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BEHAVIOUR AND ECOLOGY OF TWO SPECIES OF HONEYEATER

DAVID C. McFARLAND* and PETER F. SALE

School of Biological Sciences, Sydney University, Sydney, NSW 2006.
* Present address: Department of Zoology, University of New England, Armidale, NSW 2351.

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During the autumn and winter of 1980, the general behaviour and ecology of New Holland Honeyeaters and Little Wattlebirds was studied in heath and dry sclerophyll forest in the Royal National Park, NSW. The availability of certain foods (flying insects and nectar) was also measured. Both bird species had similar time budgets and engaged in inter- and intraspecific aggression. Hawking activity did not appear to be affected by the abundance of flying insects on either a daily or seasonal basis. Each honeyeater exhibited preferences in the plants used as nectar sources. Even though the abundance of all honeyeaters in the area increased as the density of *Banksia* inflorescences increased, when individual species were examined only two of the five present showed significant relationships.

INTRODUCTION

Several previous studies have described the behaviour and ecology, particularly that relating to foraging, of a number of honeyeater species (Keast and Condon 1968; Gravatt 1971; Recher 1977; Halse 1978; Thomas 1980). Recently more emphasis has been placed on measuring how much food, especially nectar, is present and how this affects the behaviour and abundance of honeyeaters (Ford 1979; Collins 1980; Ford and Paton 1982; Pyke 1983). In this paper we present data on the behaviour (time budgets and aggression) and ecology (relative abundance of birds, habitat and food resource use) of two sympatric species of honeyeater.

Over a period of six months between 28 February and 22 August 1980, two species of honeyeater were studied in the Royal National Park near Sydney, NSW. The species observed, the New Holland Honeyeater *Phylidonyris novaehollandiae* and the Little Wattlebird *Anthochaera chrysoptera* are both primarily nectarivorous (Pyke 1980) and are common in the coastal vegetation around Sydney (Hindwood 1944). Other honeyeater species regularly seen in the study area included the Tawny-crowned Honeyeater *Phylidonyris melanops,* Yellow-faced Honeyeater *Lichenostomus chrysops* and Eastern Spinebill *Acanthorhynchus tenuirostris.*

STUDY AREA

The work was carried out along the Uloola Ridge, which lies on the western edge of the Royal National Park, at an altitude of 200 to 240 m above sea level. Plants were identified using Beadle *et al.* (1972) and the plant communities were classified after Beadle and Costin (1952). In the study area two main types of vegetation were identified.

Heath: Expanses of heath lying along the saddle of the ridge were dominated by Proteaceae (*Banksia, Hakea* and *Isopogon* spp.). *Casuarina distyla, Angophora cordifolia* and *Darwinia fascicularis* were also common. The height of the heath ranged from 0.5 to 2.5 m.

Dry sclerophyll forest: This community consisted mostly of *Eucalyptus haemastoma, E. gummifera* and *Banksia serrata.* In some forest areas, *Banksia marginata* and *B. ericifolia* formed dense understoreys. Elsewhere the shrub layer was composed of low lying plants such as *Petrophile* and *Isopogon* spp.

The study area was completely devastated by a bushfire in November 1980.

METHODS

The activities of the birds were recorded (by DM) using 10 x 50 binoculars and a portable tape recorder. Each month at least 20 unmarked individuals of each species were observed in the morning (0700-1000 hours) and afternoon (1200-1500 hours) over four days of fine weather. Observation times averaged 111.5 ± 9.3 minutes per month for New Holland Honeyeaters and 137 ± 6.5 minutes per month for Little Wattlebirds (mean ± standard deviation, n = 6 for both). Behaviour was divided into perching (with further subdivisions of calling and preening), flying (which included hawking flights and chases), and foraging (which included probing of flowers, gleaning of insects and non-flight movements). As part of the time budget, how long each bird stayed at heights greater than and less than four metres in plants, and the type of plant visited, was also noted. Codewords were used to describe the actions and locations of the birds. The information was later transcribed from cassettes to a pen recorder from which the frequency and duration of behaviours were measured.

