

The foraging profile of a wandoo woodland avifauna in early spring

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Abstract This study reports on the foraging profile of a wandoo woodland avifauna at Dryandra in Western Australia, Australia. Despite its geographical isolation, wandoo woodland shares a large number of species with woodland bird communities in eastern Australia and there are broad similarities in community foraging profiles. Insect-eating birds using ground, bark, foliage, and aerial substrates dominate eucalypt bird communities. Nectar-feeding and seed/fruit-eating guilds are important components of the Australian avifauna, but have fewer species, and vary in composition and abundance as nectar, seed, and fruit availability changes seasonally and from year to year, and from one locality to another. Despite similarities, there are also differences between the foraging profile of the wandoo avifauna and those in eastern Australia. Specifically, the wandoo avifauna is characterized by a high proportion of ground-foraging species. In addition, many wandoo woodland birds appear to spread their foraging over a wider range of substrates (i.e., ground, bark, and foliage) than eastern species. Differences in habitat structure do not explain these differences in community foraging profiles, and there may be differences in the abundance, kind, and spatial distribution of resources between different eucalypt ecosystems. Possibly the eastern communities have lost ground-dwelling components of their avifauna since European settlement, while the woodlands at Dryandra retain a more intact avifauna. The reasons why some species and not others are lost from woodlands as a result of European land management practices are discussed.

Key words: community structure, eucalypt woodland, foraging ecology, habitat fragmentation, threatened species, Western Australia.

INTRODUCTION

The structure of bird communities can be described by the way species obtain food, the types of food taken, the foraging substrates exploited, and the heights at which different species forage (Recher *et al.* 1985; Holmes 1990; MacNally 1994; Noske 1996). These data provide a 'profile' of the foraging ecology of the community and can be used to compare communities within and between habitats (Holmes & Recher 1986; MacNally 1994, 1996). The use of food and foraging ecology in describing avian community structure is derived from the pioneering studies (Lack 1954, 1971; MacArthur 1972; Cody 1974 and others) which emphasized the significance of competition for food resources in the evolution of species and the convergence of communities towards an equilibrium and a common structural organization. Although the role of competition and the notion of equilibria in the development of communities has been questioned (Wiens 1984), using the foraging ecology of species to describe avian communities is useful for the identification of differences and similarities between communities that may be geographically isolated and have different

evolutionary histories (Holmes & Recher 1986). The patterns uncovered in this way can then be used to address questions ranging from the evolution of communities and community structure (Holmes & Recher 1986) to the relative importance of different resources for the conservation and management of ecosystems (Recher 1991).

In this paper we describe the foraging profile of a wandoo woodland avifauna at Dryandra on the western edge of the Western Australian wheatbelt, Australia. Eucalypt woodlands have been extensively cleared for agriculture and remnants are fragmented, isolated, and frequently degraded (Well *et al.* 1984; Resource Assessment Commission 1992). Moreover, selective logging, changed fire regimes, grazing by domestic stock, and weed invasion have changed the structure and floristic composition of the vegetation within the majority of remnants. A consequence is the loss of significant components of the avifauna with remnants commonly dominated by a core of widely distributed, abundant, and often aggressive species (Saunders 1989; Lynch & Saunders 1991; Barrett *et al.* 1994).

The status of the wandoo woodland avifauna is typical of temperate woodland birds throughout Australia (Robinson & Traill 1996). Throughout the central wheatbelt of Western Australia, wandoo woodlands

were preferentially cleared for farming and most remnants are small and isolated (Saunders 1989; Saunders & Ingram 1995). For reasons that are not clear, even the largest remnants rapidly lose species, retaining only a subset of the original avifauna (Saunders 1989; Lynch & Saunders 1991; Saunders & Ingram 1995). To the best of our knowledge, the wandoo woodland avifauna at Dryandra retains the full complement of bird species, including those lost from remnants in the central wheatbelt and provides a unique opportunity to describe the structure of the original community.

We compare our description of the foraging profile of the woodland avifauna at Dryandra with those of eucalypt communities in eastern Australia. We have two objectives in doing this. First, we document differences and similarities in foraging profiles and use these to identify differences and similarities in the structural and resource components of different ecosystems. Although geographically isolated, the communities compared have a common evolutionary history and should have similar community structures. Differences in foraging profiles may therefore indicate differences in resources (Holmes & Recher 1986) or be the result of recent environmental events. Thus, differences between Dryandra and the eastern communities may identify components of woodland avifaunas most likely to be affected by European land management practices. Our second objective is to contribute to an understanding of the reasons for the loss of species from remnant woodlands. This is necessary for the development of an appropriate and effective conservation strategy for woodlands where such species still survive and for the restoration of the avian community where species have been lost. We use our observations to speculate on the reasons why some species and not others are lost from remnants, and to recommend long-term management strategies for fragmented woodland ecosystems.

METHODS

Foraging data were collected from 6–15 August 1995 in wandoo (*Eucalyptus wandoo* and *Eucalyptus accedens*) woodlands in Dryandra State Forest and the 14 Mile Brook Nature Reserve near the town of Narrogin, Western Australia (32°53'S, 117°10'E, 410–430 m a.s.l.). Observations commenced shortly after sunrise and continued to dusk each day.

Study area

Dryandra is a Class A conservation reserve of 27 947 ha comprised of 17 blocks ranging in size from 87 to 12 283 ha. We worked in the largest block which contains extensive areas of *E. wandoo* and *E. accedens* woodlands. These extend throughout the reserve inter-

spersed with plantations of *Eucalyptus astringens*. Although the woodlands in Dryandra are fragmented, they are not isolated. The 14 Mile Brook Nature Reserve (44.8 ha) is 12 km from the main Dryandra block and linked by almost continuous bands of vegetation along roads and across farmland.

At Dryandra, *E. wandoo* forms nearly pure stands of open woodlands on mid- to lower slopes and low lying areas (Coates 1993). These are 'run-on' areas receiving water and nutrients from higher ground and are characterized by deep sandy to sandy loam soils over clay (Coates 1993). Wilson (1997) measured the vegetation at three locations in *E. wandoo* woodlands at Dryandra. She found the projected foliage cover of the canopy averaged 45%, that of the subcanopy averaged 14%, while that of the shrub layer ranged from 14 to 42%. *Acacia lasiocarpa*, *Hibbertia commutata*, *Bossiaea spinescens*, *Bossiaea eriocarpa*, *Gastrolobium microcarpum*, and *Astrolobia* spp. are the dominant shrubs within the woodlands at Dryandra. *E. accedens* dominates ridges and upper to mid-slopes ('run-off' areas) below lateritic plateaux with sandy and gravelly duplex soils (Coates 1993). Shrub communities dominated by *Dryandra* spp. occur among the *E. accedens* woodlands around the tops of lateritic residuals (Coates 1993), but shrubs and patches of shrubs are scattered through the wandoo woodlands from ridge to flats.

Wandoo woodlands have a sparse ground vegetation dominated by annual plants which germinate with the commencement of winter rains and dry-off by October. Ground vegetation is low (< 8 cm) and reaches its best development on the flats dominated by *E. wandoo*. Where litter occurs it tends to be a thin layer (< 1.5 cm) of dead leaves; there are extensive areas of bare soil. Logs and coarse woody debris are abundant.

