

Foraging ecology of ground-feeding woodland birds in temperate woodlands of southern Australia

Mark J. Antos^{A,B} and Andrew F. Bennett^A

^ALandscape Ecology Research Group, School of Life and Environmental Sciences,
Deakin University, 221 Burwood Highway, Burwood, Vic. 3125, Australia.

^BCorresponding author. Present address: Birds Australia, 415 Riversdale Road, Hawthorn East,
Vic. 3123, Australia. Email: antos@deakin.edu.au or m.antos@birdsaustralia.com.au

Abstract. Ground-foraging birds of temperate woodlands of southern Australia are prominent among bird species considered to be susceptible to population decline. We examined the foraging ecology, including foraging substrates, actions and heights, of 13 ground-foraging species at four woodland sites in northern Victoria. Nine species are regarded as declining in southern Australia and four are considered common. Ten foraging substrates were identified, of which leaf-litter (54% of observations) and bare ground (17%) were most frequently used. In all woodland sites, litter was used more frequently than expected from its proportional cover. Bare ground was frequently used as a substrate by individual species, and fallen timber and grass were important for some species. Most species were generalists in their use of substrates. Six foraging actions were observed, of which gleaning and pouncing were most frequently recorded. All species foraged close to the ground and four foraged almost entirely at ground level. For pouncing birds, dead branches and fallen timber were the most important launch substrates from which pouncing actions were initiated. Eight of the 13 species differed in some aspect of their foraging ecology between woodland sites, especially in relation to the use of substrates (seven species). Fewer species (four) displayed differences in foraging ecology between seasons, with the greatest seasonal variation being in use of foraging substrates (three species). Overall, no significant differences were evident in the foraging ecologies of common and declining species. Species in both groups encompassed a wide range of foraging behaviours. Owing to this range in foraging ecology, the conservation of diverse assemblages of ground-foraging birds requires the maintenance of heterogeneous ground layers and careful management of disturbance processes.

Introduction

The foraging behaviour and foraging ecology of bird species have received considerable attention over the last few decades. Many studies have focused on theoretical issues relating to competition and niche overlap of sympatric species (e.g. Recher 1989; Robinson 1992; Mac Nally 2000; Salewski *et al.* 2003). The investigation of foraging ecology can also provide valuable insights into the organisation of bird assemblages (Sabo and Holmes 1983; Recher *et al.* 1985; Recher and Davis 1997) as well as provide information regarding food types and foraging sites that can be used to aid species conservation (Weikel and Hayes 1999; Zanette *et al.* 2000; Sierro *et al.* 2001).

In Australia, many studies of bird foraging behaviour have focused on mesic and tropical forests and woodlands (e.g. Crome 1978; Wooller and Calver 1981; Frith 1984; Recher *et al.* 1985; Mac Nally 2000). However, despite a large portion of southern Australia supporting open, temperate woodlands (Yates and Hobbs 2000) there have been comparatively few studies of the foraging behaviour of birds in these habitats until recently (e.g. Ford *et al.* 1990; Recher and

Davis 1998; Cousin 2004; Luck *et al.* 2001). A notable feature of the avifauna of Australian temperate woodlands is the high proportion of species that forage mainly on the ground (Recher and Davis 1998; Antos and Bennett 2005).

Knowledge of the foraging ecology and behaviour of the ground-feeding bird assemblage of the temperate woodlands of southern Australia is important for two main reasons. First, because such high proportions of species in these woodlands forage on the ground, it is of interest to examine how they use and partition this resource to reduce the potential for interspecific competition. Foraging height frequently serves as the principal dimension for segregation of foraging in bird assemblages (Crome 1978; Frith 1984), but in the case of ground-foraging species factors such as foraging behaviour and substrate are likely to play a more important discriminatory role. Second, many bird species of the temperate woodlands are believed to be in a state of population decline (Robinson and Traill 1996; Reid 1999; Garnett and Crowley 2000; Ford *et al.* 2001). Of the 41 species identified by Robinson (1994) as being in decline, more than half forage (at least in part) on the ground. Investigating the for-

aging ecology of declining species is important in identifying vital foraging resources and ultimately can contribute to their conservation through better understanding and management of their habitat (Luck *et al.* 2001).