The relative abundance of the honeyeaters in the study area was estimated by walking along a 0.75 km transect at 0700 hours three to four times each month. The numbers of each honeyeater species found within 50 m of either side of the path were recorded.

Availability of nectar, as densities of fresh flowers or inflorescences, was determined using four sites. Each site was of 30 m diameter with two located in the heath and two in the forest. In all sites the main flowering plants were *Banksia* species. Only fresh inflorescences, i.e. those with some styles extended, were counted since they were the only ones seen visited by the honeyeaters. Other flowering plants in the sites included *Darwinia fascicularis* and *Lambertia formosa.*

The abundance of airborne arthropods was measured using 12 small, plywood boards coated with a sticky gum ("Bird Tanglefoot"). The boards were arranged vertically at various heights (0.5-8.0 m above the ground) between 0630 and 1030 hours and again between 1100 and 1500 hours. After each period the boards were collected and the arthropods identified and counted. Insects were classified to Order using Grigg (1977). Since 94% of all animals collected were insects from here on the term "insects" will signify all arthropods.

RESULTS

Time Budgets

Table 1 summarises the information as to how the two honeyeater species spent their time awake. For each species all data were combined since there were no biologically significant differences in the mean percentage times over either the months or time of day (three-factor ANOVAs*).

In general, the New Holland Honeyeaters were more active than the Little Wattlebirds, spending significantly more time flying and foraging (Table 1). The wattlebirds perched for longer periods of time and engaged in calling to a greater extent than the New Holland Honeyeaters. Both spent similar proportions of time preening.

Aggression

Both New Holland Honeyeaters and Little Wattlebirds attacked other honeyeater species as

**Analysis of variance*

TABLE 1

Time budgets of New Holland Honeyeaters and Little Wattlebirds (mean ± standard deviation).

Species[a]	Total time (h)	Percentage total time spent				
		Perching	Calling	Preening	Flying	Foraging
LW	12.7	81.1 ± 2.2	2.7 ± 0.8	1.4 ± 1.1	6.3 ± 1.4	8.5 ± 1.7
NHH	11.6	75.8 ± 1.6	0.9 ± 0.6	1.4 ± 0.6	11.1 ± 1.9	10.5 ± 1.5
Significance[b]		**	**	N.S.	**	**

a — Little Wattlebird and New Holland Honeyeater have been abbreviated in tables and figures as LW and NHH respectively.

b — differences found between species using three factor analysis of variance (ANOVA); ** = $p < 0.01$, N.S. = non-significant.

well as conspecifics (Table 2). In all cases observed the attacker was successful in driving off the other bird. The proportion of attacks by New Holland Honeyeaters that were intraspecific was significantly greater than that of the wattlebirds (Contingency $X^2 = 7.1$, df = 1; $p < 0.01$). While the two species differed in their degree of intraspecific aggression (New Holland Honeyeater = 7.3, Little Wattlebird = 1.3 attacks/hour observed), both had similar rates of interspecific aggression (New Holland Honeyeater = 2.6, Little Wattlebird = 2.7 attacks/hour). Even though wattlebirds are larger than New Holland Honeyeaters (70g cf. 20g Paton 1979), the former were still often attacked by the latter (Table 2). Most interspecific encounters involved a pair of New Holland Honeyeaters chasing a single wattlebird.

Although no birds were banded it appeared that certain individuals of both species were defending territories. This was based on observations of birds, found in certain locations, which were consistently aggressive toward other honeyeaters that moved into the area. For the Little Wattlebirds these areas included particular *B. ericifolia* and *Erythrina* trees which were flowering, while for New Holland Honeyeaters the areas were those containing a nest. Active nests of New Holland Honeyeaters were found in March (1 nest), April (3), May (3), June (1) and August (1). Most (6 nests) were located in the heath but this may have been biased since birds defending sites in the heath were more easily noticed than those in the forest. No active wattlebird nests were found during the study.

Honeyeater Abundance

The mean number of each species (birds/transect) observed each month is shown in Figure 1. New Holland Honeyeaters were by far the most common species, with relatively constant numbers throughout the study. Second most common were the Little Wattlebirds which became less abundant as the study progressed. Yellow-faced Honeyeaters were only common in April, Eastern Spinebills during May to June, while small numbers of Tawny-crowned Honeyeaters were reported in all months .