On moist sites in association with granite, *Allocasuarina huegeliana* and *Acacia acuminata* replace the eucalypts as dominants (Coates 1993). *Eucalyptus loxophleba* occurs in association with *A. acuminata*, while *Eucalyptus calophylla* occurs in association with *E. wandoo* on grey sandy soils (Coates 1993). The 14 Mile Brook Nature Reserve is an area of wandoo woodland similar to that at Dryandra.

Foraging data

Foraging data were collected at 10 different sites in Dryandra and at the 14 Mile Brook Nature Reserve; we worked at different sites each day and changed sites between morning and afternoon. Some sites were visited on two or more occasions. Our objective was to sample the range of wandoo habitats in the reserves and we allocated our time between *E. wandoo* and *E. accedens* woodlands in about the proportion that each occurred. Shrublands dominated by *Dryandra* species were avoided and are the subject of a separate study of honeyeater foraging ecology.

Foraging observations were recorded for all species of birds encountered. For each individual, we recorded up to five consecutive prey attacks following the procedures of Recher *et al.* (1985). Such data are not independent, however Recher & Gebski (1989) showed that there are no significant differences in results when two or more observations per individual are recorded as opposed to only one observation.

As our objective was to describe the foraging profile of the wandoo avifauna during a short time period, multiple observations on individual birds increased the chance of recording infrequent or unusual behaviour (Recher *et al.* 1985), while providing a large data set for analysis.

Following Recher *et al.* (1985), only foraging manoeuvres in which the bird obtained or attempted to obtain a prey item were recorded. These are called prey attacks. For each of these, we recorded the species of bird, the substrate and height of the prey, and the attack or foraging behaviour used by the bird. Foraging behaviours were described as glean, snatch, pounce, probe, hover, and hawk following the terminology of Recher *et al.* (1985). For substrates, we recorded the following categories: 1, ground (including ground vegetation, litter, logs, and coarse woody debris); 2, bark (including branches, and the main stem or trunk), substrates with loose or decorticating bark were recorded separately from other bark surfaces; 3, foliage (including twigs, petioles, eucalypt seed capsules, and leaves); 4, flowers (nectar); and 5, air (for aerial prey). Dead substrates were distinguished from live substrates, but sample sizes for dead substrates and for decorticating bark were too small to justify separate analysis. Height was estimated to the nearest 0.1 m below 2 m and to the nearest 0.5 m above 2 m. Plants on which birds were foraging were identified to genus and, where possible, to species. All trees were identified to species.

An estimate of the abundances of all bird species was made at 14 Mile Brook Nature Reserve and at eight of the 10 sites in Dryandra where we recorded foraging data. These estimates were made over several hours as a 'running tally' of birds detected during the collection of foraging data. Although these estimates cannot be used as measures of absolute abundances or to compare population densities between species and sites, they do indicate relative numbers and are an index of variation in the composition and species richness of the avifauna on the sites where we collected foraging data.

Data analysis and presentation

For each species we present the total number of prey attacks observed and calculate the percentage use of substrates, prey attack behaviours, and foraging heights based on these totals. Species for which we recorded

fewer than 10 prey attacks are not analysed, but, for discussion, some are put into foraging guilds based on unpublished observations made in other woodlands.

RESULTS

We obtained foraging data for 33 species. Observations of 50 or more prey attacks were obtained for 24 species, 34–41 observations were obtained for four species, while for five species we made only 10–20 observations.

Numbers and distribution of woodland birds

Of the 62 species of woodland birds we noted at Dryandra (Table 1), 52 were recorded while collecting foraging data (Table 2). The number of species recorded per count ranged from 15 to 28 (mean 21 ± 5) (Table 2).

Only the weebill was recorded at all the sites where we collected foraging data (Table 2). Six species, broad-tailed thornbill, grey shrike-thrush, rufous treecreeper, western thornbill, western warbler, and yellow-plumed honeyeaters were recorded at eight sites, while the Port Lincoln parrot and white-browed babbler were found on seven (see Table 1 for Latin names of birds). Thirty-two species, 60% of the species censused, were recorded on four or fewer of the sites. Fifteen species were recorded only once (Table 2). Brown, New Holland, and western spinebill honeyeaters were recorded infrequently during censuses, but were abundant in patches of *Dryandra* shrublands where there was a rich source of nectar. Because we avoided them, few of these shrublands were sampled.

Foraging heights

Of the 33 species for which more than 10 foraging observations were obtained, 18 species (56%) took more than half their food from the ground and/or ground vegetation (Tables 3 and 4). Five of these species took 89% or greater of their food from the ground. Australian magpie, fan-tailed cuckoo, mallee fowl, painted quail, and red-capped robin, for which we obtained fewer than 10 foraging observations, are also ground-foragers and take more than 90% of their food from the ground, litter, and low vegetation (unpublished data from other habitats).

Including ground-foragers, 21 species (66%) took more than half their prey from within 1 m of the ground (Table 3). Ground, ground vegetation, litter, logs, debris, and low shrubs were the substrates used in this height range by 18 of the 21 species. Grey fantail, jacky winter, willie wagtail, and western spinebill took a large proportion of their aerial prey within 1 m of the ground

(Table 3). Despite extensive ground-foraging, most species in this category foraged throughout the vegetation profile (Table 3). Three species, blue-breasted fairy wren, western spinebill, silvereye, and broad-tailed thornbill, foraged extensively in low shrubs (0.2–1 m) and piles of debris (Table 3). Broad-tailed thornbills also foraged in taller shrubs and the canopy. Eleven species took more than 40% of food items from the ground and ground vegetation, but also foraged more than 1 m above the ground in taller shrubs and the canopy (Table 3). Between 0.1 and 1 m above the ground, rufous treecreepers and scarlet robins took insects from logs, stumps, and tree trunks.

Twelve species took more than 60% of their food items from tall shrubs and the canopy. Except for the Port Lincoln parrot and golden whistler, they rarely foraged on the ground or in low shrubs. Shrub and canopy foragers included brown and New Holland honeyeaters and the little wattlebird which fed mainly on *Dryandra* nectar and foraged almost exclusively in patches of tall shrubs. The remaining species foraged mainly in eucalypts, while the western spinebill took nectar from a variety of low shrubs (e.g., *Astrolooma*, *Grevillea*), as well as *Dryandra*. Tree martins hawked

flying insects throughout and above the canopy layer (Table 3).

Substrates

Ground, including litter, logs, and debris, but excluding the foliage of ground vegetation, was the most frequently used substrate with 17 species taking more than 40% of their food from the ground (Table 4). Nine species took more than 75% of their prey from the ground and ground litter. Because prey taken from ground vegetation is categorized in Table 4 as foliage, there are differences in the grouping of species between Tables 3 and 4.

