adjacent to, and striking, two plants of each species, between 1100 and 1400 h during each visit.

#### *Direct Observation of Honeyeater Foraging Behaviour*

Numerous measurements of foraging behaviour were made for *L. indistincta* and *P. nigra*, fewer for *M. brevirostris*. In addition to the determination of which plant species were visited during the first 3 h after dawn, the relative occurrences of individual flower visitation, hawking and gleaning for arboreal arthropods were also documented; the technique used was to follow individual birds for as long as possible, scoring each feeding action as a separate observation.

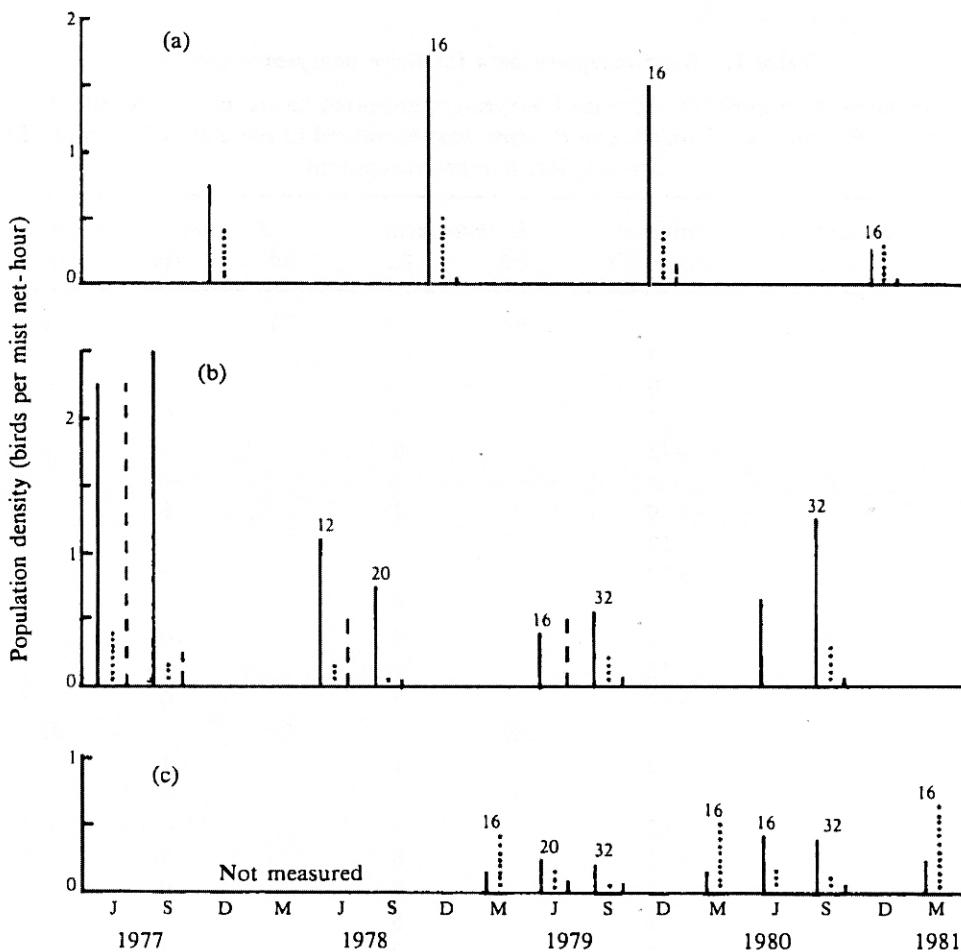
#### *Circumstantial Evidence relating to Foraging Behaviour*

Foreheads, throats and beaks of birds trapped in the mist nets were wiped with small, fresh cubes of gelatin containing basic fuchsin dye (Wodehouse 1965; Tullis and Wooller, personal communication). The cubes were melted onto microscope slides beneath coverslips, thus providing stained permanent mounts of pollen grains present on the birds. Birds were then placed in clean paper bags until they released faecal samples. Faecal material was later moistened, scraped from the paper bags onto microscope slides, then stained and mounted in a manner similar to the above. Pollen grains present in each mount were identified by comparison with type specimens taken from known plants, and their

densities estimated by counting the numbers in four, randomly chosen 1800- $\mu\text{m}$  diameter fields of view on an Olympus CHB stereomicroscope. Arthropod remnants found in the faecal samples were scored on an absent–rare–common basis, and identified to Order level where possible (Calver and Wooller 1982).