TABLE 2

Records of aggressive encounters where Little Wattlebirds and New Holland Honeyeaters were the attacking species. (Data from all time budgets combined, number in parentheses is % encounters that were intraspecific.)

Species attacked	Species attacking	
	LW	NHH
Little Wattlebird	16	16
New Holland Honeyeater	26	85
Yellow-faced Honeyeater	5	6
Eastern Spinebill	3	8
Total	50 (32.0)	115 (73.9)

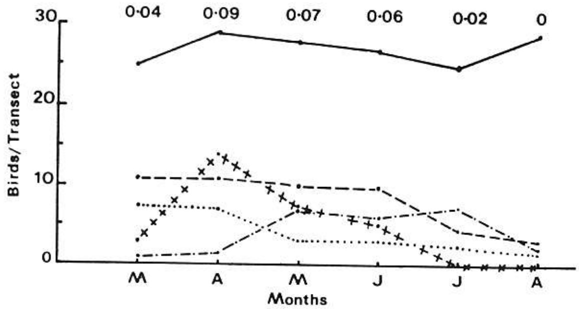

Figure 1. *Mean number of honeyeaters observed per transect over six months (———New Holland Honeyeater; - - - Little Wattlebird; . . . Tawny-crowned Honeyeater; xxxx Yellow-faced Honeyeater; — . — . — . Eastern Spinebill). Numbers above each month are the mean densities of productive Banksia inflorescences in the area (inflorescences/m²).*

All species, with the exception of the Little Wattlebirds and the Tawny-crowned Honeyeaters, were found in both heath and forest habitats. The wattlebirds were only seen in the forest while the Tawny-crowned Honeyeaters were only in the heath.

The numbers given in Figure 1 must be considered coarse estimates since each honeyeater species would have different levels of detectability in the forest and heath, and the results for each were not kept separate.

Habitat Use

While the Little Wattlebirds were only found in the dry sclerophyll forest, the New Holland Honeyeaters used both the forest and heath (Table 3). For both species, use of the banksias increased markedly when the plants flowered (Table 3). From July onwards however, each honeyeater began using different nectar sources with Little Wattlebirds in *Erythrina* trees and New Holland Honeyeaters in the *Darwinia* shrubs (both plants designated as 'Others' in Table 3). Throughout the study, eucalypts were used a great deal by both honeyeaters irrespective of whether there were flowers present or not.

Generally, wattlebirds used forest vegetation above the four metre level rather than below, while the New Holland Honeyeaters visited each zone for approximately equal amounts of time. New Holland Honeyeaters in the heath used plants mostly below four metres simply because there was little vegetation taller than three metres. These birds however did show a distinct

TABLE 3

Habitat use by the Little Wattlebird and New Holland Honeyeater (numbers are the percentages of the time the birds were observed in vegetation; flowering periods of the plants are in parentheses).

Plant	Height	Mar.			Apr.			May			June			July			Aug.		
group	(m)	LW	NH[a]	NH[b]	LW	NH	NH	LW	NH	NH	LW	NH	NH	LW	NH	NH	LW	NH	NH
Eucalyptus species	>4	44	56	25	66	34	13	75	48	14	67	40	16	58	46	13	60	37	15
(Mar.)	<4	24	22	36	8	28	27	4	20	31	8	24	24	2	18	25	2	24	28
Banksia serrata	>4	10	0	0	0	1	0	0	0	4	0	2	0	0	3	0	0	0	0
(Mar.)	<4	19	8	8	2	4	14	0	5	1	1	3	3	1	4	2	0	4	4
B. marginata	>4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
(Mar. - June)	<4	0	4	11	17	8	15	9	7	10	5	11	0	2	4	3	0	4	2
B. ericifolia	>4	0	0	0	0	0	0	1	0	0	12	0	0	18	7	0	1	5	0
Apr. - Aug.)	<4	2	1	3	6	19	14	9	14	24	6	12	28	3	11	16	2	11	5
'Others'[c]	>4	0	0	0	0	0	0	0	1	0	0	0	0	10	1	0	31	5	2
(June - Aug.)	<4	1	9	17	1	6	17	2	5	16	1	8	29	6	6	41	4	10	44

a — New Holland Honeyeaters in forest.
b — New Holland Honeyeaters in heath.
c — includes *Erythrina* sp. (used by Little Wattlebirds) and *Darwinia, Leptospermum* and *Casuarina* spp. (used by New Holland Honeyeaters).

preference for those eucalypts over four metres. The recorded amount of time spent in those trees was possibly biased since birds sitting in them were more easily noticed and observed than those within the heath.