Bark, especially loose and decorticating bark, was an important substrate for 14 species which took 15% or more of their prey from branches and tree trunks (Table 4). In addition, 13% of the prey of broad-tailed thornbills and 12% of the prey of western thornbills were taken from bark. Only three species (black-capped sittella, white-naped honeyeater, and yellow-plumed honeyeater) took more than half their prey from bark. The sittella was the only species that foraged exclusively on branches and tree trunks. Seven of the species which frequently foraged on bark (> 15% of prey attacks) took

Table 1. Alphabetical index of common and scientific names of birds observed at Dryandra during August 1995.

| | | | |
|---------------------------|-------------------------------------|--------------------------|--------------------------------------|
| Australian magpie | <i>Gymnorhina tibicen</i> | Painted Quail | <i>Turnix varia</i> |
| Australian raven | <i>Corvus coronoides</i> | Peregrine Falcon | <i>Falco peregrinus</i> |
| Black-capped sittella | <i>Daphoenositta pileata</i> | Pipit | <i>Anthus novaeseelandiae</i> |
| Black-faced cuckoo shrike | <i>Coracina novaehollandiae</i> | Port Lincoln Parrot | <i>Barnardius zonarius</i> |
| Blue-breasted fairy wren | <i>Malurus pulcherrimus</i> | Red Wattlebird | <i>Anthochaera carunculata</i> |
| Broad-tailed thornbill | <i>Acanthiza apicalis</i> | Red-capped Parrot | <i>Purplecephalus spurius</i> |
| Brown falcon | <i>Falco berigora</i> | Red-capped Robin | <i>Petroica goodenovii</i> |
| Brown goshawk | <i>Accipiter fasciatus</i> | Regent Parrot | <i>Polytelis anthopeplus</i> |
| Brown honeyeater | <i>Lichmera indistincta</i> | Restless Flycatcher | <i>Myiagra inquieta</i> |
| Brown-headed honeyeater | <i>Melithriptus brevirostris</i> | Rufous Treecreeper | <i>Climacteris rufa</i> |
| Crested shrike tit | <i>Falcunculus frontatus</i> | Rufous Whistler | <i>Pachycephala rufiventris</i> |
| Common bronzewing | <i>Phaps chalcoptera</i> | Scarlet Robin | <i>Petroica multicolor</i> |
| Crested bellbird | <i>Oreocica gutturalis</i> | Silvereye | <i>Zosterops lateralis</i> |
| Crested pigeon | <i>Ocyphaps lophotes</i> | Singing Honeyeater | <i>Meliphaga virescens</i> |
| Dusky woodswallow | <i>Artamus cyanopterus</i> | Splendid Fairy Wren | <i>Malurus splendens</i> |
| Fan-tailed cuckoo | <i>Cuculus pyrrhophanus</i> | Spotted Scrubwren | <i>Sericornis maculatus</i> |
| Galah | <i>Cacatua roseicapilla</i> | Striated Pardalote | <i>Pardalotus striatus</i> |
| Golden whistler | <i>Pachycephala pectoralis</i> | Wedge-tailed Eagle | <i>Aquila audax</i> |
| Grey currawong | <i>Strepera versicolor</i> | Weebill | <i>Smicrornis brevirostris</i> |
| Grey fantail | <i>Rhipidura fuliginosa</i> | Western Rosella | <i>Platycercus icterotis</i> |
| Grey shrike-thrush | <i>Colluricincla harmonica</i> | Western Spinebill | <i>Acanthorhynchus superciliosus</i> |
| Hooded robin | <i>Melanodryas cucullata</i> | Western Thornbill | <i>Acanthiza inornata</i> |
| Horsfield bronze cuckoo | <i>Chrysococcyx basalis</i> | Western Warbler | <i>Gerygone fusca</i> |
| Jacky winter | <i>Microeca leucomela</i> | Western Yellow Robin | <i>Eopsaltria griseogularis</i> |
| Laughing kookaburra | <i>Dacelo gigas</i> | White-browed Babbler | <i>Pomatomus superciliosus</i> |
| Magpie-lark | <i>Grallina cyanoleuca</i> | White-cheeked Honeyeater | <i>Phylidonyris nigra</i> |
| Mallee fowl | <i>Leipoa ocellata</i> | White-eared Honeyeater | <i>Meliphaga leucomelas</i> |
| Mistletoe bird | <i>Dicaeum hirundinaceum</i> | White-naped Honeyeater | <i>Melithreptus lunatus</i> |
| Nankeen kestrel | <i>Falco cenchroides</i> | Willie Wagtail | <i>Rhipidura leucophrys</i> |
| New Holland honeyeater | <i>Phylidonyris novaehollandiae</i> | Yellow-plumed Honeyeater | <i>Lichenostomus ornatus</i> |
| Pallid cuckoo | <i>Cuculus pallidus</i> | Yellow-rumped Thornbill | <i>Acanthiza chrysorrhoa</i> |

more than 40% of their prey from the ground, while bark was the second most important substrate for four species which took more than half their prey from

foliage. For the grey fantail and restless flycatcher bark was their second most important foraging substrate (Table 4).

Table 2. Bird species and number of individuals or groups (grp) censused at eight different sites at Dryandra (A-H) and 14 Mile Brook Nature Reserve (I) in wandoo woodland during August 1995