In this paper we describe the foraging ecology of a suite of common and declining ground-foraging species at four woodland sites representing different woodland types of south-eastern Australia. Specifically, we:

- provide a quantitative description of the foraging substrates, foraging actions and foraging heights for these species;
- compare the foraging behaviour of species among woodland sites, and
- compare foraging behaviour between breeding and non-breeding seasons.

We also test whether declining species are more specialised in their foraging ecology than common and widespread species.

Methods

Study area

The Northern Plains of Victoria, Australia, encompass the largely flat plains between the Great Dividing Range to the south and the Murray River to the north. Mean annual rainfall ranges between 250 and 600 mm, with annual rainfall highest in the south-east and progressively decreasing to the north-west. Summers are hot and winter months are cool, with mean daily maxima of approximately 30°C during summer and 13°C during winter (LCC 1983). Today only ~6% of the Northern Plains supports tree cover, compared with ~76% in 1869. Most land (91%) is privately owned and supports < 3% tree cover (Bennett and Ford 1997). Large remnants of woodland occur mainly on public land along the floodplains of the major rivers, including the Murray, Ovens, Goulburn and Loddon systems. Away from the rivers, woodland remnants are relatively small and fragmented (DNRE 2001).

Four main types of woodland, based on dominant tree species, occur in the western portion of the Northern Plains (Antos and Bennett 2005): White Cypress-pine (*Callitris glaucophylla*) woodland, Black Box (*Eucalyptus largiflorens*) woodland, Grey Box (*E. microcarpa*) woodland, and River Red Gum (*E. camaldulensis*) woodland. White Cypress-pine woodland has been extensively modified by silvicultural activities, and severely reduced by clearing (LCC 1983). Terrick Terrick National Park contains the only large tract (2493 ha) on the Northern Plains (Parks Victoria 2002). Black Box woodland commonly occurs as pure stands of well-spaced trees, associated with irregularly inundated land, mostly along the margins of watercourses and wetlands. Grey Box woodland is now scarce because vast areas were cleared for agriculture and few large remnants (e.g. >200 ha) persist. Large areas of River Red Gum woodland remain because it typically occurs on flood-prone areas not suited to agriculture, and River Red Gum woodland is now the most widespread woodland type on the Northern Plains (LCC 1983). More detailed descriptions of the vegetation and study sites, including an area map, can be found in Antos and Bennett (2005).

Study design and site selection

The foraging ecology of ground-feeding birds was investigated at sites located in each of the four woodland types. To reduce geographical and climatic variation, all were located in a region of 80 × 80 km. The largest blocks (> 1500 ha) of each woodland type were selected to reduce the potential effects of habitat fragmentation on the composition of the avifauna. The White Cypress-pine study area was in Terrick Terrick National Park (2493 ha), the Black Box study area in Leaghur

State Park (1680 ha), and the Grey Box study area and the River Red Gum study area were in Gunbower State Forest (19500 ha).

In each woodland type, a study plot of 100 ha (1 km × 1 km) was established. These plots were large enough to sample the heterogeneity of the woodland habitat and were located at least 1 km from the nearest woodland boundary with farmland, to reduce potential edge effects. However, as only one plot was studied in each woodland type we cannot draw strong conclusions on differences in foraging between woodland types *per se*. Rather, we refer to differences between the four woodland sites that were studied.

Foraging observations

Foraging observations were made for woodland-dependent ground-foraging species (excluding parrots). Observations were conducted by slowly walking from one end of each study plot to the other, in lines ~100 m apart, thus covering its full area. Although this did not eliminate the risk of observing the same bird repeatedly, it ensured that birds throughout the study plot had an equal chance of being observed during each session. Each observation session began from a different starting point and was carried out over at least 3 h. This ensured that the entire plot was surveyed on each occasion. Six observation sessions were carried out during each survey round.

Foraging observations were conducted during two non-breeding seasons (March–August of 2000 and 2001) and two breeding seasons (September–February of 2000–01 and 2001–02). In total, there were five survey rounds for each study plot during the breeding season and four during the non-breeding season over the 2-year period. The River Red Gum plot could not be sampled during the breeding season of 2000–01 because flooding restricted access, and consequently all breeding season observations were made during 2001–02.

During each survey round the six observation sessions were held over 4 consecutive days. Observations were conducted during mornings (dawn till 1200 hours) and afternoons (1400 hours to dusk) each day to account for potential diurnal changes in foraging behaviour (see Timewell and Mac Nally 2004). All observations were conducted on days of calm weather.