Use of Food Resources. I — Flying Insects

The numbers of aerial insects in both the morning and afternoon periods changed markedly over time in both habitats (Figure 2). However the mean total numbers for both periods combined did not vary greatly from month to month, with the exception of July (Figure 2). Insect sizes were not recorded but it was noticed that the majority of insects caught in winter were smaller ($<$ 5 mm in length) than those trapped in early autumn.

In every month except May, the total numbers of flying insects in the forest were significantly greater than in the heath (X^2 tests, $p < 0.05$). Most of the insects captured were dipterans (78.8%,) ranging from tiny midges to large flies. Hymenopterans (winged ants and wasps) accounted for 10.4% while 4.8% were coleopterans. The remaining 6.0 % of the animals trapped included hemipterans, lepidopterans and arachnids.

An analysis of the number of hawking flights undertaken by honeyeaters revealed significant differences between the species and among the six months (three factor ANOVA, $F_{1,456} = 4.0$, $p < 0.01$). New Holland Honeyeaters, in both in the morning and afternoon, hawked significantly more than the Little Wattlebirds (Figure 3; Student Newman Keuls, $p < 0.05$ in all cases; overall means New Holland Honeyeater $= 1.5$ and Little Wattlebird $= 0.4$ hawking flights/min observed). While the New Hollands showed significant changes in hawking during the study (each month's average was significantly different from the previous month, SNK, $p < 0.05$ in all cases), the hawking of the Little Wattlebirds varied only slightly over the same period (Figure 3).

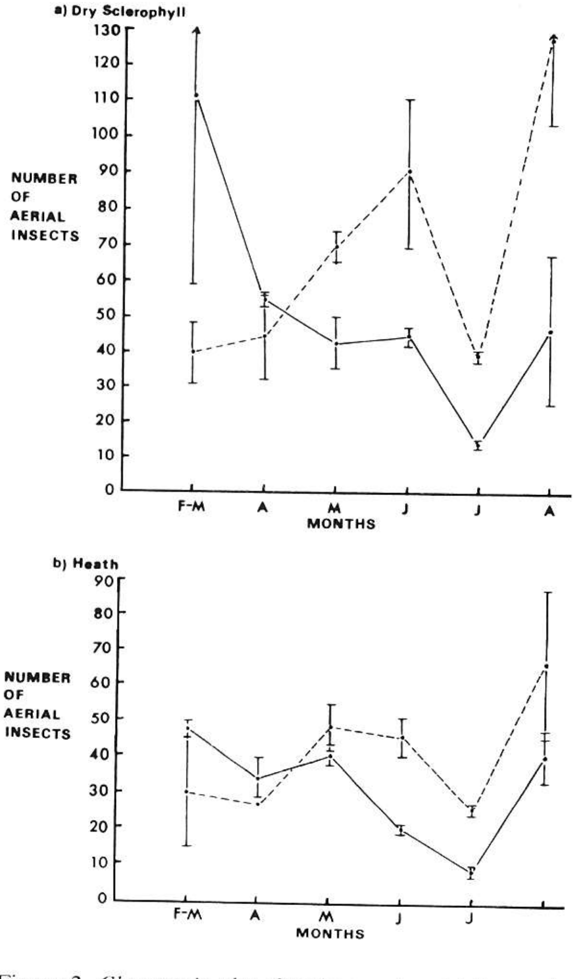

Figure 2. *Changes in the abundance of aerial insects in the morning (———) and afternoon (- - - -) in dry sclerophyll forest and heath. (Numbers of flying insects caught/4h; mean ± standard deviation.)*

