

## Observations on the foraging ecology of honeyeaters (Meliphagidae) at Dryandra Woodland, Western Australia

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**Abstract.** Dryandra Woodland, a Class A conservation reserve, on the western edge of the Western Australian wheatbelt lacks the large congregations of nectar-feeding birds associated with eucalypt woodlands to the north and east of the wheatbelt. Reasons for this are not clear, but the most productive woodlands (Wandoo *Eucalyptus wandoo*) at Dryandra are dominated by Yellow-plumed Honeyeaters (*Lichenostomus ornatus*), which exclude smaller honeyeaters from their colonies. There is also comparatively little eucalypt blossom available to nectar-feeders during winter and spring when we conducted our research at Dryandra. During winter and spring, honeyeaters are dependent on small areas of shrublands dominated by species of *Dryandra* (Proteaceae), with species segregated by size; the smaller species making greater use of the small inflorescences of *D. sessilis* and *D. armata*, while the large wattlebirds used the large inflorescences of *D. nobilis*. Honeyeaters at Dryandra also use other energy-rich sources of carbohydrates, such as lerp and honeydew, and take arthropods, segregating by habitat, foraging behaviour, and substrate. The importance of *Dryandra* within Dryandra Woodland is particularly relevant to fire management. If *Dryandra* shrublands are burnt for fire management without ensuring adequate numbers of mature *Dryandra* plants are retained in the reserve, the nectar available to nectar-feeders could be reduced to levels at which some species could not be sustained within the reserve. Given the extensive land-clearing in the wheatbelt, this could adversely affect species survival in a regional context and affect the pollination of native plants.

**Keywords.** Honeyeaters, Meliphagidae, eucalypt woodlands, *Dryandra*, nectar-feeding, Western Australia.

### Introduction

Many honeyeaters depend on flowering plants for nectar throughout the year, and rely on a range of plant species that flower at different times of the year and have different floral characteristics (Keast 1968; Ford 1977; Ford and Paton 1977; Halse 1978; Pyke 1980). Other species use alternative carbohydrates (sap, honeydew, lerp, and manna) as their principal sources of energy (Paton 1980; Woinarski 1984; Loyn 1985; Recher *et al.* 1985). All honeyeaters require arthropods for protein, especially during moult and when breeding

(Recher and Abbott 1970; Ford and Paton 1976; Ford 1977; Pyke 1980).

Honeyeaters are dispersive species reliant on a sequence of nectar resources that differ in their spatial and temporal availability (Keast 1968; Ford 1977; Ford and Paton 1977; Halse 1978; Pyke 1980). Identifying nectar and other food resources in major habitat types is necessary to ensure that conservation of honeyeaters occurs on spatial and temporal scales large enough to accommodate the requirements of the birds. Without integrated landscape management, the risk is that the incremental loss of even small nectar resources in the sequence will cause the progressive decline of honeyeaters, regardless of the amount of nectar available at other times or locations (Recher 1999; Ford *et al.* 2001; H. A. Ford personal communication).

Dryandra Woodland is one of the largest remaining areas of natural vegetation in the Western Australian Wheatbelt and is notable for its comparatively intact



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biota. Dryandra Woodland has a rich honeyeater avifauna, but the Wandoo (*Eucalyptus wandoo*) and Powderbark Wandoo (*E. accedens*) woodlands characteristic of Dryandra are dominated by Yellow-plumed Honeyeaters (*Lichenostomus ornatus*), a colonial species, which excludes smaller birds from their colonies (Recher and Davis 1998; Wilson and Recher 2001; Recher and Davis unpublished data). This contrasts with the eucalypt woodlands to the north and east of the wheatbelt where nectar-feeders are abundant (Chapman and Kealley 2001; Recher and Davis 2002, 2010, unpublished data) and there are extensive woodlands, with abundant nectar, that are not dominated by Yellow-plumed Honeyeaters.

An objective of our work in Western Australia is to compare bird assemblages, including nectar-feeders, of different eucalypt woodlands. We therefore extended our studies at Dryandra to include shrublands where nectar-feeders congregated. In addition, we continued to work in wandoo woodlands to increase our observations of species for which we had limited data (see Recher and Davis 1998). The study reported here complements our earlier research, concentrating on areas of high nectar production, and focusing on honeyeaters. Our aims were to determine what honeyeaters were present at Dryandra Woodland during winter and spring, what nectar resources were available, and temporal patterns of nectar availability and use. In addition, we summarize the foraging ecology of honeyeaters in wandoo woodlands, adding data collected from 1996 to 2004 to that previously published (Recher and Davis 1998). Our objective was to contribute to a comprehensive account of the foraging ecology of honeyeaters at Dryandra, with the aim of assisting in the conservation and management of Dryandra's avifauna and of honeyeaters in southwestern Western Australia.