| Species | A | B | C | D | E | Site F | Site G | | | No. sites recorded |
|---------------------------|-------|-------|-------|-------|-------|-----------|-----------|-------|-------|--------------------|
| | | | | | | | H | I | J | |
| Port Lincoln parrot | 2 | 0 | 0 | 6 | 10 | 6 | 2 | 5 | 10+ | 7 |
| Australian magpie | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 2 |
| Australian raven | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 3 |
| Black-capped sittella | 1 grp | 0 | 0 | 1 grp | 0 | 1 grp | 0 | 1 grp | 1 grp | 5 |
| Black-faced cuckoo shrike | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 4 |
| Blue-breasted fairy wren | 2 grp | 0 | 0 | 0 | 2 grp | 0 | 0 | 0 | 0 | 2 |
| Broad-tailed thornbill | 2 | 1 | 2 | 1 | 3 | 0 | 4 | 1 | 4 | 8 |
| Brown goshawk | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| Brown honeyeater | 10+ | 0 | 0 | 0 | 0 | 10+ | 4 | 0 | 0 | 3 |
| Brown-headed honeyeater | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 1 | 0 | 2 |
| Crested shrike tit | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Fan-tailed cuckoo | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 |
| Dusky woodswallow | 0 | 15 | 15 | 0 | 10+ | 0 | 0 | 0 | 0 | 3 |
| Galah | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| Golden whistler | 1 | 0 | 0 | 1 | 3 | 4 | 4 | 6 | 0 | 6 |
| Grey currawong | 2 | 1 | 1 | 1 | 3 | 1 | 0 | 0 | 0 | 6 |
| Grey fantail | 0 | 0 | 0 | 1 | 6 | 0 | 0 | 0 | 3 | 3 |
| Grey shrike-thrush | 1 | 1 | 4 | 10 | 8 | 2 | 0 | 2 | 10 | 8 |
| Horsfield bronze cuckoo | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 4 | 4 |
| Jacky winter | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 1 |
| Laughing kookaburra | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 2 |
| Mallee fowl | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| New Holland honeyeater | 0 | 0 | 0 | 0 | 0 | 10+ | 0 | 0 | 0 | 1 |
| Painted quail | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 |
| Peregrine falcon | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 1 |
| Red wattlebird | 0 | 2 | 2 | 5 | 0 | 2 | 1 | 0 | 0 | 5 |
| Red-capped parrot | 2 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 2 |
| Red-capped robin | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 3 |
| Regent parrot | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 1 |
| Restless flycatcher | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 4 |
| Rufous treecreeper | 8 | 10 | 10 | 8 | 6 | 0 | 4 | 10+ | 5 | 8 |
| Rufous whistler | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 2 |
| Scarlet robin | 4 | 0 | 0 | 2 | 2 | 1 | 2 | 1 | 0 | 6 |
| Silveryeye | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Singing honeyeater | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| Spotted scrubwren | 0 | 2 | 2 | 0 | 4 | 4 | 0 | 1 | 0 | 5 |
| Striated pardalote | 3 | 0 | 0 | 5 | 5 | 6 | 0 | 2 | 1 | 6 |
| Tree martin | 10+ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10+ | 2 |
| Wedge-tail eagle | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Weebill | 10+ | 2 | 2 | 8 | 12 | 15 | 10 | 8 | 10+ | 9 |
| Western rosella | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 |
| Western spinebill | 3 | 0 | 0 | 0 | 0 | 5 | 4 | 0 | 0 | 3 |
| Western thornbill | 3 grp | 1 grp | 1 grp | 1 grp | 2 grp | 1 grp | 2 grp | 1 grp | 0 | 8 |
| Western warbler | 1 | 0 | 0 | 2 | 6 | 2 | 2 | 1 | 4 | 8 |
| Western yellow robin | 1 | 8 | 8 | 1 | 4 | 0 | 0 | 4 | 1 | 7 |
| White-browed babbler | 0 | 1 grp | 1 grp | 1 grp | 1 grp | 0 | 0 | 1 grp | 1 grp | 6 |
| White-cheeked honeyeater | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| White-eared honeyeater | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| White-naped honeyeater | 3 | 0 | 0 | 1 | 6 | 0 | 2 | 0 | 1 | 5 |
| Willie wagtail | 0 | 4 | 4 | 6 | 0 | 0 | 0 | 0 | 1 | 4 |
| Yellow-plumed honeyeater | 10+ | 10+ | 10+ | 10+ | 10 | 0 | 4 | 10+ | 10+ | 8 |
| Yellow-rumped thornbill | 0 | 0 | 0 | 1 grp | 1 grp | 0 | 0 | 0 | 2 grp | 3 |
| No. species | 24 | 17 | 17 | 27 | 28 | 19 | 15 | 19 | 26 | |

Eucalyptus wandoo and *E. accedens* shed bark from branches and trunk. Almost all foraging on branches was by birds taking prey from under loose and decorative bark. This also tended to be the case on the trunks of *E. wandoo* and *E. accedens* where prey attacks were often directed towards small (< 15 mm in diameter) irregularities and depressions characterized by a rough and flaky bark surface. Inspection showed that these irregularities contained numbers of small insects (< 1 mm in length) and it was probably these that the birds were taking. Honeyeaters, such as the western spinebill, extracted prey from these depressions using their tongues similar to the way they take nectar from a flower.

After ground substrates, foliage (including twigs and petioles) was the most important foraging substrate. Six species took more than 50% of their prey from foliage (Table 4). Another eight species took more than 20% of their prey from foliage. Birds that took the majority of prey from foliage also foraged on the ground (three of six species) or took prey from bark (four of six) and the air (three of six).

Four species took 40% or more of their prey from the air, but the tree martin was the only exclusively aerial forager. The large percentage of hawking by western spinebills (43% of prey attacks; Table 5), and by brown (12%) and New Holland honeyeaters (21%), was related to their catching insects to feed young. Jacky

Table 3. Means and standard deviations of foraging height (m) and percentage use of vegetation layers by foraging birds in wandoo woodland during August 1995

| Species/foraging layer (sample size) | Foraging height (m) | | | | Mean (SD) |
|--------------------------------------|---------------------|-------|-------|-----|------------|
| | 0–0.1 | 0.2–1 | 1.1–5 | > 5 | |
| Ground | | | | | |
| Splendid fairy wren (12) | 100 | 0 | 0 | 0 | 0 (0) |
| Yellow-rumped thornbill (131) | 99 | 0 | 1 | 0 | 0.01 (0.1) |
| Spotted scrubwren (53) | 89 | 2 | 9 | 0 | 0.2 (0.6) |
| Western yellow robin (109) | 96 | 1 | 3 | 0 | 0.7 (0.4) |
| Dusky woodswallow (101) | 90 | 1 | 4 | 5 | 1.1 (4.4) |
| Ground and shrub | | | | | |
| Willie wagtail (71) | 77 | 19 | 4 | 0 | 0.2 (0.5) |
| Hooded robin (41) | 80 | 18 | 2 | 0 | 0.2 (0.6) |
| Blue-breasted fairy wren (82) | 80 | 20 | 0 | 0 | 0.7 (0.5) |
| Western spinebill (14) | 21 | 36 | 43 | 0 | 1.8 (1.7) |
| Ground and canopy | | | | | |
| Jacky winter (100) | 67 | 4 | 29 | 0 | 0.7 (1.0) |
| White-browed babbler (161) | 76 | 4 | 13 | 7 | 0.8 (1.8) |
| Scarlet robin (62) | 77 | 5 | 18 | 0 | 0.8 (1.9) |
| Grey currawong (19) | 79 | 0 | 21 | 0 | 1.1 (2.1) |
| Rufous treecreeper (363) | 65 | 8 | 20 | 7 | 1.3 (2.3) |
| Western thornbill (178) | 64 | 2 | 26 | 8 | 1.4 (2.1) |
| Grey shrike-thrush (85) | 63 | 5 | 14 | 18 | 2.0 (3.2) |
| Rufous whistler (18) | 61 | 0 | 26 | 13 | 3.4 (2.2) |
| Silveryeye (78) | 54 | 0 | 15 | 31 | 3.6 (4.3) |
| Restless flycatcher (37) | 68 | 0 | 0 | 32 | 4.2 (5.8) |
| Port Lincoln parrot (80) | 40 | 0 | 0 | 60 | 4.7 (3.9) |
| Golden whistler (111) | 20 | 12 | 34 | 34 | 4.0 (3.5) |
| Shrub and canopy | | | | | |
| Little wattlebird (10) | 0 | 0 | 100 | 0 | 1.8 (0) |
| Broad-tailed thornbill (148) | 8 | 47 | 29 | 16 | 1.9 (2.6) |
| New Holland honeyeater (38) | 0 | 5 | 95 | 0 | 2.0 (0.6) |
| Grey fantail (182) | 14 | 37 | 41 | 8 | 2.0 (2.3) |
| Brown honeyeater (34) | 0 | 0 | 82 | 18 | 2.7 (1.8) |
| Canopy | | | | | |
| Western warbler (122) | 0 | 4 | 74 | 22 | 4.1 (2.2) |
| Yellow-plumed honeyeater (237) | 0 | 1 | 38 | 61 | 6.7 (3.3) |
| Striated pardalote (66) | 0 | 0 | 45 | 55 | 7.6 (3.6) |
| White-naped honeyeater (58) | 0 | 0 | 9 | 91 | 7.7 (3.0) |
| Weebill (261) | 0 | 4 | 42 | 54 | 8.4 (5.9) |
| Black-capped sittella (108) | 0 | 0 | 21 | 79 | 9.2 (4.2) |
| Above canopy | | | | | |
| Tree martin (110) | 0 | 0 | 0 | 100 | 17.9 (2.9) |

winter (26% of prey attacks), willie wagtail (39%), western warbler (14%), and yellow-plumed honeyeater (15%) also took large numbers of flying insects. Dusky woodswallows took most (90%) of their prey from the ground during the times we observed them foraging, but we also noticed woodswallows above the canopy where they hawked flying insects.