## Results

Estimates of relative population densities of honeyeaters, expressed as birds captured per mist net-hour during the first 4 h after dawn, are given in Fig. 1.



**Fig. 1.** Relative population densities of *L. indistincta* (—), *P. nigra* (···), and *M. brevirostris* (---) at Wongamine, every 3 months between June 1977 and March 1981. (a) Site 1. (b) Site 2. (c) Site 3. Only birds caught during the first 4 h after dawn are included; each individual is counted once only. Sampling effort was usually of 8 mistnet-hours; greater efforts are indicated on the graph. Note that the regular 3-monthly netting did not always catch honeyeaters.

Although these in no way indicate the absolute numbers of birds present, there is a clear pattern of seasonal variation in the abundance of *L. indistincta*, *M. brevirostris* and *P. nigra* at each of the three sites: site 1 is favoured in summer, site 2 in winter and spring, and site 3 from autumn to spring. There is also some evidence of bird movement between the sites (Table 1).

Densities of plants visited by honeyeaters, and seasonal variations in the mean numbers of flowers on marked plants at the three sites, are outlined in Table 2 (patterns were similar from 1977 to 1981). In general, there is a variety of flowers present, although those of one or two plant species predominate for any given season or site. Standing crops of nectar and equivalent sucrose concentrations are

indicated in Table 3. Standing crops, in particular, vary considerably according to plant species and season.

Relative abundances of soil, litter and arboreal arthropods at different times of the year are indicated in Table 4. As would be expected, the apparent availability of arthropods is least in June (winter), and greatest in September (spring) and December (summer). Data were gathered only at the site(s) where honeyeaters were most abundant in each season.

**Table 1. Band-recapture data for three honeyeater species**

— Recaptures virtually impossible, because honeyeaters appeared to be absent. At site 3, only six *L. indistincta* and 11 *P. nigra* were banded; one *P. nigra* was recaptured at site 2 after 3 months. Bd, number banded; Rc, number recaptured

Banding site	Recapture site	Interval (months)	<i>L. indistincta</i> Bd	<i>L. indistincta</i> Rc	<i>P. nigra</i> Bd	<i>P. nigra</i> Rc	<i>M. brevirostris</i> Bd	<i>M. brevirostris</i> Rc
1		98			34		6	
1	1	3		—	—	—	—	—
		9		—	—	—	—	—
		12		2	0	0	0	0
		>12		0	1	1	0	0
1	2	3		—	—	—	—	—
		9		3	1	1	1	1
		12		—	—	—	—	—
		>12		1	0	0	0	0
1	3	3		0	1	0	0	0
		9		0	0	0	0	0
		12		—	—	—	—	—
		>12		0	0	0	0	0
2	1	169			22		25	
		3		1	1	1	0	0
		9		—	—	—	—	—
		12		—	—	—	—	—
		>12		0	2	2	1	1
		3		2	0	0	0	0
		9		5	0	0	1	1
		12		9	1	1	0	0
2	2	>12		7	1	1	2	2
		3		0	0	0	0	0
		9		0	0	0	0	0
		12		0	0	0	0	0
2	3	>12		0	1	1	0	0

The relative incidence of visitation to individual flowers, hawking and gleaning for arthropods on bark and leaves during different seasons is indicated in Table 5. Data provided do not include foraging in the ground litter, which was rarely observed (five out of 1732 observations). More than 96% of all foraging records for *P. nigra* and *L. indistincta* were of birds visiting flowers. *P. nigra* and *L. indistincta* appeared to differ significantly in the main flowers that they used in March, but not in December. In June and September, populations of *P. nigra* were very small, making it difficult for us to gather an adequate number of observations of foraging behaviour. Nevertheless, *P. nigra* appeared to be less inclined to forage on flowers, bark or leaves in eucalypt species than was *L. indistincta* at these times. *M.*

