*Emu*, 2001, **101**, 7–12

# The structure and dynamics of an assemblage of small birds in a semi-arid eucalypt woodland in south-western Australia

*W. J. Morris and R. D. Wooller*[A]

Biological Sciences, Murdoch University, WA 6150, Australia.
[A]To whom correspondence should be addressed.

*Abstract.* The small birds present in 25 ha of dry sclerophyll woodland near Kalgoorlie, Western Australia, were monitored twice weekly over 18 months. The birds that fed solely upon invertebrates were largely resident and their abundances fluctuated little. The numbers of species and the abundances of honeyeaters varied much more, but with no clear relationship to the nectar present in the erratically flowering eucalypts present. Some resident meliphagid honeyeaters were either predominantly gleaners or only opportunistic flower-feeders. Only larger-scale studies are likely to resolve patterns among the more mobile birds in such assemblages.

## Introduction

Nectar-feeding birds, especially honeyeaters (Meliphagidae), are a major component of many avian assemblages within Australia, often reaching densities much greater than insect-feeding birds (Ford 1989). In some areas, honeyeater densities appear to change in relation to nectar availability (Ford and Paton 1976; Ford and Pursey 1982; Ford 1983*a*; McFarland 1986*b*), but elsewhere patterns seem less clear (Pyke 1983, 1985; Pyke and Recher 1988; Pyke *et al.* 1993). Difficulties in interpreting the changing presence and abundance of honeyeaters stem from their mobility in relation to the scale of most studies (Mac Nally and McGoldrick 1997). Moreover, some honeyeater species are relatively sedentary and territorial, often relying almost entirely on non-floral carbohydrates (lerp, manna, etc.) and insects, which may bring them into potential conflict with other wholly insectivorous passerine birds (Mac Nally and McGoldrick 1997).

Most detailed studies of honeyeaters have been carried out in coastal heathlands where they are often the most abundant birds, with fewer studies in eucalypt forests and woodlands (Mac Nally and McGoldrick 1997). In an effort to explore the influence of eucalypt flowering upon honeyeaters in south-western Australia, we detailed the structure and dynamics of an assemblage of small birds in one small area of eucalypt woodland in the eastern Goldfields region of Western Australia over 18 months. This paper reports the results of this study.

## Methods

The study area was near Kambalda (31°12′S, 121°38′E), 58 km south of Kalgoorlie. It was 25 ha (500 m × 500 m) of almost flat, mature open woodland between two dry creeks, within a larger area of dry sclerophyll woodland of the Coolgardie system (Beard 1969). The dominant trees, about 8 m tall, were *Eucalyptus salmonophloia, E. salubris, E. lesoueffi, E. stricklandii* and *E. torquata,* together with smaller numbers of *E. transcontinentalis* and *E. celestroides*. The shrub layer, 1–2 m tall, comprised mostly *Eremophila* spp., *Melaleuca pauperiflora, Dodonaea lobulata, Acacia* spp. and *Santalum* spp., with only 10–30% ground cover and typical clumping of shrubs.

The average temperature and rainfall for the semi-arid area, summarised in Fig. 1, shows little difference between summer and winter rainfall, but summer rain is associated with thunderstorms. The actual pattern of rainfall during the study is shown in Fig. 2. In this area there can be a fourfold difference in annual rainfall. Temperatures rise as high as 46°C in summer and fall to –3°C in winter with frequent, but not severe, frosts.

Observations were made throughout the study area between 0500 and 0900 h twice each week from February 1981 to June 1982, except for October and November. Each bird seen foraging was noted, together with its mode of feeding and height. On the basis of up to 30 h of observations each month throughout the study area, monthly indices of relative abundance were derived for each species, ranging from 0 (absent) and 1 (least common) to 4 (most common). Mist-netting was carried out intermittently throughout the study period and was highly dependent on weather conditions. Up to sixteen 13 m × 2 m nets were operated for 3 h in the early morning for 2–3 consecutive mornings at different sites throughout the study area. Birds caught in mist-nets were individually marked with coloured leg-bands and records kept of subsequent sightings of these individuals. Captured individuals were measured and pollen and faecal samples obtained from them using the methods of Wooller *et al.* (1983) and Calver and Wooller (1982).