## Methods

### Study area

Dryandra Woodland is a Class A Conservation Reserve (centred on 32°45'S, 116°55'E) near the town of Narrogin 180 km southeast of Perth, Western Australia. Plots were chosen for an abundance of nectar-rich flowers, ease of access, and proximity to the wandoo woodlands studied by Recher and Davis (1998). The shrublands (Dry Ridge, Fire Tower, Malleefowl, Possum, and Sessilis) were dominated by one or more species of *Dryandra* (*D. nobilis*, *D. sessilis*, and *D. armata*). *Dryandra nobilis* is a tall shrub (to 3 m in height), with large inflorescences (8–22 cm long by 5–22 cm wide) on sturdy branches. *Dryandra sessilis* is also tall (to 6 m), but has smaller inflorescences and less sturdy branches. *Dryandra armata* is a generally a low shrub (<1 m), but can grow to 3 m. *Dryandra armata* had the smallest inflorescences and least sturdy branches.

Shrubland plots ranged in size from 2.2 to 10.1 ha (Table 1). Only *Dryandra sessilis* occurred on Sessilis. *Dryandra sessilis* was absent from Firetower, but *D. sessilis*, *D. nobilis*, and *D. armata* were present on Malleefowl, Dry Ridge, and Possum (Table 1). *Sessilis* was divided by a narrow (<2.5 m wide) dirt road and occurred on deep sandy soil at mid-slope where it was flat. The other plots were along ridges on lateritic soils adjacent to narrow roads.

WED recorded honeyeater foraging and estimated nectar abundance between 1 July and 7 October 1997. In November 1997, the density (no./m<sup>2</sup>) of each *Dryandra* species on the shrubland plots was measured. HFR censused the shrubland plots, recorded honeyeater foraging and estimated floral abundance between May 1998 and August 1999. HFR also recorded honeyeater foraging behaviour in wandoo woodlands at Dryandra between 1996 and 2004.

Dryandra Woodland is subject to annual fuel reduction burning. At the time the study was initiated, all plots had been unburnt for more than ten years. Shortly after HFR commenced counts in May 1998, Dry Ridge was burnt, while Sessilis was burnt after counts in August 1999, both as part of fuel reduction burns. After burning, work on both plots ended, because no dryandras were flowering.

### Floristics and flower abundance

The area and density of bird-pollinated species in shrubland plots were measured in November 1997. Transects through the plots were positioned centrally along the long axis and 10 x 10 m quadrats randomly located along the transects. On Sessilis, quadrats were 10 x 10 m and 5 x 5 m (because of narrowing of the stand), with the larger quadrats divided by four for calculations of average plant density. The number of quadrats differed between plots, but a minimum of 5% of the patch was sampled if less than 2 ha; 2.5% between 2 and 5 ha; and, 1.25% if the patch was greater than 5 ha. For some small stands, all plants were counted. Mean density of each species of *Dryandra* was calculated using the average number of plants per quadrat and the total area of the plot. The height of each plant within the sampling quadrats was measured to the nearest 0.25 m and used to calculate average heights.

WED estimated the number of inflorescences for each species of *Dryandra* between 15 July and 7 August 1997 by counting the inflorescences on 10 randomly selected plants of each species on each of the shrubland plots. When WED scored inflorescences on Dry Ridge and Possum, *D. armata* was not in bloom. The number of inflorescences for *D. armata* was therefore estimated from the average number per plant on Firetower and Malleefowl.

Using the density of plants, size of patches of each species within a plot, and the mean number of inflores-

**Table 1.** Patch area and mean *Dryandra* species density, height, and number of inflorescences per plant, with an estimated total number of inflorescences/species for five shrubland plots in Dryandra Woodland during July/August 1997. Species density and heights differed among mono-specific stands within each patch; the range of densities and heights are given. The number of inflorescences was calculated separately for each species stand within the patch and summed to provide a value for the stand as a whole. Numbers provide an indication of the total floral resource, as a measure of nectar availability, around the time of peak floral abundance in these shrublands.

Plot (ha)	Species	Density (no./m <sup>2</sup> )	Mean height/Patch (m)	Inflorescences (mean no./plant)	Est. total inflorescences
Dry Ridge (3.1)	<i>D. nobilis</i>	0.1-0.3	2.5	47	262000
	<i>D. sessilis</i>	0.1-0.3	3.5	17	6000
	<i>D. armata</i>	0.1	1.5	41	18500
Firetower (2.2)	<i>D. nobilis</i>	0.2	2.5	79	226000
	<i>D. sessilis</i>	nil	nil	nil	nil
	<i>D. armata</i>	0.1-0.5	1.3-1.5	42	102000
Malleefowl (10.1)	<i>D. nobilis</i>	0.1-0.3	2.5-3.0	47	438000
	<i>D. sessilis</i>	0.2-0.3	2.3-4.5	10	30500
	<i>D. armata</i>	0.2-0.3	2.0	41	171000
Possum (4.6)	<i>D. nobilis</i>	0.2-0.4	2.0-2.5	45	533500
	<i>D. sessilis</i>	0.2	4.0-5.0	44	76000
	<i>D. armata</i>	<0.1	1.3	41	4000
Sessilis (6.8)	<i>D. nobilis</i>	nil	nil	nil	nil
	<i>D. sessilis</i>	0.3-0.5	5.0	23	570000
	<i>D. armata</i>	nil	nil	nil	nil

cences on a plant, an estimate was made of the total number of inflorescences on each plot, for each species. The number of inflorescences estimated provides an index of differences in nectar abundance between plots and illustrates the amount of nectar these shrublands provide nectar-feeders.