**Table 2. Abundances and mean flower densities of plant species visited by honeyeaters**

The term 'flower' is used loosely; for *B. attenuata*, *D. sessilis*, *B. prionotes* and *D. carduacea* it denotes inflorescences composed of numerous tightly packed florets. Counts for sites 1 and 2 are means for seasons from 1977 to 1980, those for site 3 are means for seasons from 1979 to 1981

Plant species	Plants per ha	Flowers per plant				Flowers per hectare			
		Mar.	June	Sept.	Dec.	Mar.	June	Sept.	Dec.
Site 1									
<i>Adenanthes argyrea</i>	35	—	—	—	8	—	—	—	280
<i>Banksia attenuata</i>	5	—	—	—	3	—	—	—	15
<i>Calothamnus quadrifidus</i>	8145	—	—	—	135	—	—	—	$1 \times 10^6$
<i>Eucalyptus macrocarpa</i>	3	—	—	—	22	—	—	—	6
Site 2									
<i>A. argyrea</i>	61	—	—	11	—	—	—	671	—
<i>A. cygnorum</i>	182	—	5	25	—	—	910	4550	—
<i>Anigozanthos humilis</i>	70	—	—	3	—	—	—	210	—
<i>C. quadrifidus</i>	47	—	—	25	120	—	—	1175	5640
<i>C. sanguineus</i>	23	—	55	—	—	—	1265	—	—
<i>Dryandra sessilis</i>	214	—	7	16	—	—	1498	3424	—
<i>Eucalyptus drummondii</i>	56	—	700	500	—	—	39200	28000	—
<i>E. wandoo</i>	51	—	1200	—	—	—	—	61200	—
Site 3									
<i>A. cygnorum</i>	4	15	30	21	—	60	120	84	—
<i>Banksia prionotes</i>	5	6	1	—	—	30	5	—	—
<i>Dryandra carduacea</i>	17	—	—	211	—	—	—	3587	—
<i>D. sessilis</i>	15	2	12	47	—	30	180	705	—
<i>E. wandoo</i>	41	5	1000	20	—	205	41000	820	—

**Table 3. Mean standing crops and equivalent sucrose concentrations (w:v) of nectar from plants**

Values for standing crops are means from 20 flowers sampled during approximately the first and third hours after dawn, 10 flowers in each hour. Data from sites 1 and 2, except for March (site 3)

Plant species	Nectar crop ( $\mu\text{l}$ per flower)				Sucrose concentration (%)			
	Mar.	June	Sept.	Dec.	Mar.	June	Sept.	Dec.
<i>A. argyrea</i>	—	—	4.1	1.3	—	—	30.4	27.8
<i>A. cygnorum</i>	0.7	0.5	7.0	—	22.3	7.0	21.7	—
<i>A. humilis</i>	—	—	5.6	—	—	—	20.5	—
<i>B. attenuata</i>	—	—	—	100.2	—	—	—	15.5
<i>B. prionotes</i>	67.8	16.0	—	—	18.2	16.1	—	—
<i>C. quadrifidus</i>	—	—	5.8	5.0	—	—	26.7	25.4
<i>C. sanguineus</i>	—	0.9	—	—	—	25.7	—	—
<i>D. carduacea</i>	—	—	17.4	—	—	—	27.9	—
<i>D. sessilis</i>	—	27.1	43.5	—	—	22.5	25.2	—
<i>E. drummondii</i>	—	0.5	9.6	—	—	21.1	23.8	—
<i>E. macrocarpa</i>	—	—	—	82.0	—	—	—	12.0
<i>E. wandoo</i>	—	1.1	—	—	—	20.7	—	—

**Table 4. Relative abundances of arthropods collected in pitfall traps and sweep nets**

Values are numbers of species, followed by numbers of individuals. Data for March from site 3, for June and September from site 2, for December from site 1. Ants were invariably the most abundant of the Hymenopterans trapped