Of the 12–31 individuals of each of the *Eucalyptus* species present in the study area, ten were selected at random, marked at the start of the study and their flowering status recorded twice each month as: 0 (no flowers open), 1 (1–10% of all flowers open), 2 (11–50% of all flowers open), or 3 (≥51% of all flowers open.

Ten individuals of the major nectar-producing shrub *Eremophila oldfieldii* were marked and monitored in the same way. Indices of the standing crop of nectar per hectare soon after dawn were derived by multiplying the density of a species by the average number of flowers per plant and by the average amount of nectar per flower, following procedures similar to those used by Paton (1985). Nectar volumes of ten uncovered flowers were measured early in the morning using microcapillary tubes and sugar concentrations of nectar determined with a hand-held refractometer. The energy content of this nectar was


10.1071/MU00062 0158-4197/01/010007

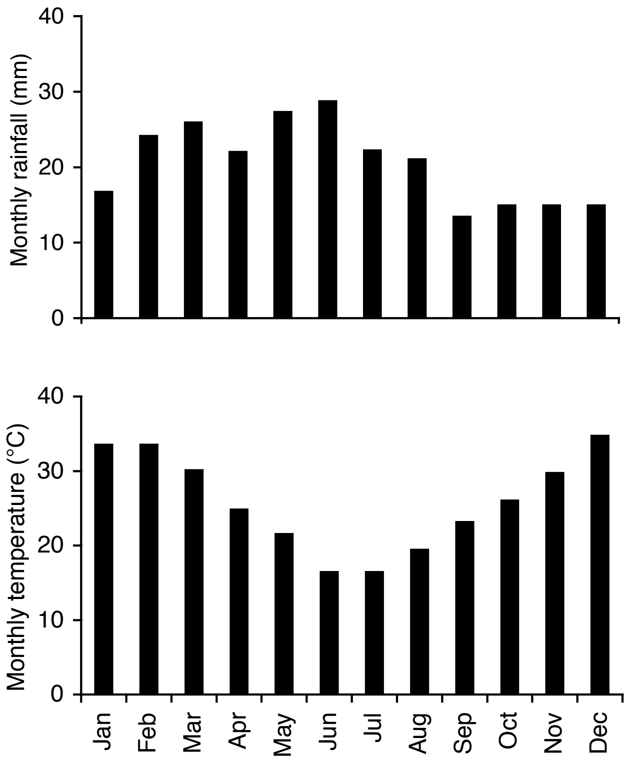


**Fig. 1.** The mean monthly rainfall (upper) and temperature (lower) at Kalgoorlie, Western Australia (1900–79).

then calculated (Paton 1985) and indices of the amounts of energy present at the eucalypts and the *Eremophila* understorey were estimated separately.

## Results

The birds most frequently seen and caught in the study area consisted of nine meliphagid honeyeaters and a similar number of other passerines (Table 1). Less often seen were the Black-faced Cuckoo-shrike (*Coracina novaehollandiae*), Willie Wagtail (*Rhipidura leucophrys*), Chestnut Quail-thrush (*Cinclosoma castanotus*), Striated Fieldwren (*Calamanthus fuliginosus*), Western Gerygone (*Gerygone fusca*), Varied Sittella (*Daphoenositta chrysoptera*), Magpie Lark (*Grallina cyanoleuca*), Grey and Pied Butcherbirds (*Cracticus torquatus* and *C. nigrogularis*), Australian Magpie (*Gymnorhina tibicen*), Grey Currawong (*Strepera versicolor*) and Little Crow (*Corvus bennetti*). Overall, only 7 of 33 honeyeaters marked were recaptured, compared with 21 of 48 non-honeyeaters (Table 1). Honeyeaters often showed marked changes in abundance throughout the study (Table 2), whereas the more sedentary non-honeyeaters changed little in abundance. One exception was the White-eared Honeyeater (*Lichenostomus leucotis*), which showed few seasonal changes in abundance and was recaptured relatively often.