Each time a target species was encountered a record was made of its foraging substrate, the action used and the height at which the action occurred. Foraging actions are defined in Table 1. Birds foraging > 8 m above the ground were excluded, as were immature individuals likely to be reliant on parents for supplementary feeding. Sequential observations of foraging behaviour were made with a maximum of five observations per bird at any one time. Sequential observations allow less-obvious foraging methods to be detected compared with single point observations (Morrison 1984) and they help to reduce discovery bias (Wiens 1994) as well as allowing a larger amount of data to be collected for each species (Recher and Gebiski 1990). Individual birds could not be differentiated and so it is likely that multiple observations were recorded for some individuals in separate observation sessions.

Analysis

Foraging observations were pooled for the 2 years of the study, a necessary step because breeding season observations in River Red Gum woodland were collected only in one year owing to flooding. However, data from each woodland site and from breeding and non-breeding seasons were collated separately for comparison.

Niche breadth can be calculated using a number of different indices (see Krebs 1999; Mac Nally 1995), as a measure of the degree of specialisation shown by a species in its foraging ecology. The Shannon-Wiener diversity index (*H*) has been used in many studies (e.g. Frith 1984; Ford *et al.* 1986; Recher 1989; Mac Nally 1995). However, the size of *H* is sensitive to the number of resource states (e.g. foraging substrates) and so cannot be reliably used for comparisons among different niche dimensions. Consequently, we used the standardised form of the Shannon-Wiener index, termed evenness (*J*), for which values range

Table 1. Descriptions and examples of foraging actions used by ground-foraging birds in temperate woodlands of the Northern Plains, Victoria (adapted from Recher *et al.* 1985)

| Foraging action | Description | Example |
|-----------------|--|--|
| Glean | Bird moves along substrate and takes prey or seed from its surface | Diamond Firetail taking seeds from bare ground |
| Probe | Bird extracts prey from beneath the surface of substrates such as soil, litter or fallen timber | White-browed Babbler extracting prey from underneath leaf-litter |
| Pounce | Bird flies down from a perch to land on a substrate and take prey | Hooded Robin flying down from dead branch to take insect from bare ground |
| Hawk | Bird takes insect from the air whilst flying | Willie Wagtail taking an insect in mid air |
| Snatch | Bird flies from a perch to take prey off a substrate without landing and consuming it on another perch | Jacky Winter flying down from a perch to pick an insect off ground herbs and consuming it on a dead branch |
| Wing-flush | Bird moves over substrate and opens its wings repeatedly to flush prey | Red-capped Robin hopping through leaf-litter, opening wings to flush small moths |

between 0 and 1 (Krebs 1999). We subjectively recognised species that had an evenness index of $J \geq 0.6$ as being generalists in relation to a particular niche dimension, and those with $J \leq 0.4$ as being specialists (see also Frith 1984).

A second simple measure of niche breadth is the number of frequently used resources (Krebs 1999), which we defined as the number of resource states (e.g. foraging substrates, foraging heights) that represented at least 5% of all observations for a species.

Differences in evenness (J) of use of resource states by common and declining species were compared using t -tests. Declining species were those identified by Robinson (1994) or Reid (1999). The use of different foraging substrates, heights and actions between different woodland sites and seasons were compared by using chi-square tests. Significance levels for all chi-square tests were set at $P < 0.01$ to partly compensate for reduced independence of foraging observations based on sequential samples from individuals (Recher 1989).

To compare foraging behaviour among species, a similarity matrix was developed by using the Bray–Curtis index based on the substrates, actions and heights used by each species. Variables were standardised to represent the proportional use of each resource state for each species. All niche dimensions (substrate, action, height) were incorporated in the analysis because niche separation often involves several aspects of behaviour and habitat use (Wiens 1994). Differences in foraging behaviour between declining and common species were tested by using analysis of similarity (ANOSIM) (Clarke and Warwick 1994). Multi-

dimensional scaling (MDS) was used to obtain an ordination of species, also based on foraging substrates, foraging actions and foraging heights. Cluster analysis (CLUSTER) was carried out using an hierarchical agglomerative procedure based on Bray–Curtis similarity. The ANOSIM, MDS and CLUSTER procedures were conducted using the PRIMER software package (Clarke and Warwick 1994).