Order	Number in pitfall traps				Number in sweep nets			
	Mar.	June	Sept.	Dec.	Mar.	June	Sept.	Dec.
Acarina	—	3, 3	—	4, 11	—	—	—	—
Araneae	3, 3	—	2, 8	—	2, 3	3, 3	3, 4	4, 4
Blattodea	—	—	—	—	1, 1	—	—	—
Coleoptera	3, 5	3, 3	8, 230	—	6, 10	1, 1	9, 11	3, 8
Collembola	4, 4	23, 70	2, 14	2, 8	—	2, 4	1, 1	—
Dermaptera	1, 1	1, 1	—	1, 1	—	—	—	—
Diptera	3, 39	1, 1	8, 38	5, 9	—	4, 6	8, 14	1, 3
Heteroptera	1, 1	—	—	—	4, 31	2, 7	5, 6	1, 1
Homoptera	1, 1	—	1, 2	1, 1	1, 10	1, 1	3, 3	1, 1
Hymenoptera	16, 81	7, 21	6, 145	5, 200	1, 1	2, 2	3, 12	6, 13
Lepidoptera	1, 1	1, 1	—	—	—	—	1, 1	2, 4
Neuroptera	—	—	—	—	—	—	1, 1	—
Orthoptera	1, 1	—	1, 3	—	—	—	1, 1	—
Psocoptera	—	—	—	—	—	1, 1	2, 2	1, 1
Thysanoptera	—	—	—	—	1, 1	—	—	1, 1
Total	34, 139	39, 100	28, 440	18, 230	16, 57	16, 25	37, 56	20, 36

**Table 5. Relative incidence of flower-probing, hawking, and gleaning of arthropods from bark and leaves**

Observations made June 1979–March 1981; foraging in ground litter excluded. Values in parentheses under 'Probing of flowers' are the percentages for the two major plant species probed: *Ac*, *Adenanthera cygnorum*; *Bp*, *Banksia prionotes*; *Cq*, *Calothamnus quadrifidus*; *Ds*, *Dryandra sessilis*; *Ed*, *Eucalyptus drummondii*; *Ew*, *E. wandoo*

Month	Species	No. of birds	Total No. of feeding actions	Probing of flowers (%)	Hawking (%)	Gleaning (%)
Mar.	<i>L. indistincta</i>	12	116	98·2 (86·2 <i>Bp</i> , 7·8 <i>Ew</i> )	0·9	0·9
	<i>P. nigra</i>	47	530	96·8 (89·6 <i>Bp</i> , 4·7 <i>Ac</i> )	1·5	1·7
June	<i>L. indistincta</i>	19	200	99·1 (87·5 <i>Ew</i> , 10·5 <i>Ds</i> )	0·5	0·5
	<i>P. nigra</i>	2	9 <sup>A</sup>	—	—	—
Sept.	<i>L. indistincta</i>	43	437	96·6 (52·2 <i>Ed</i> , 27·7 <i>Ds</i> )	1·6	1·8
	<i>P. nigra</i>	2	12 <sup>A</sup>	—	—	—
Dec.	<i>L. indistincta</i>	29	308	98·0 (97·7 <i>Cq</i> )	1·3	0·7
	<i>P. nigra</i>	15	115	98·2 (98·2 <i>Cq</i> )	0·9	0·9

<sup>A</sup> Not enough birds observed for percentages to be calculated.

**Table 6.** Arthropod material and pollen grains present in faecal samples

Arthropod abundance: rare, <3 arthropods per sample; common, >3. Values in parentheses are percentages of groups in samples (hymenopterans mainly ants). Pollen abundance: +, <5 grains per field of view; ++, 5–20; +++, >20. *Ds*, *D. sessilis*; *Ac+Aa*, *A. cygnorum*+*A. argyrea*; *Cq+Cs*, *C. quadrifidus*+*C. sanguineus*; *Ed+Ew*, *E. drummondi*+*E. wandoo*; *Ah*, *A. humilis*; *Em*, *E. macrocarpa*; *Ba+Bp*, *B. attenuata*+*B. prionotes*