Some honeyeater species were seen mostly at flowers whereas other honeyeaters spent much of their time foraging at other substrates, often for insects (Table 3). The extent of nectarivory and insectivory varied not only between species but also seasonally. For instance, the White-eared Honeyeater fed extensively at flowers in spring and summer but was mainly a bark-prober and gleaner for the rest of the year (Table 4). In general, honeyeaters foraged less on the ground and more in the air than the wholly insectivorous birds and tended to glean insects from higher strata (Table 3). Analysis of faecal samples obtained from birds caught in mist-nets indicated that the exclusively insectivorous species ate mainly beetles; honeyeaters ate fewer beetles, but many more termites and flying insects (flies, wasps, etc.) than the obligate insectivores (Table 5). On average, the prey items taken by honeyeaters were smaller (2–4 mm long) than those taken by the obligate insectivores (4–6 mm).

Many of the eucalypts monitored did not flower during the 15-month study period. None of the ten marked *Eucalyptus salmonophloia* or *E. salubris* flowered, and only two of the *E. lesoueffii* and *E. celestroides*, three of the *E. torquata* and *E. stricklandii* and four of the *E. transcontinentalis* flowered. In contrast, eight of the ten marked shrubs of *Eremophila oldfieldii* flowered. *Eucalyptus stricklandii*, a major source of nectar in 1981, produced very few flowers in 1982 (Fig. 2). *Eucalyptus celestroides* and *E. transcontinentalis* were in flower by June in 1981, but did not flower until later (August/September) in 1982. *Eucalyptus torquata* produced some flowers in September 1981, but many buds did not open until after significant rains fell in April 1982, when a second, separate flowering period occurred (Fig. 2).

Although nine species of honeyeater were recorded during the study, on no occasion were all nine detected in the study area simultaneously (Table 2). Only four honeyeaters were present throughout the study. Of these, the Yellow-throated Miner (*Manorina flavigula*) and Brown-headed Honeyeater (*Melithreptus brevirostris*) were largely gleaners (Table 3). The White-eared Honeyeater was the only species recorded sufficiently often to permit a seasonal analysis of its foraging. It was primarily a gleaner for much of the year, but became more of a flower visitor from August to December (Table 4), when many of the eucalypts were in flower (Fig. 2). The Red Wattlebird (*Anthochaera carunculata*) was the only markedly flower-feeding bird present all year. It was also the largest and most aggressive nectarivore, often recorded defending clumped nectar sources, such as the flowers of *Eucalyptus transcontinentalis*. Red Wattlebirds were also recorded all year in the township of Kambalda, about 5 km from the study area. The more protracted flowering of eucalypts in Kambalda may account, in part, for the otherwise anomalous presence of wattlebirds all year within the study area. In general, however, there was little correspondence between rainfall and indices of nectar availability, or between nectar levels and the numbers of honeyeaters (Fig. 2).

**Table 1. The mean sizes (±s.d.), relative abundances and recapture rates of the most common small insectivorous and nectarivorous birds in the study area**