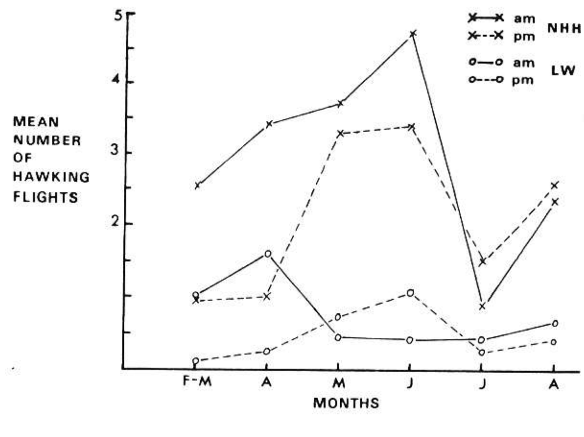

Figure 3. *Number of Hawking Flights, in the morning and afternoon, by Little Wattlebirds and New Holland Honeyeaters (flights/100 s of observation).*

TABLE 4

Vertical distributions of honeyeater hawking activity and flying insects.

Bird species	Height (m)	No. (& %) Hawking Flights	Proportion Time in Height Zone	Total No. Insects Caught Per Board*
LW (forest)	>4	210 (78.4)	74%	48.0
	<4	58 (21.6)	26%	64.9
NHH (forest)	>4	232 (48.0)	48%	48.0
	<4	251 (52.0)	52%	64.9
NHH (heath)	>4	48 (8.9)	17%	17.5
	<4	494 (91.1)	83%	45.4

* Each board had 157 cm^2 of sticky surface.

For both species of honeyeater, the number of hawking flights in particular height zones was proportional to the percentage of time they spent in those zones (Table 4). In the forest and heath the distribution of hawking flights by New Holland Honeyeaters also corresponded to the abundance of aerial insects in the two height zones. Overall, the Little Wattlebirds hawked more often above four metres even though there were just as many insects in the lower zone.

We tested to see if the abundance of flying insects in the habitats, at particular times of the day over the six months, was correlated with the number of hawking flights made by the honeyeaters in the same periods. For the wattlebirds a significant correlation occurred only in the afternoon (am, $r = 0.67$, $p > 0.05$; pm, $r = 0.82$, $p < 0.05$; $n = 6$ for both). For forest dwelling New Holland Honeyeaters (am, $r = -0.12$; pm, $r = 0.77$, $p > 0.05$ and $n = 6$ for both) and those in heath (am, $r = 0.50$; pm, $r = 0.65$; $p > 0.05$ and $n = 6$ for both) there were no significant correlations. In all cases the afternoon coefficients were higher than the morning ones.

Use of Food Resources. II — Nectar.

For most of the study banksias were the main flowering plants in the sites. *Banksia ericifolia* dominated the heath while *B. serrata* was found in the forest. A few *B. marginata* were scattered in both the heath and forest sites. *Lambertia* flowers were uncommon and *Darwinia* was a totally unexpected nectar source since it has been previously noted as only one of many minor plants visited by honeyeaters (Recher 1971). In July it became a major nectar source for New Holland Honeyeaters in the heath (Table 3). During August most nectar feeding by Little Wattlebirds was on the flowers of five Coral Trees (*Erythrina* sp.) sited between a road and the edge of the dry sclerophyll forest. New Holland Honeyeaters in the forest continued to feed on the remaining *B. ericifolia* inflorescences.

The extent to which each nectar source was used by the two honeyeater species was determined by comparing the total number of birds observed feeding at the various sources (Table 5). *Banksia serrata, B. marginata* and the *Erythrina* sp. were visited more frequently by Little Wattlebirds than New Holland Honeyeaters, while the reverse was true for *B. ericifolia* and *D. fascicularis* (Table 5).

TABLE 5

Nectar sources used by Little Wattlebirds and New Holland Honeyeaters (total of 240 birds observed for each species, N.S. = non-significant).