Species	Month	<i>N</i>	Arthropod abundance	Major arthropod group(s)	<i>Ds</i>	Abundance of pollen grains from:					
						<i>Ac+Aa</i>	<i>Cq+Cs</i>	<i>Ed+Ew</i>	<i>Ah</i>	<i>Em</i>	<i>Ba+Bp</i>
<i>L. indistincta</i>	Mar.	5	Rare	Hymenoptera (100) Larvae (40)		+		++			++
	June	10	Rare	Hymenoptera (80)	+		++	+++			
	Sept.	27	Rare-common	Hymenoptera (81)	++	+	+	++			
	Dec.	7	Rare-common	Diptera (71) Lepidoptera (43)		+	++			+	
<i>P. nigra</i>	Mar.	9	Rare	Hymenoptera (67)	+	+	+	++			++
	June	2	Rare	?	+	+		+			
	Sept.	5	Rare-common	Hymenoptera (80)	++	+	++				
	Dec.	10	Rare-common	Hymenoptera (90) Diptera (40)			++			+	+
<i>M. brevirostris</i>	Mar.	0	—	—				+			
	June	2	Rare	?					+		
	Sept.	2	Common	?	+	+	+	++			
	Dec.	2	Common	?		+	+			+	

Table 7. Source of pollen grains in smears taken from beaks, throats and foreheads of honeyeaters

Abbreviations of plant species as in Table 6

Species	Month	N	Total pollen grains counted	Ds	Percentage of pollen grains from:					
					Ac + Aa	Cq + Cs	Ed + Ew	Ah	Em	Ba + Bp
<i>L. indistincta</i>	Mar.	5	2553	0·2	69·8	2·4	0·7	—	—	26·9
	June	20	7590	12·2	—	78·1	9·7	—	—	—
	Sept.	33	22345	5·9	48·6	43·3	2·0	0·2	—	—
	Dec.	9	7682	—	9·1	90·8	—	—	0·01	—
<i>P. nigra</i>	Mar.	13	5351	2·4	47·3	—	0·5	—	—	49·6
	June	5	4029	12·7	0·3	86·3	0·7	—	—	—
	Sept.	8	6306	2·1	48·3	46·3	2·8	0·5	—	—
	Dec.	12	7965	—	6·9	89·8	—	—	2·1	1·2
<i>M. brevirostris</i>	Mar.	0	—	—	—	—	—	—	—	—
	June	4	1040	5·6	0·9	57·4	36·1	—	—	—
	Sept.	2	930	3·4	30·1	17·0	47·3	2·2	—	—
	Dec.	3	1355	—	17·3	82·7	—	—	—	—

*brevirostris* was observed foraging in the vegetation on only a few occasions, mainly in winter and spring; at these times, it fed on flowers, bark and leaves in eucalyptus as well as in various components of the shrub layer.

Results obtained by microscopic analysis of facial and faecal smears are summarized in Tables 6 and 7. It is apparent that arthropods are ingested by all three species of honeyeater at different times of the year. There is also some evidence to suggest differences in preferences for arthropods, although samples are small and the technique used gives no indication of the absolute quantities of material ingested. The pollen grain data confirm direct observations that each honeyeater species visits a variety of plant species, with no clearcut fidelity to species. They also suggest that the three honeyeater species are similar in the range of plants visited during a given season.

## Discussion

Evidence obtained in this investigation clearly supports the contention that there were seasonal variations in the population densities of *L. indistincta*, *P. nigra* and *M. brevirostris* at the three study sites. Despite a general decline in relative densities from 1977 to 1979, which may have been associated with a period of below-average rainfall in the Wongamine region (Masters, personal communication), those honeyeaters present in the reserve appeared to be concentrated at sites where plants were in flower (Fig. 1; Table 2). Disregarding apparently low densities of birds in December of 1977 and 1980, when conditions were very windy and not conducive to the use of mist nets, densities for *L. indistincta*, *P. nigra* and *M. brevirostris* were higher in summer than at other times of the year. This does not imply large-scale migration of these species into the reserve from other areas. It is more likely that the high December values were due to the concentration of birds already in the reserve into site 1, which contained virtually the only plants in flower there at this time. Site 1 was so small, in relation to the reserve, that there was probably significant emigration from the reserve during summer. In support of this contention, Collins (1980) has indicated a dearth of nectarivores in the reserve during January and February, when there were virtually no plants in flower. Nevertheless, banding-recapture data indicate that some honeyeaters moved seasonally within the reserve, to regions where there were suitable food supplies (Table 1). The overall level of recapture for banded birds was not high (12.1%), yet the fact that 24 banded birds were netted at the same sites 12 months or more later suggests that at least some members of the nectarivore populations may have been relatively sedentary. Keast (1968) has suggested that *L. indistincta* shows a much greater degree of nomadism than *P. nigra* or *M. brevirostris*. Insufficient data have been collected in the present study, however, to permit speculation on this point for the Wongamine region.