| | Body mass (g) | Beak length (mm) | Relative abundance | Individuals recaptured / individuals banded | Percentage of individuals sighted that were banded (sample size) |
|---|---|---|---|---|---|
| Insectivores | | | | | |
| Weebill (*Smicrornis brevirostris*) | – | – | 4 | 1/4 | 0 (23) |
| Inland Thornbill (*Acanthiza apicalis*) | 7.3 ± 2.2 | 9.3 ± 1.5 | 3 | 3/6 | 43 (28) |
| Chestnut-rumped Thornbill (*Acanthiza uropygialis*) | 7.2 ± 1.7 | 8.6 ± 0.6 | 3 | 5/11 | 36 (28) |
| Redthroat (*Pyrrholaemus brunneus*) | 11.6 ± 1.2 | 12.9 ± 2.6 | 2 | 2/4 | 10 (20) |
| White-browed Babbler (*Pomatostomus superciliosus*) | 36.0 ± 6.5 | 25.6 ± 5.0 | 2 | 3/7 | 33 (37) |
| Red-capped Robin (*Petroica goodenovii*) | 8.0 ± 0.5 | 11.1 ± 1.2 | 2 | 6/9 | 41 (32) |
| Striated Pardalote (*Pardalotus striatus*) | – | – | 2 | 0/3 | 0 (4) |
| Yellow-rumped Thornbill (*Acanthiza chrysorrhoa*) | 5.8 ± 0.1 | 11.3 ± 0.1 | 1 | 1/3 | 25 (4) |
| Crested Bellbird (*Oreoica gutturalis*) | 66.0 | 21.6 | 1 | 0/1 | 70 (10) |
| Grey Shrike-thrush (*Colluricincla harmonica*) | – | – | 1 | – | – |
| Honeyeaters | | | | | |
| Yellow-throated Miner (*Manorina flavigula*) | 46.2 ± 1.1 | 23.4 ± 4.4 | 2–4 | 0/11 | 0 (44) |
| Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*) | 45.0 ± 1.0 | 26.7 ± 1.8 | 0–4 | 0/3 | 0 (5) |
| White-eared Honeyeater (*Lichenostromus leucotis*) | 19.5 ± 4.3 | 17.2 ± 2.5 | 2–3 | 5/7 | 30 (74) |
| Brown-headed Honeyeater (*Melithreptus brevirostris*) | – | 12.8 | 0–3 | – | – |
| Yellow-plumed Honeyeater (*Lichenostomus ornatus*) | 19.5 | 15.5 | 0–3 | 0/1 | 0 (17) |
| White-fronted Honeyeater (*Phylidonyris albifrons*) | 16.6 ± 6.6 | 20.6 ± 1.5 | 0–3 | 2/6 | 10 (20) |
| Brown Honeyeater (*Lichmera indistincta*) | 7.9 ± 0.6 | 16.4 ± 4.7 | 0–3 | 0/5 | 0 (6) |
| Red Wattlebird (*Anthochaera carunculata*) | – | – | 1–2 | – | – |
| Singing Honeyeater (*Lichenostomus virescens*) | – | – | 0–1 | – | – |

## Discussion

This study had obvious limitations in terms of its duration and the use of indices rather than standardised quantification to score abundances. Despite this, some trends emerged from an area for which there is a dearth of studies. The bird assemblage studied, like those in other arid areas, contained a core of resident species augmented by more nomadic and opportunistic species (Recher and Davis 1997). In common with other eucalypt woodlands and forests, most bird species ate insects from the ground, bark, foliage and air; there were fewer nectar-, seed- and fruit-eating species (Recher and Davis 1998). The foraging habits of those passerines that fed solely

**Table 2. Seasonal changes in the relative abundances of nine honeyeater species present in the study area**
Values in italics indicate flocking

| Species | 1981 | | | | | | | | | | | 1982 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun |
| Yellow-throated Miner | *3* | *3* | *3* | *2* | *3* | *4* | *3* | *2* | – | – | *2* | *2* | *2* | *2* | *3* | *3* | *3* |
| White-eared Honeyeater | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | – | – | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| Red Wattlebird | 2 | *2* | *2* | 1 | 2 | 2 | 2 | 2 | – | – | 1 | 1 | 1 | *1* | *1* | 1 | 2 |
| Brown-headed Honeyeater | 0 | *3* | *2* | *2* | *2* | *3* | *3* | *2* | – | – | *1* | *1* | *2* | *2* | *3* | *3* | *3* |
| Yellow-plumed Honeyeater | 2 | 2 | 2 | 2 | 3 | 3 | 2 | 0 | – | – | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| White-fronted Honeyeater | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 3 | – | – | 3 | 2 | 1 | 1 | 1 | 0 | 0 |
| Brown Honeyeater | 3 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | – | – | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| Spiny-cheeked Honeyeater | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | – | – | *3* | *2* | 2 | 3 | 3 | 4 | 3 |
| Singing Honeyeater | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | – | – | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

**Table 3. Percentage frequency distributions of the modes and heights of feeding of the most common small birds in the study area**