Plant group	Number of birds visiting plant to feed		Significance
	LW	NNH	(X^2 test)
Eucalyptus species	17	15	N.S.
Banksia serrata	17	5	$p<0.05$
B. marginata	39	21	$p<0.05$
B. ericifolia	59	93	$p<0.005$
Darwinia fascicularis	0	27	$p<0.005$
Erythrina species	28	1	$p<0.005$

Within the sites the trees used most for nectar feeding were those with the greatest numbers of inflorescences. A correlation between the total time spent in a particular *B. serrata* plant (during which probing was observed) by either honeyeater species, and the number of productive inflorescences in that plant was significant ($r = 0.97$, $n = 6$; $p < 0.05$). There was also a positive correlation between the time spent in *B. ericifolia* bushes and the number of productive inflorescences they carried ($r = 0.89$, $n = 4$; $p > 0.05$). In *Darwinia,* the density of flower clusters and the time spent in the clump by New Holland Honeyeaters was significantly correlated ($r = 0.88$, $n = 12$; $p < 0.01$).

To examine the relationship between flowering and honeyeater abundance we performed correlations using the mean density of productive banksia inflorescences (Figure 1, inflorescences/ m^2) and the mean numbers of birds seen on a transect each month (Figure 1). The coefficient for all honeyeaters combined was highly significant but among the individual species the coefficients were of variable significance (Table 6). Examination of the r^2 values (Table 6) revealed that of the five honeyeater species only for the Little Wattlebirds and Yellow-faced Honeyeaters was a substantial amount of the variation in bird numbers accounted for by inflorescence density. As always one must be careful when inferring casualty from statistical correlations (Nie *et al.* 1975).

TABLE 6

Relations between mean numbers of honeyeaters observed per month (birds/transect) and the mean density of productive banksia inflorescences inflorescences/ cm^2) ($n = 6$ in all cases).

Birds	Correlation coefficient (r)	r^2	Significance
All honeyeaters	0.928	0.861	$p<0.01$
Little Wattlebird	0.856	0.733	$p<0.05$
New Holland Honeyeater	0.249	0.062	$p>0.10$
Tawny-crowned Honeyeater	0.469	0.220	$p>0.10$
Yellow-faced Honeyeater	0.941	0.885	$p<0.01$
Eastern Spinebill	0.021	0.000	$p>0.10$

DISCUSSION

Given that the two species studied are so different in size it is not surprising that there are some differences in their time budgets. However, despite the statistical significance of the differences, New Holland Honeyeaters and Little Wattlebirds had similar divisions of time. Birds of both species spent most of their time perching with only 15 to 21% of their time allocated to foraging and flying activities. This is quite different to the time budgets recorded for the same species in Victoria (Paton 1979, 1982a). Paton (*loc. cit.*) observed New Holland Honeyeaters spending between 45 and 93% of their time feeding on *Banksia marginata,* while Little Wattlebirds spent an average of 42% of their of their time nectar feeding. These percentages are markedly greater than those we recorded. The differences may be due to variations in the nectar sources used, e.g. differences in flower structure, density and richness (J/flower), which may result in the birds requiring more or less foraging time to satisfy their daily energy needs.

Honeyeaters are generally regarded as being pugnacious toward both their own and other species (Immelmann 1961). Both the New Holland Honeyeaters and Little Wattlebirds observed in this study exhibited intra- and interspecific aggression. The frequency of attacks by these species against conspecifics and other honeyeater species was proportional to the overall mean abundance of each species attacked, as determined by transect counts (New Holland Honeyeater $r = 0.99$, Little Wattlebird $r = 0.93$, $n = 4$ and $p < 0.02$ in both cases). It appears then that the frequency of aggression by New Holland Honeyeaters and wattlebirds toward other honeyeaters (including conspecifics) is influenced by the relative abundance of, and hence the likelihood of encounter with, other honeyeaters in the area.

The basic aim of aggression is to gain access to some resource, e.g., food, mates, shelter (Kaufman 1983). In this study Little Wattlebirds appeared to be actively defending nectar resources by the use of aggression and calling (McFarland 1984). The same species has also been observed defending nectar sources in Victoria (Paton 1979). New Holland Honeyeaters are known to hold feeding territories (Paton 1982a) but in this study only nest sites seemed to be defended. New Holland Honeyeaters occupying small breeding territories centred on the nest has been noted by Recher (1971) in a population north of Sydney.