The six species of honeyeaters (Meliphagidae) for which we obtained foraging data visited flowers and took nectar (Table 4). Some may have been attracted by the insects found at flowers rather than the nectar. The red wattlebird, a species for which we obtained few foraging records, visited flowers for nectar, but was also

observed probing under loose bark on branches and trunks. The brown-headed honeyeater, another species with few foraging observations, was only observed to glean foliage. Honeyeaters, other than the yellow-plumed honeyeater, congregated in patches of *Dryandra*, which were in full bloom and rich in nectar.

Prey attack behaviour

Gleaning was the most common foraging behaviour used by birds in wandoo woodland (Table 5). Nine species took 80% or more of their prey by gleaning, while another 10 species used gleaning more than 40%

Table 4. The percent use of substrates by a wandoo woodland avifauna at Dryandra during August 1995

| Species/guild (sample size) | Ground | Bark | Foliage | Air | Flower |
|------------------------------------|--------|--------|---------|-----|--------|
| | | Branch | Trunk | | |
| Ground foragers | | | | | |
| Splendid fairy wren (12) | 100 | 0 | 0 | 0 | 0 |
| Western yellow robin (109) | 96 | 0 | 4 | 0 | 0 |
| Spotted scrubwren (53) | 91 | 6 | 0 | 4 | 0 |
| Dusky woodswallow (101) | 90 | 1 | 0 | 1 | 8 |
| Yellow-rumped thornbill (131) | 84 | 0 | 0 | 5 | 11 |
| Scarlet robin (62) | 77 | 6 | 3 | 5 | 8 |
| Ground and bark foragers | | | | | |
| White-browed babbler (161) | 82 | 17 | 1 | 0 | 0 |
| Hooded robin (41) | 80 | 0 | 15 | 5 | 0 |
| Rufous treecreeper (362) | 70 | 19 | 10 | 1 | 0 |
| Grey shrike-thrush (85) | 53 | 27 | 1 | 19 | 0 |
| Silveryeye (78) | 41 | 29 | 6 | 23 | 0 |
| Ground and foliage foragers | | | | | |
| Rufous whistler (18) | 44 | 22 | 0 | 28 | 6 |
| Western thornbill (178) | 62 | 11 | 1 | 26 | 0 |
| Blue-breasted fairy wren (82) | 71 | 0 | 0 | 29 | 0 |
| Grey currawong (19) | 79 | 0 | 0 | 21 | 0 |
| Ground and aerial foragers | | | | | |
| Jacky winter (100) | 66 | 2 | 6 | 0 | 26 |
| Willie wagtail (70+A55) | 44 | 0 | 0 | 17 | 39 |
| Bark foragers | | | | | |
| Black-capped sitella (114) | 0 | 80 | 20 | 0 | 0 |
| Bark and foliage foragers | | | | | |
| White-naped honeyeater (59) | 0 | 54 | 5 | 24 | 0 |
| Yellow-plumed honeyeater (235) | 0 | 44 | 12 | 20 | 15 |
| Foliage foragers | | | | | |
| Striated pardalote (56) | 0 | 0 | 0 | 100 | 0 |
| Weebill (265) | 0 | 12 | 3 | 85 | 0 |
| Broad-tailed thornbill (148) | 8 | 11 | 2 | 74 | 4 |
| Port Lincoln parrot (86) | 27 | 0 | 0 | 73 | 0 |
| Western warbler (126) | 0 | 8 | 13 | 62 | 17 |
| Golden whistler (111) | 20 | 21 | 3 | 52 | 1 |
| Hawkers | | | | | |
| Tree martin (110) | 0 | 0 | 0 | 100 | 0 |
| Grey fantail (182) | 2 | 0 | 14 | 7 | 77 |
| Restless flycatcher (39) | 21 | 21 | 0 | 13 | 45 |
| Western spinebill (14) | 0 | 0 | 7 | 36 | 43 |
| Nectar feeders | | | | | |
| Little wattlebird (10) | 0 | 0 | 0 | 0 | 100 |
| Brown honeyeater (34) | 0 | 0 | 0 | 6 | 12 |
| New Holland honeyeater (38) | 0 | 0 | 0 | 13 | 21 |
| | | | | | 66 |

of the time. Probing, a foraging behaviour similar to gleaning, but directed into (e.g., flowers for nectar) or under a substrate (e.g., decorticating bark) was a principal foraging behaviour (> 45% of prey attacks) for six species.

Three of the six species classed as 'probers' were honeyeaters that visited flowers for nectar (Table 4). Two other honeyeaters, white-naped and yellow-plumed, probed under loose bark on branches and trunks where they probably obtained insects, manna, and honeydew. Probing was the second-most frequent foraging behaviour of black-capped sittella (Table 5). Sittellas gleaned prey (53% of prey attacks) from bark surfaces or probed under loose bark or into cracks and crevices (47%). Occasionally (< 5% of foraging

manoeuvres), sittellas lifted up and removed bark to expose prey (flaking), but we classed this as probing.

Pouncing to take prey on the ground was the principal foraging behaviour (> 60% of prey attacks) of five species (Table 5). It was also used by the restless flycatcher (21% of prey attacks). Two species, red-capped robin and fan-tailed cuckoo, for which we obtained fewer than 10 foraging observations, are also pouncers that take prey from the ground (unpubl. data). Willie wagtail, grey fantail, and restless flycatcher were constantly in motion, moving between perches, hovering over the ground, and moving from ground level into the upper canopy. At times, restless flycatchers hovered over a spot before pouncing on or snatching prey from the ground or ground vegetation.