HFR estimated flower abundance for *Dryandra* and other nectar-rich plants in the shrublands on a scale of 0 to 10 in May, July, August, September, and October 1998, and again in August 1999 when birds were censused. To illustrate the pattern of blossoming, scores for all plots were summed for each scoring period.

### Bird counts

We use two measures of honeyeater abundances. As the shrublands were dense and birds difficult to follow as they moved, WED estimated species abundance as the number of foraging observations recorded per hour of observation. This also compensated for the fact that WED spent more time on some plots than others (see below). Data were collected on each bird encountered without selecting for species. This measure of abundance cannot be used to calculate species densities or to compare the abundances of different species, but measures the relative abundances of the species between plots.

HFR also spent different lengths of time at each plot, but used a modified area search procedure and kept a running tally of individuals of all species on each plot. See Recher and Davis (1998, 2002) for a fuller description and justification of this procedure.

HFR censused the shrubland plots in May, July, August, September, and October 1998, and again in August 1999, but ceased censusing after *Sessilis* was burned.

### Foraging behaviour

Apart from limited visibility in shrublands, the honeyeaters studied were easy to approach and observe foraging; usually at distances of 10-30 m. WED collected foraging data on honeyeaters from 1 July through 8 August, 30 September through 6 October, and 2-5 November 1997, and 20-22 August 1999. The August 1997 and August 1999 data have been combined. Plots were visited by WED between 0700-1200 hrs, with a few visits in the afternoon. WED concentrated on areas where there was an abundance of blossom and honeyeaters were abundant. He recorded the bird species, a single foraging manoeuvre for each bird foraging on nectar, and the plant species. As in 1995, WED and HFR recorded up to five foraging manoeuvres (e.g. glean, hawk, probe) for each individual encountered foraging on arthropods and carbohydrates other than nectar (e.g. lerp, honeydew). Details of these procedures, including descriptions of foraging manoeuvres, are given by Recher *et al.* (1985). HFR visited the shrubland plots throughout the day.

To ascertain the pattern of plant species use by honeyeaters, the number of foraging manoeuvres per hour of observation by WED for each species of plant was calculated. To examine the shift in plant use by each bird species with time, the number of foraging

**Table 2.** Relative floral abundances on shrubland plots at Dryandra as scored by HFR during 1998-9 on a scale of 0-10. Abundances have been summed across plots.

Species	early May	early July	early August	mid-August	mid-Sept.	late October
<i>Dryandra nobilis</i>	1	12.5	22	5.5	3	0
<i>Dryandra sessilis</i>	2	11.5	14	12	4	0
<i>Dryandra armata</i>	0	0	2	24.5	4	2
<i>Astroloma</i> sp.	5	2.5	0	0	0	0

manoeuvres per hour of observation for each bird species at inflorescences was calculated for each month of observation, with numbers expressed as percentages of observations for each species of honeyeater by month.

## Results

### *Plant heights and flower abundance in 1997*

With an average height for each site of 3.5 to 5 m, the tallest plants were *D. sessilis*. *Dryandra nobilis* averaged 2 to 3 m, with the tallest plants on Malleefowl. *Dryandra armata* averaged 1.3 to 2 m, with the tallest plants on Malleefowl (Table 1).

Gauged by the estimated abundances of *Dryandra* and *Astroloma* inflorescences (Table 2), nectar was available in the shrublands from early May to late October. *Dryandra nobilis* flowered first, with *D. sessilis* flowering later, overlapping with *D. nobilis*. *Dryandra armata* flowered last, when *nobilis* had passed its peak (Table 2). *Dryandra nobilis* averaged 45 to 79 inflorescences per plant, *D. sessilis* 10 to 44 inflorescences, and *D. armata* 41-42 inflorescences (Table 1). The estimated total number of inflorescences over the winter and spring for individual plots was large: from four to six thousand for *D. armata* (Possum) and *D. sessilis* (Dry Ridge) (respectively) to more than 500,000 for *D. nobilis* (Possum) and *D. sessilis* (Sessilis; Table 1).

### *Honeyeater species observed*

Sufficient data for analysis (>50 foraging observations after Recher *et al.* 1985) were obtained for eight species of honeyeater; Brown Honeyeater (*Lichmera indistincta*), Brown-headed Honeyeater (*Melithreptus brevirostris*), Western Wattlebird (*Anthochaera lunulata* [formerly Little Wattlebird *A. chrysoptera*]), New Holland Honeyeater (*Phylidonyris novaehollandiae*), Red Wattlebird (*A. carunculata*), Western Spinebill (*Acanthorhynchus superciliosus*), White-naped Honeyeater (*M. lunatus*), and Yellow-plumed Honeyeater. We observed five other honeyeaters, but obtained insufficient data for analysis, although some are mentioned in discussion; Singing Honeyeater (*Lichenostomus virescens*), Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*), Tawny-crowned Honeyeater (*Glyciphila melanops*), White-cheeked Honeyeater (*P. niger*), and White-eared Honeyeater (*L. leucotis*).