Results

Foraging observations were recorded for 19 species of ground-feeding birds from the four woodland sites, but adequate numbers of observations were obtained for 13 species (Table 2). These consisted of nine declining and four common ground-foraging birds (see Table 2 for scientific names and status of species). There were too few observations for Common Bronzewing (*Phaps chalcoptera*), Gilbert's Whistler (*Pachycephala inornata*), Sacred Kingfisher (*Todiramphus sanctus*), Painted Button-quail (*Turnix varia*), Pallid Cuckoo (*Cuculus pallidus*) and Restless Flycatcher (*Myiagra inquieta*) to be used in analyses.

The largest numbers of observations were obtained for the Brown Treecreeper, White-winged Chough, Red-capped

Table 2. Number of foraging observations obtained for 13 species of ground-foraging birds in different woodland sites and seasons on the Northern Plains, Victoria

| Species | Woodland type | | | | Breeding season | Non-breeding season | Total |
|---|--------------------|-----------|----------|---------------|-----------------|---------------------|-------|
| | White Cypress-pine | Black Box | Grey Box | River Red Gum | | | |
| Brown Treecreeper (<i>Climacteris picumnus</i>) ^A | 113 | 177 | 172 | 182 | 330 | 314 | 644 |
| Chestnut-rumped Thornbill (<i>Acanthiza uropygialis</i>) ^A | 70 | 10 | 36 | 0 | 84 | 32 | 116 |
| Diamond Firetail (<i>Stagonopleura guttata</i>) ^A | 74 | 98 | 6 | 7 | 83 | 102 | 185 |
| Hooded Robin (<i>Melanodryas cucullata</i>) ^A | 113 | 74 | 17 | 5 | 93 | 116 | 209 |
| Jacky Winter (<i>Microeca fascians</i>) ^A | 64 | 0 | 57 | 101 | 95 | 127 | 222 |
| Red-capped Robin (<i>Petroica goodenovii</i>) ^A | 176 | 97 | 144 | 62 | 252 | 227 | 479 |
| Scarlet Robin (<i>Petroica multicolor</i>) ^A | 0 | 0 | 75 | 12 | 34 | 53 | 87 |
| Southern Whiteface (<i>Aphelocephala leucopsis</i>) ^A | 67 | 0 | 58 | 0 | 86 | 39 | 125 |
| Superb Fairy-wren (<i>Malurus cyaneus</i>) | 0 | 147 | 85 | 62 | 175 | 119 | 294 |
| White-browed Babbler (<i>Pomatostomus superciliosus</i>) ^A | 76 | 0 | 82 | 0 | 100 | 58 | 158 |
| Willie Wagtail (<i>Rhipidura leucophrys</i>) | 39 | 77 | 16 | 71 | 113 | 90 | 203 |
| White-winged Chough (<i>Corcorax melanorhamphos</i>) | 127 | 139 | 139 | 94 | 275 | 224 | 499 |
| Yellow-rumped Thornbill (<i>Acanthiza chrysorrhoa</i>) | 114 | 30 | 56 | 8 | 98 | 110 | 208 |

^ASpecies identified as declining by Robinson (1994) or Reid (1999).

Robin and Superb Fairy-wren (Table 2). Morrison (1984) suggested that a minimum of 30 individual foraging observations is required to provide a representative picture of the foraging behaviour of a species. We analysed data for species only if there were >60 observations. Large numbers of foraging observations were obtained from all woodland sites for some species (e.g. Brown Treecreeper, White-winged Chough), but for others, observations were derived mainly from two or three sites (e.g. White-browed Babbler, Diamond Firetail; see Table 2).

Foraging substrates

In total, 10 substrates were identified as being used for foraging by the 13 species examined (Fig. 1). Litter was the most important, accounting for 54% of foraging observations (pooled across all species). Other important substrates included bare ground (17%) and fallen timber (9%). Above-ground substrates such as branches, tree canopy and shrubs were used infrequently (1.8, 0.6 and 1.2% respectively). The proportional use of substrates varied significantly among woodland sites ($\chi^2 = 303.7$, d.f. = 27, $P < 0.001$). Some of the greatest differences occurred in the relative use of bare ground for foraging. This substrate was used 30% more often than expected in the Black Box site and 37% less than expected in the Grey Box site. Grass was used 48% and 40% more often than expected in the White Cypress-pine and Black Box sites, respectively, and 91% less often than expected in River Red Gum, and not at all at the Grey Box site.