Table 5. Per cent use of prey-attack manoeuvres by a wandoo woodland avifauna during August 1995

| Behaviour Species/guild (sample size) | Pounce | Probe | Glean | Hover | Snatch | Hawk |
|--|--------|-------|-------|-------|--------|------|
| Pounce | | | | | | |
| Western yellow robin (109) | 97 | 0 | 0 | 0 | 3 | 0 |
| Dusky woodswallow (101) | 90 | 0 | 0 | 1 | 1 | 8 |
| Hooded robin (41) | 80 | 0 | 15 | 0 | 5 | 0 |
| Jacky winter (100) | 66 | 0 | 0 | 0 | 8 | 26 |
| Scarlet robin (62) | 61 | 17 | 2 | 2 | 10 | 8 |
| Probe | | | | | | |
| Little wattlebird (10) | 0 | 100 | 0 | 0 | 0 | 0 |
| Brown honeyeater (34) | 0 | 69 | 13 | 3 | 3 | 12 |
| New Holland honeyeater (38) | 0 | 66 | 0 | 0 | 13 | 21 |
| White-naped honeyeater (59) | 0 | 57 | 41 | 0 | 2 | 0 |
| Yellow-plumed honeyeater (235) | 0 | 47 | 28 | 5 | 5 | 15 |
| Black-capped sittella (114) | 0 | 47 | 53 | 0 | 0 | 0 |
| Glean | | | | | | |
| Grey currawong (19) | 0 | 0 | 100 | 0 | 0 | 0 |
| Port Lincoln parrot (86) | 0 | 0 | 100 | 0 | 0 | 0 |
| Splendid fairy wren (12) | 0 | 0 | 100 | 0 | 0 | 0 |
| Spotted scrubwren (53) | 0 | 0 | 100 | 0 | 0 | 0 |
| Striated pardalote (56) | 0 | 0 | 100 | 0 | 0 | 0 |
| Yellow-rumped thornbill (131) | 0 | 0 | 89 | 0 | 0 | 11 |
| Western thornbill (178) | 0 | 4 | 88 | 6 | 2 | 0 |
| Blue-breasted fairy wren (82) | 0 | 0 | 83 | 0 | 17 | 0 |
| Grey shrike-thrush (85) | 0 | 11 | 82 | 1 | 6 | 0 |
| White-browed babbler (161) | 0 | 21 | 79 | 0 | 0 | 0 |
| Rufous treecreeper (362) | 0 | 22 | 78 | 0 | 0 | 0 |
| Silveryeye (78) | 0 | 18 | 76 | 6 | 0 | 0 |
| Willie wagtail (71) | 3 | 0 | 55 | 0 | 3 | 39 |
| Glean and snatch | | | | | | |
| Broad-tailed thornbill (148) | 0 | 1 | 67 | 7 | 21 | 4 |
| Rufous whistler (18) | 0 | 0 | 72 | 0 | 22 | 6 |
| Golden whistler (111) | 0 | 4 | 56 | 0 | 39 | 1 |
| Western warbler (126) | 0 | 4 | 29 | 21 | 32 | 14 |
| Restless flycatcher (39) | 21 | 0 | 0 | 26 | 32 | 21 |
| Glean and hover | | | | | | |
| Weebill (265) | 0 | 0 | 45 | 45 | 10 | 0 |
| Hawk | | | | | | |
| Western spinebill (14) | 0 | 15 | 21 | 21 | 0 | 43 |
| Grey fantail (182) | 1 | 0 | 1 | 14 | 7 | 77 |
| Tree martin (110) | 0 | 0 | 0 | 0 | 0 | 100 |

The weebill was the only species to take a major proportion (45% of prey attacks) of prey while hovering (Table 5). We were careful to distinguish between hovering behaviour that was exploratory (searching) and hovering while taking prey. Weebills did both, but only movements directed against prey are presented here. Hovering was a common behaviour used by the western warbler (21% of prey attacks), restless flycatcher (26%), grey fantail (14%), and western spinebill (14%). With grey fantails, hovering was directed against prey on tree trunks as part of a foraging behaviour in which individuals moved rapidly over the bark surface searching for and flushing prey. Spinebills hovered to take prey from bark and foliage, but also hover at flowers to probe for nectar (H. F. Recher pers. obs. 1986 and other habitats during August 1995).

Five species took more than 20% of their prey by snatching (Table 5). Snatching was the most frequent prey attack behaviour of the western warbler and restless flycatcher, and the second most frequent manoeuvre of golden and rufous whistlers, and the broad-tailed thornbill. Nine species obtained 10% or more of their prey by snatching. The same number of species took 10% or more of their prey by hawking. Five of these took more than 25% of their prey by hawking. Hawking was the principal foraging behaviour of western spinebills (43% of prey attacks), grey fantails (77%), and tree martins (100%; Table 5). Thirty-nine

per cent of prey attacks by willie wagtails were hawks, with the bird often hawking insects that it had flushed from the ground as it moved along the ground or from perch to perch.

Plant species

Eucalyptus wandoo was the most frequently used tree species by foraging birds (Table 6). However, these data should not be taken as evidence that birds preferred one species of eucalypt as a foraging substrate to another. During observations, there was no indication that birds preferred one species over another. Where the different eucalypts occurred together, birds foraged in all (Table 6). We avoided areas where some species were most abundant and made our foraging observations in woodlands dominated by *E. wandoo* and *E. accedens*. However, as we spent equal amounts of time in woodlands dominated by *E. wandoo* and those dominated by *E. accedens*, birds may forage preferentially in *E. wandoo* woodlands, but we lack data on tree species frequencies and cannot confirm this suggestion. Where *Acacia acuminata* and *Allocasuarina huegeliana* occurred, they were used by birds as foraging substrates. The frequent use of *Dryandra* spp. by honeyeaters reflects the abundance of blossom at the time of the study, despite our avoiding *Dryandra* shrublands.

Table 6. Per cent use of plant species for foraging by a wandoo woodland avifauna during August 1995. Only species with 10 or more prey attacks in which prey is taken from vegetation are presented. Others include ground vegetation, other eucalypts, sheoak, wattles, and shrubs

| Plant species Bird species (sample size) | Wandoo | Powderbark wandoo | Marri | Dryandra | Other |
|---|--------|----------------------|-------|----------|-------|
| Rufous treecreeper (95) | 92 | 5 | 0 | 0 | 3 |
| Port Lincoln parrot (38) | 89 | 0 | 0 | 0 | 11 |
| Black-capped sittella (114) | 84 | 5 | 10 | 0 | 0 |
| Restless flycatcher (14) | 79 | 0 | 0 | 0 | 21 |
| White-naped honeyeater (59) | 76 | 22 | 2 | 0 | 0 |
| Grey fantail (37) | 76 | 0 | 3 | 3 | 19 |
| Yellow-plumed honeyeater (102) | 72 | 26 | 0 | 0 | 2 |
| Grey shrike-thrush (42) | 69 | 0 | 0 | 0 | 31 |
| Silveryeye (42) | 67 | 0 | 10 | 0 | 24 |
| Weebill (264) | 65 | 31 | 1 | 0 | 4 |
| Striated pardalote (66) | 64 | 18 | 27 | 0 | 9 |
| Western warbler (110) | 62 | 15 | 5 | 0 | 18 |
| Western thornbill (69) | 38 | 0 | 32 | 0 | 30 |
| Golden whistler (56) | 34 | 4 | 14 | 0 | 48 |
| Little wattlebird (10) | 0 | 0 | 0 | 100 | 0 |
| Brown honeyeater (28) | 7 | 0 | 0 | 89 | 4 |
| New Holland honeyeater (30) | 0 | 17 | 0 | 50 | 33 |
| Willie wagtail (12) | 0 | 0 | 0 | 0 | 100 |
| Yellow-rumped thornbill (15) | 0 | 0 | 0 | 0 | 100 |
| Blue-breasted fairy wren (38) | 5 | 0 | 0 | 0 | 95 |
| Broad-tailed thornbill (132) | 30 | 5 | 1 | 0 | 64 |