The movement of honeyeaters into areas where there is an abundance of flowers is not unique to Wongamine, and has been documented elsewhere by several investigators (e.g. Keast 1968; Ford and Paton 1977; Ford 1979; Pyke 1980). An obvious interpretation of this phenomenon is that the birds rely upon the flowers. It is by no means certain, however, that nectar is the sole proximate reason for this association. For instance, the almost universal occurrence of arthropods in faecal samples produced by honeyeaters at Wongamine, together with the low incidence of hawking and gleaning, suggests that birds may have ingested arthropods during part of the time that they probed flowers (Tables 5, 6). This proposition is supported by

the fact that many of the flowers, especially those of *Dryandra sessilis*, *D. carduacea*, *Banksia attenuata* and *B. prionotes*, had an attendant arthropod fauna of ants, flies, bees and moths at various times of the year; fragments of such arthropods were frequently identified in faecal samples (Table 6). Nevertheless, the substantial reductions in the standing crops of nectar, during the first few hours after dawn (Collins, unpublished data), are reminiscent of the situation in South Australia described by Ford (1979), and suggest that the honeyeaters were also ingesting significant quantities of nectar. This explanation is consistent with the observation that, in general, the plant species with the greatest nectar energy potential in any given season were the ones whose flowers were most frequently visited by honeyeaters (Tables 5, 8).

**Table 8. Ranking of plant species according to their importance as sources of pollen grains, and of available energy from nectar**

Abbreviations for plant species as in Table 6; species listed in order of decreasing importance. Energy available from nectar in early morning calculated from data in Tables 2 and 3, assuming 1 mg sucrose in nectar equivalent to 16.74 J of energy

Pollen	Ranking of plant species in:			
	Mar.	June	Sept.	Dec.
<i>L. indistincta</i>				
Facial	<i>Ac, Bp, Cs</i>	<i>Cs, Ds, Ed+Ew</i>	<i>Ac+Aa, Cs+Cq, Ds</i>	<i>Cq, Aa, Em</i>
Faecal	<i>Bp, Ew, Ac</i>	<i>Ed+Ew, Cs, Ds</i>	<i>Ed+Ew, Ds, Ac+Aa</i>	<i>Cq, Aa, Em</i>
<i>P. nigra</i>				
Facial	<i>Bp, Ac, Ds</i>	<i>Cs, Ds, Ed+Ew</i>	<i>Ac+Aa, Cs+Cq, Ed+Ew</i>	<i>Cq, Aa, Em</i>
Faecal	<i>Bp, Ew, Ac</i>	<i>Ds, Ac, Ed+Ew</i>	<i>Ds, Cs+Cq, Ac+Aa</i>	<i>Cq, Ba, Em</i>
<i>M. brevirostris</i>				
Facial	—	<i>Cs, Ed+Ew, Ds</i>	<i>Ed+Ew, Ac+Aa,</i> <i>Cs+Cq</i>	<i>Cq, Aa</i>
Faecal	—	<i>Ed+Ew</i>	<i>Ed+Ew, Ds, Ac+Aa</i>	<i>Cq, Em, As</i>
Availability of energy	<i>Bp, Em, Ac</i>	<i>Ed+Ew, Em, Ac</i>	<i>Ed+Ew, Ds, Ac+Aa</i>	<i>Cq, Ba, Aa</i>

Pollen grains were present in virtually all of the faecal samples examined. Pollen is, however, unlikely to be of great nutritional significance to honeyeaters (Hopper and Burbidge 1979; Paton 1981), and is probably ingested accidentally with nectar and arthropods. Nevertheless, a study of pollen grains in the faecal samples and facial smears provides evidence in support of that gained by direct observation of honeyeaters' foraging behaviour. For instance, it confirms that honeyeaters do not rely upon single plant species when foraging, and extends the range of species to include plants that were rarely seen to be visited. Caution should be exercised, however, in the attempt to predict flower preferences on the basis of relative abundance of pollen grains in facial and faecal smears. The morphology of flowers and of honeyeaters' heads undoubtedly influence the quantities of pollen that the birds pick up and consume. Flowers could also vary in the amounts of pollen that they produce. Nevertheless, it is of interest that the plant species whose pollen grains are most abundant in faecal and facial smears are generally those seen to be most frequently visited by honeyeaters, and which offer the greatest nectar energy (Tables 6–8; in 9 out of 11 possible comparisons of energy availability with presence

of faecal pollen, at least one of the two top-ranking plant species was common; comparisons of energy availability and presence of faecal pollen rankings showed similar overlap in 11 out of 11 cases).