Honeyeaters forage extensively on arthropods, but require carbohydrates as a source of energy (Recher and Abbott 1970; Paton 1980). Of the 13 species of honeyeaters we recorded, eight have relatively long, decurved bills (Table 3) and forage on nectar as their principal source of energy (Higgins *et al.* 2001). The remaining five species have relatively short, straight bills (Table 3) and forage predominantly on alternative carbohydrates (lerp, honeydew, manna, and sap). The honeyeaters at Dryandra occur in a variety of habitats, but the smaller, more nectarivorous species were most commonly encountered in shrublands or in eucalypt dominated woodlands with a well-developed and floristically diverse shrub layer (Table 3). The larger species of long-billed honeyeaters were more commonly encountered in eucalypt woodlands, but also frequented shrublands when nectar was abundant. The short-billed honeyeaters were more frequent in eucalypt woodlands (Table 3).

### *Honeyeater abundances*

During 1998-1999, HFR recorded 11 species of honeyeaters on the shrubland plots (Table 4). Censuses during May 1998 are not included in Table 4, as there were no shrubs in bloom. Brown and New Holland Honeyeaters, and Western Spinebill were the most abundant honeyeaters censused by HFR in the shrubland plots (Table 4). Brown-headed and Yellow-plumed Honeyeaters were the next most abundant, with smaller numbers of Western and Red Wattlebirds, and White-naped Honeyeaters. Only single individuals of Singing and White-eared Honeyeaters were recorded. A pair of Tawny-crowned Honeyeaters was resident on each of Malleefowl and Sessilis. Yellow-plumed Honeyeaters were only abundant on Possum and not recorded on Sessilis. Wattlebirds were absent from Sessilis, and Red Wattlebirds were absent from Fire Tower (Table 4). The zeros in Table 4 do not mean that a particular species did not occur on a plot, only that it was not recorded during censuses.

WED recorded seven species of honeyeaters on the shrubland plots (Table 4). Using the number of foraging observations recorded per hour as an index of abundance, Brown and New Holland Honeyeaters, Red Wattlebird, and Western Spinebill were the most abundant honeyeaters during July (Table 5). Yellow-plumed and Tawny-crowned Honeyeaters, and Western

**Table 3.** Morphological characteristics of Dryandra Woodland honeyeaters observed in this study. Measurements are means or ranges depending on the data available; weights from Johnstone and Storr (2004); head/bill length from de Rebeira (2006). Male and female honeyeaters generally differ in size and bill length, but the differences cannot be distinguished in foraging birds and are not shown here. Habitat and status are based on the observations of HFR and WED in Dryandra Woodland. See text for scientific names.

Species	Weight (gm)	Mean Head Bill Length (mm)	Bill Shape	Habitat	Status at Dryandra
Brown Honeyeater	7-13	32-35	long, decurved	shrublands, woodland with dense shrub layer; riparian	common, abundant
New Holland Honeyeater	15-22	42-44	long, decurved	shrublands, woodland & forest with dense shrub layer; riparian	abundant in shrublands
Red Wattlebird	131	58-65	long, decurved	woodland & forest, visits shrublands	common, abundant
Spiny-cheeked Honeyeater	38-53	48	long, decurved	shrublands, woodland with dense shrub layer	rare vagrant
Tawny-crowned Honeyeater	16-19	40	long, decurved	shrublands, esp. low, open shrublands	uncommon
Western Wattlebird	48-75	59	long, decurved	woodland & forest, visits shrublands	uncommon
Western Spinebill	9-12	40	long, decurved	shrublands, woodland & forest with dense shrub layer; riparian	common, although not abundant outside shrublands
White-cheeked Honeyeater	12-19	41-45	long, decurved	shrublands, woodland with dense shrub layer	uncommon
Brown-headed Honeyeater	11-13	30	short, straight	woodland & forest, visits shrublands	common
Singing Honeyeater	20-39	39	short, straight	restricted to anthropogenic habitats	uncommon
White-eared Honeyeater	21-24	38	short, straight	woodland & forest with dense shrub layer; riparian	common, patchy distribution
White-naped Honeyeater	11-17	33	short, straight	woodland & forest, visits shrublands	common
Yellow-plumed Honeyeater	14-24	35	short, straight	woodland & forest, visits shrublands	common, very abundant

Wattlebird were also frequent. Numbers of Brown Honeyeater, Red Wattlebird, and Yellow-plumed Honeyeater declined after July, but Brown and New Holland Honeyeaters, Western Spinebill, and Western Wattlebird remained relatively common in the shrublands through October (Table 5).