Table 7. The use of substrates by bird species in three eucalypt woodlands. The number of species in each category is the number taking more than 20% of their prey from that substrate. Species may be counted in more than one category with the percentage based on the total number of species for which data were recorded in each woodland. Percentages therefore exceed 100.

| Substrate | Dryandra, WA | No. species (%) | |
|---------------|--------------|---------------------------|---------------------------|
| | | Southern Tablelands, NSW* | Northern Tablelands, NSW† |
| Ground | 20 (61) | 14 (34) | 15 (38) |
| Bark | 10 (30) | 10 (24) | 7 (18) |
| Foliage | 16 (49) | 16 (39) | 18 (45) |
| Aerial | 7 (21) | 6 (15) | 7 (18) |
| Nectar | 3 (9) | 4 (10) | 6 (15) |
| Seeds/fruit | 0 (0) | 2 (5) | 3 (8) |
| Total species | 33 | 41 | 40 |

*Recher *et al.* 1985; †Ford *et al.* 1986.

DISCUSSION

Foraging ecology of eucalypt avifaunas

Recher *et al.* (1985) and Ford *et al.* (1986) used similar procedures to our work at Dryandra to describe the foraging ecology of bird communities in eucalypt forest and woodland on the Southern and Northern Tablelands of New South Wales. Most other studies of the foraging ecology of eucalypt birds have either focused on single species (Bell 1986), on guilds of closely related species (Bell 1985; Noske 1985; Recher 1989; Robinson 1992), or did not consider all bird species within the community (Calver & Wooller 1981; Wooller & Calver 1981; Cale 1994). Osborne and Green (1992) reported on avian foraging ecology of birds at high elevation in the Snowy Mountains where there are relatively few species. The communities studied by Recher *et al.* (1985) and Ford *et al.* (1986) had similar numbers of bird species to the wandoo woodlands at Dryandra. Although both studies were of longer duration and obtained foraging data for more species than did we at Dryandra, we compare the guild structure and use of substrates by birds in the three communities to identify major differences and similarities between the respective communities. The presentation here is preliminary and intended to highlight major differences and similarities as the basis for subsequent, more detailed analyses.

Recher *et al.* (1985) and Ford *et al.* (1986) obtained data for 41 and 40 species of birds, respectively. However, as at Dryandra, the study areas in New South Wales each had 50–60 regularly occurring breeding bird species (Ford *et al.* 1985; Recher & Holmes 1985; H. F. Recher pers. obs. 1979–1995). Despite their geographical separation, there is a broad overlap in species between the three locations. Of a combined total of 53 species for which foraging data were obtained on the Tableland plots, 28 (53%) occurred on both the Northern and Southern Tablelands. Of a total of 45

species, 28 (62%) were shared between the Northern Tablelands and Dryandra, and of 51 species, 23 (45%) were shared between the Southern Tablelands and Dryandra. In calculating species overlaps, we considered ecologically equivalent and taxonomically related species (e.g., brown *Acanthiza pusilla* and broad-tailed thornbills, eastern *Eopsaltria australis* and western yellow robins, fuscous *Lichenostomus flavescens* and yellow-plumed honeyeaters) as being functionally the same species.

With the broad similarity in species it is not surprising that the three locations have similar guild structures. Insect-eating birds using ground, bark, foliage, and aerial substrates are the species-rich guilds in eucalypt forests and woodlands (Ford *et al.* 1985; Recher *et al.* 1985; see Holmes & Recher 1986 for a comparison of guild structure in forest bird communities between continents). Nectar-feeding and seed/fruit-eating birds are additional guilds with fewer species, and show considerable temporal change in species composition and abundances as nectar, seed, and fruit availability changes seasonally and from year to year (Recher *et al.* 1980, 1983; Ford *et al.* 1985).

The relative importance of each guild can be assessed in two ways. In Table 7, we allocated birds to foraging guilds based on the substrates from which a species took 20% or more of its prey; species could therefore occur in more than one guild. Table 8 presents the proportion of foraging observations recorded for each guild based on substrate type. Although there are obvious and inherent biases in collecting foraging data across foraging guilds (e.g., ground-foraging birds are more conspicuous than foliage-foragers in the canopy), errors in observation are likely to be consistent between locations and observers; in addition, one observer (HFR) was responsible for a substantial proportion of the observations for two of the studies being considered.

The guild structures in these three avian communities have similarities and differences, which are the same regardless of whether species (Table 7) or pro-

Table 8. Per cent of foraging observations (prey attacks) of birds taking prey from different substrates in three eucalypt woodlands

| Substrate | Proportion of observations | | |
|------------------|----------------------------|---------------------------------|---------------------------------|
| | Dryandra, WA | Southern Tablelands, NSW* | Northern Tablelands, NSW† |
| Ground | 37 | 18 | 21 |
| Bark | 19 | 25 | 21 |
| Foliage | 28 | 37 | 40 |
| Aerial | 13 | 11 | 9 |
| Nectar | 3 | 3 | 8 |
| Seeds/fruit | 0 | 6 | 1 |
| No. observations | 3280 | 27116 | 9862 |

*Recher *et al.* 1985; †Ford *et al.* 1986.

portion of observations (Table 8) are considered. At Dryandra, a much larger proportion of species (61%) than on either the Southern (34%) or Northern (38%) Tablelands (Table 7) take prey from the ground. This difference is the same for the proportion of foraging observations (Table 8).

Had we been able to collect data over a longer period at Dryandra, the high proportion of ground-foragers would not change. The majority of additional species for which we would have obtained sufficient data for analysis are eight species of ground-foragers, four species of foliage-foragers, one seed/fruit eater, and an additional nectarivore. This would give a total avifauna of 47 species for analysis with ground-foragers constituting 59% (28/47 species) of the avifauna.

Although the difference is not as pronounced as with ground-foragers, a larger proportion of species at Dryandra take prey from bark, foliage, and air than on the Tablelands, while there are fewer nectar-feeders and seed/fruit eaters (Table 7). A different result emerges from consideration of the proportion of observations where foliage-foraging is much greater on the Tablelands than at Dryandra, while the proportions of bark- and aerial-foragers are similar in the three communities (Table 8). Nectar-feeders were a greater component of the community on the Northern Tablelands than either the Southern Tablelands or Dryandra. With data on additional species, the proportions of foliage- (43%, 20/47 species) and bark-foragers (21%, 10/47 species) at Dryandra would be similar to those on the Tablelands.