There is some evidence, both direct and circumstantial, of floral resource partitioning between the three honeyeater species, particularly in autumn and winter. For instance, the relatively long-billed *L. indistincta* appeared to visit flowers that have relatively long nectary-anther distances and styles, and tubular corollas (e.g. *B. prionotes*, *C. sanguineus*, *A. cygnorum* and *C. quadridifidus*), as well as those with shorter and more open flowers. *M. brevirostris*, which has a much shorter bill, seemed to be more restricted to open flowers, and was often seen foraging in eucalypts. Although *P. nigra* frequently foraged on flowers, bark or leaves in close proximity to *L. indistincta*, especially in the shrub-small tree layer of the vegetation, this species was not seen to make extensive use of eucalypt flowers. Nevertheless, circumstantial evidence for March and September suggests that *P. nigra* utilizes eucalypt flowers at least as much as does *L. indistincta* at these times (Tables 6, 7). Ford (personal communication) has found that relatively large honeyeaters, such as *Phylidonyris novaehollandiae* and wattlebirds, often feed on eucalypt flowers. The discrepancies between direct and indirect data in the present study may be due to the tight time constraints imposed by the project design. Observations were sometimes sporadic, and unequal attention was given to different patches of the vegetation, especially in seasons when several plant species were in flower.

Aggressive interaction between honeyeater species was rarely obvious at Wongamine. The only time that it has been observed was during each autumn, when nectar resources were confined mainly to the large inflorescences of *B. prionotes*. *P. nigra* was consistently more abundant than *L. indistincta* at site 3 during the morning, when standing crops of nectar were relatively large; later in the day *L. indistincta*, with its smaller total energy requirements, seemed to visit the flowers more frequently. The virtual absence of *M. brevirostris* could have been due to the difficulties that it would have encountered in extracting nectar from the deep inflorescences of *B. prionotes* (Hainsworth and Wolf 1976; Pyke 1980).

Observations reported in this paper regarding the low incidence of obvious capture of arthropods by *L. indistincta* and *P. nigra* are in accord with data obtained by some workers (e.g. Recher and Abbott 1970; Halse 1978), yet quite different from other data (e.g. Keast 1975; Recher 1977). These differences may be due to variations in the foraging strategies adopted by different populations of honeyeaters, or the time of year when observations were made. Another factor could be that some observations were biased by the inadvertent recording of the licking of manna or honeydew as gleaning for arthropods (Paton 1980). It was also suggested earlier in this paper that honeyeaters at Wongamine obtained some arthropods when probing flowers; flowers may not be such a profitable source of arthropods in other areas. Regardless of the source of arthropod material, it seems that *L. indistincta* and *P. nigra* ingest a variety of species, ranging from ants, in particular, to bees, wasps and flies. Insufficient faecal samples were obtained from *M. brevirostris* to provide a realistic indication of their arthropod preferences, although Ford (personal communication) has found that faeces from this species captured in Eastern Australia contained spiders, larvae, beetles and ants. Lea and Gray (1936) have also shown that the stomach contents of honeyeaters such as *L. indistincta*, *P. nigra*, and particularly *M. brevirostris*, contain a variety of arthropods. Virtually no other analyses of arthropod preferences by nectarivores have been reported, apart from

data obtained for the Cape sugarbird, *Promerops cafer*, feeding on *Protea repens* in South Africa (Mostert *et al.* 1980). At Wongamine there seemed to be a correlation between preferences and the availability of particular arthropod groups, apart from an apparent disinclination for honeyeaters to ingest coleopterans. This is at variance with data for *P. cafer* in South Africa, where beetles were abundant and constituted a substantial part of the diet.

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