The highest density (mean number of individuals per count/ha) of honeyeaters recorded by HFR was at Possum and Firetower, with lower numbers at Malleefowl and Sessilis (Table 4). The greater densities on Possum and Firetower were due to the large numbers of smaller honeyeaters (see Table 3). Red Wattlebirds were absent from Firetower and Sessilis, plots with the fewest *D. nobilis* inflorescences (Table 1). The smaller honeyeaters were most abundant at the plots with an abundance of *D. sessilis* and *D. armata* inflorescences (Firetower, Sessilis), although New Holland Honeyeater was absent from Sessilis (Table 4). Given the number of foraging observations/hour is affected by ease of detection of foraging birds and that wattlebirds

tend to forage on the highest inflorescences where they are conspicuous, the ranked abundances obtained by HFR and WED are broadly similar (Table 4).

### **Honeyeater abundances**

#### Food sources

Brown and New Holland Honeyeaters, Western and Red Wattlebirds, and Western Spinebill were recorded foraging on nectar for more than 60% of observations (Table 6). Three species, Brown-headed, White-naped, and Yellow-plumed Honeyeaters foraged predominantly (67-94% of observations) on foods other than nectar (Table 6). Only five observations were made of White-eared Honeyeater, all were of bark-probing. Twenty-one observations were made of Tawny-crowned Honeyeaters, which were of birds foraging on *Dryandra* nectar. Honeyeaters not feeding at flowers took a wide range of foods, including lerp, honeydew, and arthropods.

**Table 4.** Numbers of honeyeaters recorded on *Dryandra* shrubland plots during counts from July through October in 1998 and in August 1999. Numbers are the total number of individuals recorded during seven censuses (6 on Sessilis), with the average number of honeyeaters for all species combined given separately. Species are listed in order of total abundance. Only one count was completed on the Ridge plot before it was burnt in 1998 and it is excluded from this table, as are counts during May 1997 when there were no shrubs or eucalypts in bloom on the plots. WED's ranked abundance is based on number of foraging observations/species/hour of observation in 1997.

PLOT	Malleefowl	Firetower	Sessilis	Possum	Total	WED
No. Counts	7	7	6	7	Individuals	RANK
Brown Honeyeater	39	50	70	79	238	1
New Holland Honeyeater	37	32	0	100	169	4
Western Spinebill	23	35	33	67	158	3
Brown-headed Honeyeater	19	17	2	34	72	nil
Yellow-plumed Honeyeater	3	1	0	38	42	5
Red Wattlebird	18	0	0	4	22	2
White-naped Honeyeater	12	2	1	4	19	nil
Western Wattlebird	6	3	0	7	16	6
Tawny-crowned Honeyeater	3	0	4	0	7	7
White-eared Honeyeater	0	1	0	0	1	nil
Singing Honeyeater	0	0	1	0	1	nil
TOTAL	160	141	107	333	641	n/a
Mean/count	22.8	20.1	17.8	47.6	23.7	n/a
Mean/ha	2.3	9.1	2.6	10.3	6.1	n/a

**Table 5.** WED's foraging observations per hour for July-October 1997 (August 1999 data combined with August 1997) on shrubland plots. Observations/hour can be used as an index of abundance for species between months, but do not necessarily indicate differences in abundances between species.

Species	No. Foraging Obs./hour		
	July	August	October
Brown Honeyeater	3.7	1.3	1.8
New Holland Honeyeater	1.7	1.1	1.7
Red Wattlebird	2.4	0	0
Tawny-crowned Honeyeater	0.2	0.1	0
Western Spinebill	1.7	0.2	1.4
Western Wattlebird	0.5	0.4	0.7
Yellow-plumed Honeyeater	0.7	0	0

When observing foraging honeyeaters, it was not always possible to determine what was being eaten. Birds foraging at flowers take nectar and arthropods and may take pollen. However, the manoeuvres used to take nectar differ from those used to capture arthropods and it was possible to distinguish the two. With nectar-feeding, the manoeuvre is a probing action and the tongue can be observed moving in and out of the beak. Arthropods are taken from flowers with a distinctive pecking or snapping motion, or are hawked from the air. G. R. Fulton (personal communication) noted that insects are often trapped in nectar and may be taken by nectar-feeders. Pollen is known to be consumed by

honeyeaters, but it is apparent from this and other observational studies that ingestion occurs incidentally during foraging rather than through foraging specifically for pollen.

#### Foraging manoeuvre

Foraging for nectar was described as probing, as the head and beak tend to be pushed or probed into the flower or inflorescence, even by short-billed species. A greater variety of manoeuvres was used by birds feeding on lerp, honeydew, and arthropods. Gleaning, most commonly for lerp and arthropods, was the most frequent manoeuvre of six species (>44% of observations of birds foraging for food other than nectar; Table 6). Hawking insects was the most common manoeuvre of New Holland Honeyeater (50%). It was also a common manoeuvre of Brown Honeyeater (32%), Western Spinebill (28%), and Western Wattlebird (19%; Table 6). Probing for arthropods and honeydew, usually under bark, was a frequent manoeuvre of Red Wattlebird (44%), White-naped Honeyeater (32%), and Western Spinebill (39%; Table 6). 'Hang-gleaning' best represented the foraging manoeuvre of Brown-headed Honeyeaters (40% of foraging observations) and was used when probing between leaves that had been 'glued' together by larval insects and when taking lerp from leaves.