In terms of habitat use there are some marked differences between the two species, the most conspicuous being the absence of Little Wattlebirds from the heath while the New Holland Honeyeaters occupy both heath and forest habitats. Stands of tall trees (> 4m) appear to be a basic requirement for Little Wattlebirds even though they will visit shrubs below four metres to feed (Table 3). This species' tendency to use vegetation above four metres could be due to a need for a high perch for either hawking (the lower, denser foliage may reduce manoeuvreability), and/or a vantage point to watch for predators or territory intruders. New Holland Honeyeaters, being smaller than the wattlebirds, can move and hawk more easily in the denser vegetation below four metres. It may also be that the New Holland Honeyeaters are excluded, to some extent, from the higher vegetation by territorial wattlebirds. When plants are flowering the time spent by each honeyeater species in either height zone seems to be determined by the distribution of the flowers, e.g., flowers of eucalypts and *B. serrata,* were all above four metres, those of *B. ericifolia* were in both zones, while those of *B. marginata* were all below four metres. As this study was carried out over only six months of the year it is an incomplete analysis of the birds' habitat use.

New Holland Honeyeaters took far more aerial insects than the Little Wattlebirds. Wattlebirds may find hawking energetically too expensive compared to gleaning insects, and when they do hawk they may be selecting large prey items, such as moths (Recher 1971). In both the heath and forest habitats the amount of time spent and the number of hawking flights made by New Holland Honeyeaters above and below four metres corresponded closely to the abundance of aerial insects recorded in those height zones (Table 4). New Holland Honeyeaters may be dividing their time at various heights in response to the availability of flying insects, although the distribution of nectar and interactions with other honeyeaters may also influence vertical habitat use. The correlations between hawking activity and abundance of insects over the months and times of day revealed that both honeyeaters followed changes in the numbers of flying insects more closely in the afternoon. However, while insect numbers were greater in the afternoon most hawking activity by the birds took place in the morning. So while flying insects may be an important source of protein for the honeyeaters (Paton 1982a), the timing of hawking activity during the day or season by either species does not appear to be significantly influenced by the abundance of flying insects.

Honeyeaters have been reported as showing district preferences for certain species of flowers (Ford and Paton 1977). In this study New Holland Honeyeaters and Little Wattlebirds visited a range of nectar sources with some sources being used more often by a particular species of honeyeater. Reasons for such differential usage are numerous but can often be reduced to differences in the bird species energy needs, foraging efficiencies and interspecific dominance relations (Ford 1979). Although no significant correlation was found between the abundance of New Holland Honeyeaters and the density of banksia inflorescences over the months, this species did exhibit obvious preferences for those plants or areas with the highest densities of productive inflorescences (*Banksia* spp.) or flowers (*Darwinia* sp.). The importance of the extent of floral display in attracting honeyeaters has already been documented for *Correa, Callistemon* and *Eucalyptus* species (Paton 1982b).

One of the dogmas associated with honeyeaters is that the movements and abundance of birds in an area is directly related to some measure of the nectar availability in that area (e.g., J/ha or flowers/ha). With the exception of a few studies (Collins and Briffa 1982; Ford and Pursey 1982; Pyke 1983; Ford and Paton 1985) few quantitative results have been supplied to support or refute the idea. In this study we found that honeyeater numbers (birds/transect) did not necessarily fluctuate with changes in nectar availability (inflorescences/m^2). Of the five honeyeater species recorded in the area only the numbers of Little Wattlebirds and Yellow-faced Honeyeaters were highly correlated with inflorescence density (Table 6). These species may track nectar availability by either local movements, in the case of the wattlebirds, or during migrations, as in the Yellow-faced Honeyeaters (Keast 1968). The lack of correlations for the other three species (Table 6) could indicate that they do not track nectar or the results could be due to other factors, e.g., the influence of non-banksia nectar sources which were not measured

(*Darwinia* used by New Holland Honeyeaters in the heath in July and August) or changes in bird detectability (Tawny-crowned Honeyeaters not giving conspicuous flight display in winter months). Whether correlations are found to be significant or not there is unlikely to be a single factor which determines the numbers of honeyeaters in a given area.

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