| Species | No. observed feeding | Mode of feeding: At a flower | Gleaning/ hover gleaning | Probing / bark-probing | Hawking/ sallying | Ground-feeding / pouncing | Height observed feeding: <1 m | 1–3 m | >3 m |
|---|---|---|---|---|---|---|---|---|---|
| Brown Honeyeater | 30 | 90 | 3 | 0 | 6 | 0 | 0 | 48 | 52 |
| White-fronted Honeyeater | 65 | 88 | 3 | 0 | 9 | 0 | 0 | 89 | 11 |
| Red Wattlebird | 184 | 66 | 22 | 4 | 2 | 5 | 2 | 44 | 54 |
| Yellow-plumed Honeyeater | 106 | 25 | 44 | 16 | 11 | 3 | 3 | 10 | 87 |
| White-eared Honeyeater | 342 | 14 | 22 | 50 | 4 | 10 | 10 | 31 | 59 |
| Brown-headed Honeyeater | 150 | 12 | 78 | 9 | 0 | 1 | 1 | 17 | 82 |
| Yellow-throated Miner | 65 | 2 | 71 | 9 | 2 | 17 | 21 | 19 | 60 |
| Singing Honeyeater | 24 | 0 | 95 | 5 | 0 | 0 | 0 | 17 | 83 |
| Spiny-cheeked Honeyeater | 71 | 0 | 55 | 3 | 23 | 18 | 17 | 26 | 57 |
| Red-capped Robin | 66 | 0 | 12 | 1 | 1 | 85 | 1 | 82 | 18 |
| Redthroat | 38 | 0 | 43 | 0 | 3 | 53 | 73 | 26 | 0 |
| White-browed Babbler | 49 | 0 | 3 | 2 | 0 | 45 | 45 | 53 | 2 |
| Weebill | 166 | 0 | 97 | 2 | 0 | 1 | 11 | 15 | 74 |
| Chestnut-rumped Thornbill | 81 | 17 | 36 | 13 | 2 | 31 | 35 | 65 | 0 |
| Inland Thornbill | 52 | 14 | 84 | 0 | 0 | 2 | 6 | 90 | 4 |
| Striated Pardalote | 35 | 0 | 100 | 0 | 0 | 0 | 3 | 37 | 60 |

upon invertebrates appeared largely in accord with the findings of other workers in this area (Ford 1983; Recher *et al.* 1985; Recher and Davis 1997, 1998) and these species formed the core of the community. Thus, robins often pounced upon their prey, babblers commonly probed for prey, White-eared Honeyeaters probed bark, Brown-headed and Yellow-plumed Honeyeaters probed and gleaned, while Weebills often hovered as they gleaned.

It was clear, however, that not all honeyeaters were a permanent component of the assemblage. Studies elsewhere have found that although up to 12 species of honeyeaters may be recorded from an area, often only 2–4 of these are common or present at most times of year (Wooller 1981; Pyke 1983; McFarland 1986*b*). In more nectar-rich systems, priority of access to nectar appears to be based on aggressive interactions, resulting in a size-based dominance hierarchy that enables nectar specialists to be residents (McFarland 1986*a*). However, in areas where nectar availability is less predictable and at lower levels, such as the area studied, obligate nectarivores may not be a permanent component of the avian assemblage (McKenzie *et al*. 1962). This is the converse of the seasonal opportunistic nectarivory recorded for members of groups other than honeyeaters in monsoonal northern Australia (Franklin 1999).

Davies (1976) found the timing of flowering by arid-zone shrubs in Western Australia to be the same from year to year, but that the intensity of flowering varied greatly. In the present study, the seven eucalypt species flowered at slightly different times, mostly within the spring–summer period, and with very different intensities. Paton (1985) also documented temporal inconsistency in flowering by eucalypts in Victoria, with each species monitored failing to flower in one or more years of study. Thus, it is not surprising that the presence and abundance of honeyeaters in the present study showed no clear correlation with the flowering of eucalypts. Large amounts of nectar were available from *Eremophila*

**Table 4. Seasonal differences in the modes of feeding by White-eared Honeyeaters in the study area**

| | No. observed | Percentage observed: At a flower | Probing bark | Gleaning / hover gleaning | Hawking / sallying | On ground |
|---|---|---|---|---|---|---|
| February | 23 | | 100 | | | |
| March | 18 | 11 | 77 | | 6 | 5 |
| April | 20 | | 95 | 5 | | |
| May | 11 | | 82 | 9 | | 9 |
| June | 57 | 4 | 70 | 9 | 7 | 10 |
| July | 31 | 12 | 31 | 41 | 10 | 6 |
| August | 43 | 33 | 37 | 16 | 2 | 12 |
| September | 70 | 23 | 30 | 22 | | 23 |
| October | 30 | 3 | 30 | 43 | 10 | 13 |
| December | 38 | 23 | 18 | 54 | 3 | |