#### Foraging substrate

Arthropods and lerp were taken from foliage, twigs,

**Table 6.** Percent foraging for nectar compared with % foraging for arthropods and alternative carbohydrates (e.g. lerp, honeydew) by honeyeaters in Dryandra Woodland 1995 to 2004 and giving % of non-nectar foraging manoeuvres. All foraging for nectar was described as ‘probing’. *n* is the total number of foraging observations for a species. The number of observations for honeyeaters foraging for food other than nectar is given in Table 7.

Species	<i>n</i>	Nectar foraging	Non-nectar foraging	% non-nectar foraging manoeuvres					
				Glean	Hang glean	Hawk	Probe	Snatch	Hover
Brown Honeyeater	400	67.5	32.5	44.3	0	32.1	9.2	10.7	3.8
Brown-headed Honeyeater	70	32.9	67.1	46.8	40.4	2.1	10.6	0	0
New Holland Honeyeater	283	68.6	31.4	21.3	5.6	50.1	1.1	18.0	3.4
Red Wattlebird	185	78.9	21.1	46.2	2.6	0	43.6	7.7	0
White-naped Honeyeater	163	11.0	89.0	55.9	5.5	0.7	31.7	0.7	5.5
Western Spinebill	222	60.4	39.6	19.3	0	28.4	38.6	10.2	3.4
Western Wattlebird	185	80.0	20.0	54.1	0	18.9	10.8	13.5	2.7
Yellow-plumed Honeyeater	975	6.4	93.6	55.9	0.1	14.8	23.1	3.6	2.5

and buds (48-85% of observations; Table 7). Honeydew was most abundant under decorticating bark, but also occurred on branches and twigs (personal observation). Red Wattlebird (49%), White-naped (33%), and Yellow-plumed (30%) Honeyeaters probed for arthropods and honeydew under bark on branches and less often on tree trunks (Table 7). The arthropods taken by spinebills appeared small and were often clustered in small depressions in the bark or in the hollow of the cup of eucalypt capsules. New Holland, Brown, and Yellow-plumed Honeyeaters, Western Wattlebird, and Western Spinebill frequently took flying insects (15-51% of observations; Table 7). We had few observations of honeyeaters taking arthropods at flowers, despite the abundance of insects attracted to blossoms (Table 7). Only Western Spinebill and Yellow-plumed Honeyeater were seen to forage on ground or litter arthropods (<5% of observations; Table 7).

### Use of plant species

#### Nectar-feeding

All honeyeaters took nectar, with species of *Dryandra* being used most often (Table 8). Although our focus on *Dryandra* shrublands biases our observations towards species of *Dryandra*, we have few observations of honeyeaters feeding at Powderbark Wandoo, Marri (*E. calophylla*), or Jarrah (*E. marginata*) inflorescences (Table 8), despite the abundance of these trees at Dryandra. Nectar was also taken from *Astroloma*, *Grevillea*, and *Adenanthos* by the smaller honeyeaters. Although not rare, the plants in these genera at Dryandra tend to be small and patchy in distribution. Consequently they did not provide the abundance of nectar we associated with *Dryandra* spp. and failed to attract large numbers of nectar-feeders.

Among the species of *Dryandra*, *D. sessilis* was the most important source of nectar for Brown, Brown-headed, New Holland, Tawny-crowned, and Yellow-

plumed Honeyeaters, and Western Spinebill (Table 8). Red Wattlebirds foraged almost exclusively on *D. nobilis*, but also took nectar from *D. sessilis*. *Dryandra nobilis* was also used by Brown and New Holland honeyeaters, and Western Spinebill. *Dryandra armata* was a source of nectar late in the season for Brown, Brown-headed, and New Holland Honeyeaters, and Western Spinebill (Table 9). Relative to other honeyeaters, Western Wattlebirds used *Dryandra* species infrequently (Table 8). In general, honeyeaters foraged for nectar on *D. nobilis* in July then *D. sessilis* and finally *D. armata* in October (Table 9).

#### Non-nectar-feeding

Most foraging for arthropods and alternative carbohydrates by honeyeaters at Dryandra was on *Eucalyptus* species (60-90% of observations). Despite extensive use of shrublands when feeding on nectar, honeyeaters took relatively few arthropods from *Dryandra* or other shrubs and rarely foraged in *Acacia* and *Allocasuarina* or other genera of plants abundant at Dryandra. We recorded no increase in honeyeater numbers in eucalypt woodlands at Dryandra as the amount of nectar in the *Dryandra* shrublands decreased. However, wattlebirds congregated in Brown Mallet (*E. astringens*) plantations as these came into flower in late spring and early summer (HFR personal observation; G. R. Fulton personal communication).

### Discussion

Compared to other eucalypt woodlands and forests in south-western Australia (e.g. Recher and Davis 2002, 2010), nectar-feeders, including honeyeaters, are not abundant in *Dryandra* woodland (Recher and Davis 1998; personal observation). This was illustrated by the small numbers (tens and hundreds, not thousands as in some other southwest Australian woodlands; Recher and Davis unpublished data) recorded during censuses

**Table 7.** Percent use of substrates by honeyeaters foraging for arthropods and alternative carbohydrates in Dryandra Woodland, 1995-2004. Ground includes litter and logs. Foliage includes twigs, eucalypt capsules, and buds. Flower excludes foraging for nectar.