At Dryandra, many species use a wide range of substrates (i.e., ground, bark and foliage), but for the community as a whole, proportionately more prey is taken from the ground than from bark or foliage. The small number of nectar-feeders and the absence of observations on seed/fruit eaters at Dryandra can be explained by the absence of flowers from most of the sites where foraging observations were made and the general scarcity of seeds and seed eaters (e.g., quail, parrots,

finches) relative to the Tablelands. Although the number of specialist bark- and foliage-foraging species on the Tablelands is greater than at Dryandra, species use alternative substrates less frequently than at Dryandra. This explains the apparent anomaly of a smaller number of species using ground, bark, and foliage despite a larger number of species for which foraging data were obtained within the Tablelands' communities.

Possible causes of differences

Differences in community foraging profiles between the wandoo woodland avifauna and those reported for avifaunas on the Tablelands suggest different resource bases. The high proportion of ground-foragers in wandoo woodland may be explained by the openness of these habitats, the absence of dense ground vegetation, and the lack of a continuous shrub layer. Ground-foraging, particularly of pouncers, appears to be facilitated by an open habitat with areas of bare ground. Conversely, the absence of grass or a well-developed ground vegetation explains the scarcity of ground-foraging seed eaters at Dryandra.

However, differences in habitat structure are insufficient to explain the different foraging profiles within eucalypt habitats. The habitats studied by Recher and Ford and their colleagues in eastern Australia were also open with sparse to dense litter layers, an abundance of coarse woody debris, and discontinuous or absent ground and shrub layers (H. F. Recher pers. obs. 1988–1995). Thus, differences in habitat structure between these areas and Dryandra cannot entirely explain the greater abundance of ground-foragers in wandoo woodland, although it helps explain why ground-foragers may be more abundant on these sites than in denser forests and woodlands with well-developed shrub and ground vegetation, such as that in the Snowy Mountains (Osborne & Green 1992) and coastal forests of New South Wales (Milledge & Recher 1985) where there are few ground-foraging species.

Four possibilities occur to us, which we present here as hypotheses requiring testing. First, there are important differences in habitat structure that are not revealed by casual observation. For example, differences in tree heights and canopy complexity may contribute to differences in species richness and foraging behaviour among bark- and foliage-foragers. Second, despite structural similarities, it is possible that there are differences between habitats in the abundance or availability of litter and ground-dwelling prey. Such differences, if they exist, may indicate fundamental differences between eucalypt ecosystems in how and where energy and nutrients are cycled, as well as in overall productivity. This in turn results in different kinds and abundances of prey and their distribution within the ecosystem. For example, a dense growth of annual grasses and an abundance of seed characterized

Acacia aneura woodlands studied by Recher and Davis (1997). Forty per cent of the ground-foragers in *A. aneura* woodlands were seed eaters, while 60% were insectivorous. Although seed-eating ground-foragers were present at Dryandra (e.g., mallee fowl, painted button quail), and also occurred in eastern eucalypt woodlands (e.g., common bronzewing, painted button quail, diamond firetail), there was no evidence of an abundance of seeds, and ground-dwelling seed-eaters were uncommon (Recher *et al.* 1983, 1985; Ford *et al.* 1985). Our third hypothesis is that, because our data from Dryandra were obtained during a short period of time, we may simply have documented a seasonal shift to ground-foraging, such as that which Bell (1985), Recher (1989) and Robinson (1992) reported for the birds they studied. We tend to discount the latter explanation as other data (unpubl. data), which indicates that the birds we described as ground-foragers at Dryandra forage predominantly on the ground in other habitats and during other seasons, including at Dryandra. Fourth, the difference in foraging profiles between the Tablelands and Dryandra may be the result of historical changes in the avifauna as a consequence of changed grazing and fire regimes, the impact of introduced predators, such as the European fox *Vulpes vulpes* and feral cat *Felis catus*, and logging following European settlement. The greatest impact of these processes is on ground-foraging and ground-nesting birds (Garnett 1992). Dryandra has not been free of these changes or activities, but the impact may have been less (or more recent) with the result that Dryandra may retain a 'more natural or complete' avifauna relative to the eastern sites.

Threatened species

Yellow-plumed honeyeater and rufous treecreeper are two species that are abundant at Dryandra, but which fail to survive in smaller remnants (Saunders 1989; Lynch & Saunders 1991). A possible explanation for their failure to persist in remnants can be derived from their use of habitats and foraging substrates, and their social behaviour.

Both species were most abundant in the *E. wandoo* woodlands on the lower slopes and run-on areas where the largest trees occurred and were least abundant in woodlands on the slopes and laterite ridges. Neither habitat is greatly disturbed and we suggest that there is a gradient in nutrient richness and moisture from the ridges to the flats with the vegetation on the flats being more productive and having a richer and more abundant invertebrate fauna than on the slopes and ridges. Recher *et al.* (1996) have shown that arthropod abundances and species richness in the canopies of eucalypt forests are positively correlated with foliar and soil nutrient levels. Thus, although they use different

substrates and forage at different heights, rufous treecreeper and yellow-plumed honeyeater select and require the most productive habitats within a region. In addition, both species are social. The honeyeater aggregates in large, loose colonies, while the treecreeper forms breeding groups of two or more individuals within a larger clan structure. By itself, social behaviour does not mean that populations require large or continuous areas of habitat for survival. For example, P. Cale (pers. comm.) informs us that white-browed babblers have a complex social structure involving interactions within and between breeding groups, but are able to survive in relatively small patches of habitat within highly fragmented landscapes. The extent of continuous or interconnected habitat required by a social species probably depends on the extent to which breeding units within the social group are territorial and/or the size of the population needed for social facilitation and successful reproduction. Because the social behaviour of yellow-plumed honeyeaters and rufous treecreepers is not well understood, the precise relationship between habitat area, social structure, and population viability is not known. However, it is not unreasonable to suggest that meeting the population requirements of their social behaviour requires large areas of habitat; this is probably also true for babblers, but babblers may perceive the landscape at a different scale from honeyeaters and treecreepers and are able to survive in a fragmented system of small patches while the latter species would decline to extinction.

Clearing for agriculture not only fragmented the woodlands of south-western Australia, but the most productive habitats, such as wandoo woodland, were cleared preferentially. In these circumstances remnants of native vegetation are unlikely to contain a sufficient expanse of productive habitat with the necessary foraging substrates or food resources to sustain populations of either rufous treecreeper or yellow-plumed honeyeater. In our opinion, restoration of either species to regions from which it has disappeared or declined will only be possible by restoring large areas of suitably productive and linked habitat patches, an unlikely event. Ground-foraging and ground-dwelling species, as well as those requiring productive habitats, will be and are most affected by European land management practices (Garnett 1992). The conservation of these species therefore requires the retention of those areas that remain large enough to include adequate areas of the productive habitats they require and where there is minimal disturbance to ground, litter, and soil ecosystems.

ACKNOWLEDGEMENTS

As always, Jonathan Majer was generous with his hospitality during our stay in Western Australia. Geoff

Barrett, Peter Cale, Mike Calver, Robert Lambeck, Allan Keast and Richard Noske made helpful comments on earlier versions of the manuscript. The research was conducted while H. F. Recher was on the staff of the Department of Ecosystem Management at the University of New England, Armidale. The University of New England provided the research funds required for this work.

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