**Table 5. The percentage composition of invertebrate taxa identified from remains in the faeces of small birds caught in the study area**

| Bird species | No. sampled | | Percentage of invertebrates in taxon | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Birds | Invertebrates | Coleoptera | Orthoptera | Isoptera | Formicidae | Other Hymenoptera | Diptera | Lepidoptera | Araneae | Other |
| White-eared Honeyeater | 5 | 17 | | | 65 | 6 | | 6 | | 17 | 6 |
| Spiny-cheeked Honeyeater | 4 | 13 | 46 | | 23 | 8 | 23 | | | | |
| Yellow-throated miner | 5 | 35 | 37 | 3 | 43 | 11 | | | | 6 | |
| Red-capped Robin | 8 | 28 | 96 | | | 4 | | | | | |
| Inland Thornbill | 7 | 23 | 65 | 9 | | | 9 | | | 5 | 12 |
| Chestnut-rumped Thornbill | 9 | 27 | 67 | 4 | | 4 | 4 | 8 | | 9 | 4 |
| White-browed Babbler | 5 | 25 | 80 | 4 | | 8 | | | | 9 | 4 |
| All honeyeaters | 23 | 80 | 28 | 1 | 36 | 8 | 9 | 8 | 1 | 8 | 1 |
| Other species | 40 | 126 | 73 | 5 | 2 | 4 | 2 | 2 | 0 | 5 | 7 |

shrubs in June and July, but in a dispersed form that probably makes its harvesting uneconomic, except perhaps for the small honeyeaters. Overall, as others have noted (e.g. Mac Nally and McGoldrick 1997), the spatial patchiness of nectar and temporal variability in flowering in systems such as that studied make the detection of even rich nectar sources difficult for flocking or itinerant honeyeaters.

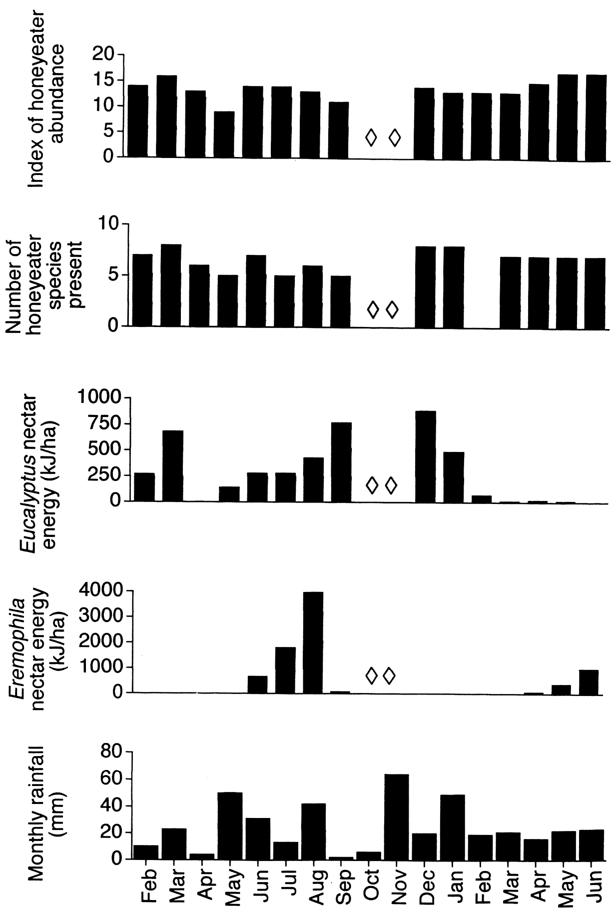


**Fig. 2.** The monthly rainfall (mm), estimated standing crop of energy available from nectar in *Eucalyptus* and *Eremophila* flowers (kJ/ha), the number of honeyeater species present in that month and monthly index of honeyeater abundance (top) in the Kambalda study area. Diamonds indicate the two months for which data were unavailable.