Species	n	% Substrate					
		Ground	Foliage	Branch	Trunk	Air	Flower
Brown Honeyeater	130	0	63.8	3.8	0	32.3	0
Brown-headed Honeyeater	47	0	85.1	10.6	0	0.2	0.2
New Holland Honeyeater	89	0	48.3	1.1	0	50.6	0
Red Wattlebird	39	0	48.7	48.7	2.6	0	0
White-naped Honeyeater	145	0	63.4	33.1	2.8	0.7	0
Western Spinebill	88	4.5	62.5	2.3	1.1	28.4	1.1
Western Wattlebird	37	0	64.9	10.8	2.7	18.9	2.7
Yellow-plumed Honeyeater	913	0.6	48.5	30.1	4.6	15.0	1.2

and the difficulty we experienced in obtaining foraging observations for most species. Although 18 species of honeyeaters have been recorded at Dryandra (G. R. Fulton unpublished data), we obtained sufficient foraging data for analysis from only eight species. Only Yellow-plumed Honeyeaters, which dominate large areas of wandoo woodlands (Wilson and Recher 2001), and Red Wattlebirds were abundant in habitats outside *Dryandra* shrublands. Although they were encountered in most habitats and some could be considered 'common' (Table 3), other honeyeaters were only abundant during winter and spring when *Dryandra* species were in bloom. Where the birds that congregated in the *Dryandra* shrublands during winter and spring moved to after *Dryandra* species finished blossoming is unknown.

### *Dryandra* shrublands

The sequential flowering of *Dryandra* species provides an important winter and spring nectar resource for honeyeaters in Dryandra Woodland. The large number of inflorescences estimated for each of the five shrublands surveyed gives an indication of the amount of nectar available from *Dryandra* species. Yet, even this abundance was insufficient to attract the large congregations of honeyeaters observed in woodlands east of the wheatbelt.

The choice of food plants by honeyeaters is influenced by size-related dominance hierarchies, with larger birds generally monopolising the most rewarding nectar resources (McFarland 1986). Red Wattlebirds defend feeding territories (Ford 1981; personal observation) and smaller honeyeater species are often relegated to smaller flowers and inflorescences or those with less nectar (Ford and Paton 1982). These generalizations are consistent with the foraging observed in the *Dryandra* shrublands. Red Wattlebirds dominated the patches of *D. nobilis* when it was the most abundant flowering plant, while the smaller honeyeaters foraged mostly on *D. sessilis*, which wattlebirds used sparingly.

Even the relatively large Western Wattlebirds foraged mostly at the edge of *D. nobilis* patches or in *D. sessilis*, suggesting that dominance of the larger Red Wattlebird may have been involved. The presence of discrete, mono-specific stands of each species of *Dryandra* on all but Sessilis plot enabled a variety of honeyeaters to co-exist without aggressive exclusion. As *D. nobilis* flowering declined, wattlebirds shifted to other nectar sources, such as Brown Mallet, while the smaller honeyeaters remained in the shrublands using nectar from the last of the *D. nobilis*, as well as *D. sessilis* and *D. armata*.

### Foraging behaviour

Ford and Paton (1976) and Ford (1977) concluded that long-billed honeyeaters were nectar-dependent, while short-billed species fed more on arthropods. This separation of long-billed and short-billed species has been modified to account for the fact that the short-billed species also feed extensively on alternative carbohydrates (Paton 1980; Recher and Davis 2002, 2010). Honeyeaters also differ in the plant species they visit for nectar. Ford and Paton (1977) found that short-billed species tended to feed at the cup-shaped flowers of eucalypts, while longer-billed species used a wider array of plants, including flowers with long corollas. Large-bodied honeyeaters are also restricted to feeding on plants with sturdy branches and inflorescences (Pyke 1980) and there is a tendency for species to segregate by body size and bill length (Ford and Paton 1976; Ford 1977). This general pattern of resource allocation among honeyeaters was also observed at Dryandra, although the separation of long- and short-billed honeyeaters in respect to eucalypt flowers was not pronounced given the limited availability of eucalypt blossom during the study reported here.

The long-billed honeyeaters in Dryandra Woodland were nectar-dependent and aggregated where nectar-rich flowers were abundant. During winter and spring, long-billed honeyeaters relied on nectar from species

**Table 8.** Use of plant species by honeyeaters foraging for nectar at Dryandra Woodland, 1995-2004. Other includes mallee eucalypts, unidentified eucalypts, *Astroloma*, *Grevillea*, and *Adenanthos*. Abbreviations: *Dn*, *Dryandra nobilis*; *Da*, *D. armata*; *Ds*, *D. sessilis*; *Ea*, *Eucalyptus astringens*; *Ew*, *E. wandoo*; *Eac*, *E. accedens*; *Ec*, *E. calophylla*.