Nevertheless, some honeyeaters, particularly White-eared and Brown-headed Honeyeaters, as well as miners, were present at relatively high densities all year. White-eared and Brown-headed Honeyeaters are known not only to take nectar but also to rely upon other sources of carbohydrates, such as the lerp and honeydew produced by insects (Recher and Holmes 1985; Recher *et al.* 1985). These foods, together with manna, fruit pulp and soft-bodied invertebrates, leave little trace in faeces, and foraging for them is not readily distinguished from gleaning for insects. Lerp, the carbohydrate-rich cases of psyllid insects, was widespread on the leaves of *Eucalyptus lesoueffi*, *E. torquata* and *E. transcontinentalis* over summer, from their first appearance in October/November until the cases fell off in February/March. Manna, the exudate from damaged plants, was abundant on several *E. salubris* during May and June 1981. Both of these foods were exploited by several honeyeater species while available, particularly by those species that remained in the study area all year. Indeed, the availability of non-floral, energy-rich carbohydrate sources may be as important to short-billed honeyeaters as nectar is to longer-billed species and play an important role in their continued presence at times when nectar is scarce. Interestingly, the Weebill, also known to feed extensively on lerp (Recher and Davis 1997), was consistently the most abundant bird in the study area.

Recher and Holmes (1985) also noted that White-eared and Brown-headed Honeyeaters fed less upon flowers and more upon insects than did many other honeyeaters, particularly by probing loose bark. Pearce (1996*b*) also characterised the White-eared Honeyeater as a bark-feeding specialist. She noted that this species is found where eucalypts with decorticating bark occur and where there is also a dense shrub layer in which it can nest. Such honeyeaters, which are only facultative nectarivores, are probably best able to utilise erratic nectar production. At other times, their gleaning habits have the potential to bring them into competition with species that feed exclusively upon invertebrates (Mac Nally and McGoldrick 1997).

Only the Singing Honeyeater (*Lichenostomus virescens*), White-eared Honeyeater and Yellow-throated Miner, all species that take substantial numbers of insects, are resident honeyeaters in reserves in the wheatbelt of Western Australia (Kitchener *et al.* 1982), the region adjacent to the goldfields where the present study was conducted. Given the mobility of many honeyeaters (Keast 1968) and their opportunistic exploitation of temporal and spatial variation in food resources, localised studies, such as the one reported here, need to be interpreted within the context of a larger regional understanding (Mac Nally 1995, 1996), as yet largely unavailable.

### Acknowledgments

We thank Tim Richards and Western Mining Corporation for their assistance in this work and Allan Burbidge and Harry Recher for their comments as referees.

### References

Beard, J. S. (1969). The natural regions of the deserts of Western Australia. *Journal of Ecology* **57**, 677–711.

Calver, M. C., and Wooller, R. D. (1982). A technique for assessing the taxa, length, dry weight and energy content of the arthropod prey of birds. *Australian Wildlife Research* **9**, 293–301.

Davies, S. J. J. F. (1976). Studies of the flowering season and production of some arid zone shrubs and trees in Western Australia. *Journal of Ecology* **64**, 655–687.

Ford, H. A. (1983*a*). Relations between number of honeyeaters and intensity of flowering near Adelaide, South Australia. *Corella* **7**, 25–31.

Ford, H. A. (1983*b*). A synthesis of the foraging ecology and behaviours of birds in eucalypt forest and woodlands. In 'Birds of Eucalypt Forest and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 249–254. (Surrey Beatty & Sons: Sydney.)

Ford, H. A. (1989). 'Ecology of Birds: an Australian Perspective.' (Surrey Beatty & Sons: Sydney.)

Ford, H. A., and Paton, D. C. (1976). Resource partitioning and competition in honeyeaters of the genus *Meliphaga*. *Australian Journal of Ecology* **1**, 281–287.

Ford, H. A., and Pursey, J. F. (1982). Status and feeding of the Eastern Spinebill *Acanthorhynchus superciliosus* at New England National Park, north-eastern NSW. *Emu* **82**, 203–211.

Franklin, D. C. (1999). Opportunistic nectarivory: an annual dry season phenomenon among birds in monsoonal northern Australia. *Emu* **99**, 135–141

Keast, A. (1968). Seasonal movement in the Australian honeyeaters (Meliphagidae) and their ecological significance. *Emu* **67**, 159–209.