Species	<i>n</i>	<i>Dryandra</i> spp.	<i>Dn</i>	<i>Da</i>	<i>Ds</i>	<i>Hakea</i> sp.	<i>Ea</i>	<i>Ew</i>	<i>Eac</i>	<i>Ec</i>	Other
Brown Honeyeater	270	20	24	22	177	3	8	7	0	1	8
Brown-headed Honeyeater	23	5	0	4	13	0	0	0	0	1	0
New Holland Honeyeater	194	5	47	46	66	2	0	7	0	0	21
Red Wattlebird	146	0	87	0	7	5	42	5	0	0	0
White-naped Honeyeater	18	0	2	0	4	2	0	10	0	0	0
Western Spinebill	134	3	16	35	72	1	0	0	0	0	7
Western Wattlebird	148	10	12	3	8	61	35	0	0	0	19
Yellow-plumed Honeyeater	62	0	2	1	27	3	0	22	0	0	7

**Table 9.** Mean number of nectar-feeding foraging observations by all species of honeyeaters combined/hour of observation for July, August, and October 1997 and August 1999 by WED at the *Dryandra* shrubland plots. Data were not collected during September. Other includes mallee eucalypts, *Grevillea*, *Adenanthos*. Data from August 1997 and 1999 have been combined.

Species	Month		
	July	August	October
<i>Dryandra nobilis</i>	4.9	0.8	<0.1
<i>D. sessilis</i>	6.6	7.8	1.8
<i>D. armata</i>	<0.1	2.3	3.3
Other	<0.1	0.5	0.7

of *Dryandra*. The short-billed species used a wider range of resources, including nectar, and tended to segregate by habitat. It is likely that some habitat segregation among short-billed honeyeaters was forced by the dominance of Yellow-plumed Honeyeaters in Wandoo woodlands. By virtue of their position in the landscape, these are the most productive woodlands at Dryandra (Majer *et al.* 2003; Fulton and Rose 2007), with honeyeaters other than Yellow-plumed Honeyeaters and wattlebirds forced to use less productive habitats on the slopes and ridges. The limited extent (most patches are less than 10 ha) and patchy distribution of *Dryandra* shrublands and the lack of flowering eucalypts may also explain the absence of large, multi-species aggregations of nectar-feeders during winter and spring. As we lack data, we cannot exclude a different pattern of honeyeater abundance during summer and autumn when Wandoo and Powderbark Wandoo bloom.

Outside the *Dryandra* shrublands, honeyeaters used a variety of foraging resources, but appeared to rely on lerp and honeydew as carbohydrates. Lerp taken from eucalypt foliage was the most important energy resource as measured by frequency of use. Decorticating bark was the second most frequently exploited substrate, presumably as a source of arthropods and honeydew. Wilson and Recher (2002) documented seasonal and year-to-year shifts in the use of substrates at

*Dryandra* by Yellow-plumed Honeyeaters, probably in response to changes in the kinds and availability of resources.

### Conservation and management

Honeyeaters at *Dryandra* used a variety of foods and foraging substrates. They also foraged over the entire height range of the vegetation in the habitats they frequented (Recher and Davis unpublished data). Their ability to exploit different resources and a variety of energy-rich carbohydrates as conditions change enables honeyeaters to use habitats that may be relatively low in productivity, with significant seasonal and year-to-year changes in food abundances. For honeyeaters in *Dryandra* Woodland, the importance of *Dryandra* shrublands during winter and spring was demonstrated by the aggregations of honeyeaters present whenever *Dryandra* spp. were in bloom. Even then, wattlebirds used the shrublands only when *D. nobilis* was in flower, with the smaller honeyeaters also using *D. sessilis* and *D. armata*.

The conservation and management of honeyeaters and other nectar-feeders in *Dryandra* Woodland requires the retention of the *Dryandra* shrublands. As these shrublands are small and patchy in distribution, even the loss of individual patches through burning, for example, may have adverse effects on honeyeaters throughout the reserve. Lambeck and Saunders (1993) noted the importance of small patches of *Banksia prionotes* for the survival of honeyeaters in the central wheatbelt of Western Australia. As with *Dryandra* spp., *B. prionotes* is a source of nectar at time of the year when little other nectar is available. Lambeck and Saunders (1993) also pointed out that honeyeaters are important pollinators of a many native plants and that the loss of a keystone species, such as *B. prionotes*, would affect more than the honeyeaters reliant on it for nectar. Similar cascading effects could be expected at *Dryandra*, where many plants are also bird-pollinated, with any decline in honeyeater abundances.

All *Dryandra* species appear sensitive to fire and rates of recovery vary significantly; *D. sessilis*, for example, appears to reach flowering maturity and size much sooner than *D. nobilis* (personal observation). As honeyeaters differ in their use of *Dryandra* spp., changes in the abundances of *Dryandra* spp. may have differential effects on honeyeater species. To avoid adverse effects, any burning of *Dryandra* shrublands should be conducted with the explicit objective of maximising the average long-term availability of nectar of all species and the sequence of flowering of different *Dryandra* spp. Further, *Dryandra* spp. may show small amounts of natural recruitment in the absence of fire, and management burns may be unnecessary to perpetuate stands (Bradshaw *et al.* 2011).

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