Kitchener, D. J., Dell, J., Muir, B. G., and Palmer, M. (1982). Birds in Western Australian wheatbelt reserves – implications for conservation. *Biological Conservation* **22**, 127–163

Mac Nally, R. C. (1995). A protocol for classifying regional dynamics, exemplified by using woodland birds in southeastern Australia. *Australian Journal of Ecology* **20**, 442–454.

Mac Nally, R. C. (1996). A winter's tale: among-year variation in bird community structure in a south-eastern Australian forest. *Australian Journal of Ecology* **21**, 280–291.

Mac Nally, R. C., and McGoldrick, J. M. (1997). Landscape dynamics of bird communities in relation to mass flowering in some eucalypt forests of central Victoria, Australia. *Journal of Avian Biology* **28**, 171–183.

McFarland, D. C. (1986*a*). The organisation of a honeyeater community in an unpredictable environment. *Australian Journal of Ecology* **11**, 107–120.

McFarland, D. C. (1986*b*). Seasonal changes in the abundance and body condition of honeyeaters (Meliphagidae) in response to inflorescence and nectar availability in the New England National Park, New South Wales. *Australian Journal of Ecology* **11**, 331–340.

McKenzie, N. L., Rolfe, J. K., and Youngson, W. K. (1992). Vertebrate fauna. In 'The Biological Survey of the Eastern Goldfields of Western Australia. Part 8. Kurnalpi–Kalgoorlie Study Area'. (Eds N. L. McKenzie and N. J. Hall.) pp. 37–64. Records of the Western Australian Museum, Supplement No. 41.

Paton, D. C. (1985). Food supply, population structure and behaviour of New Holland Honeyeaters *Phylidonyris novaehollandiae* of woodland near Horsham, Victoria. In 'Birds of Eucalypt Forest and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 219–230. (Surrey Beatty & Sons: Sydney.)

Pearce, J. (1996*a*). Habitat selection by the White-eared Honeyeater. I. Review of habitat studies. *Emu* **96**, 42–49.

Pearce, J. (1996*b*). Habitat selection by the White-eared Honeyeater. II. A case study at Yellingbo State Nature Reserve, south-east Victoria. *Emu* **96**, 50–54.

Pyke, G. H. (1983). Seasonal pattern of abundance of honeyeaters and their food resources in heathland near Sydney. *Australian Journal of Ecology* **8**, 217–233.

Pyke, G. H. (1985). The relationships between abundances of honeyeaters and their food resources in open forest areas near Sydney. In 'Birds of Eucalypt Forest and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 65–77. (Surrey Beatty & Sons: Sydney.)

Pyke, G. H., and Recher, H. F. (1988). Seasonal patterns of capture rate and resource abundance for honeyeaters and silvereyes in heathland near Sydney. *Emu* **88**, 33–42.

Pyke, G. H., O'Connor, P. J., and Recher, H. F. (1993). Relationship between nectar production and yearly and spatial variation in density and nesting of resident honeyeaters in heathland near Sydney. *Australian Journal of Ecology* **18**, 221–229.

Recher, H. F., and Davis, W. E. (1997). Foraging ecology of a mulga bird community. *Wildlife Research* **24**, 27–43.

Recher, H. F., and Davis, W. E. (1998). The foraging profile of a wandoo woodland avifauna in early spring. *Australian Journal of Ecology* **23**, 514–527.

Recher, H. F., and Holmes, R. T. (1985). Foraging ecology and seasonal patterns of abundance in a forest avifauna. In 'Birds of Eucalypt Forest and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 79–96. (Surrey Beatty & Sons: Sydney.)

Recher, H. F., Holmes, R. T., Schultz, M., Shields, J., and Kavanagh, R. (1985). Foraging patterns of feeding birds in eucalypt forest and woodland of southeastern Australia. *Australian Journal of Ecology* **10**, 399–419.

Wooller, R. D. (1981). Seasonal changes in a community of honeyeaters in south-western Australia. *Emu* **18**, 50-51.

Wooller, R. D., Russell, E. M., Renfree, M. B., and Towers, P. A. (1983). A technique for sampling pollen carried by vertebrates. *Australian Wildlife Research* **10**, 431–432.

Manuscript received 24 June 1999; accepted 20 September 1999