The use of four ground-layer substrates (litter, bare ground, grass, herbs) by all 13 species (observations pooled) was compared with a measure of their availability. The availability of ground-layer substrates was assessed (see Antos and Bennett 2005) as the percentage cover on transects in each woodland site. Significant differences were detected between the frequency of use and the frequency of occurrence (percentage cover) of these four substrates at the

White Cypress-pine ($\chi^2 = 235.11$, d.f. = 3, $P < 0.001$), Black Box ($\chi^2 = 61.38$, d.f. = 3, $P < 0.001$), Grey Box ($\chi^2 = 61.50$, d.f. = 3, $P < 0.001$) and River Red Gum ($\chi^2 = 66.28$, d.f. = 3, $P < 0.001$) sites. Rather than using substrates in proportion to their availability, the bird assemblage favoured certain substrates. Leaf-litter was used more frequently than expected based on its availability, while grass was used less frequently (Fig. 2). Bare ground was used at all sites largely in proportion to that expected, except at the Grey Box site where it was under-utilised. Herbs were also used less frequently than expected, except at the Grey Box site (Fig. 2).

All species used litter as a foraging substrate (Table 3). The Diamond Firetail showed the lowest frequency of use (22% of observations) and the White-winged Chough the greatest (85%). Others that relied heavily on this substrate included the Scarlet (75%), Hooded (70%) and Red-capped (67%) Robins. Bare ground was used most frequently by Diamond Firetails (36%), Willie Wagtails (27%) and Yellow-rumped Thornbills (26%). Grass was most frequently used by the Diamond Firetail (33%), a granivorous species, with the Yellow-rumped Thornbill being the next most frequent user (9%). Similarly, herbs were infrequently used by most species other than the Chestnut-rumped Thornbill (20%) and Southern Whiteface (22%).

The Brown Treecreeper and Chestnut-rumped Thornbill often foraged on timber on the ground (22% and 19% of observations respectively), as did the White-browed Babbler and Superb Fairy-wren to a lesser extent (14 and 12% respectively). Brown Treecreepers also foraged on tree trunks (21% of observations). The only two species observed foraging from shrubs were the Chestnut-rumped Thornbill (11%) and Superb Fairy-wren (10%). Of the few species to take prey in the air, the Willie Wagtail and Jacky Winter were most prominent (16% and 12% of observations respectively).

Six species can be regarded as generalists in their use of foraging substrates ($J \geq 0.6$; see Table 4 for J values), while

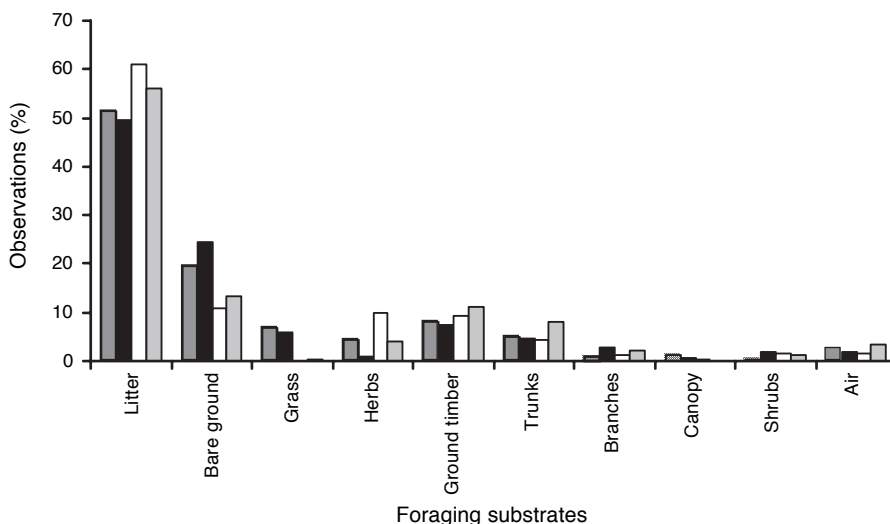


Fig. 1. Proportion (%) of foraging substrates used by 13 species of ground-foraging birds in four woodland sites in the Northern Plains, Victoria. Dark-grey bars = White Cypress-pine ($n = 1033$ observations); black bars = Black Box ($n = 853$); white bars = Grey Box ($n = 943$); and light-grey bars = River Red Gum ($n = 604$).

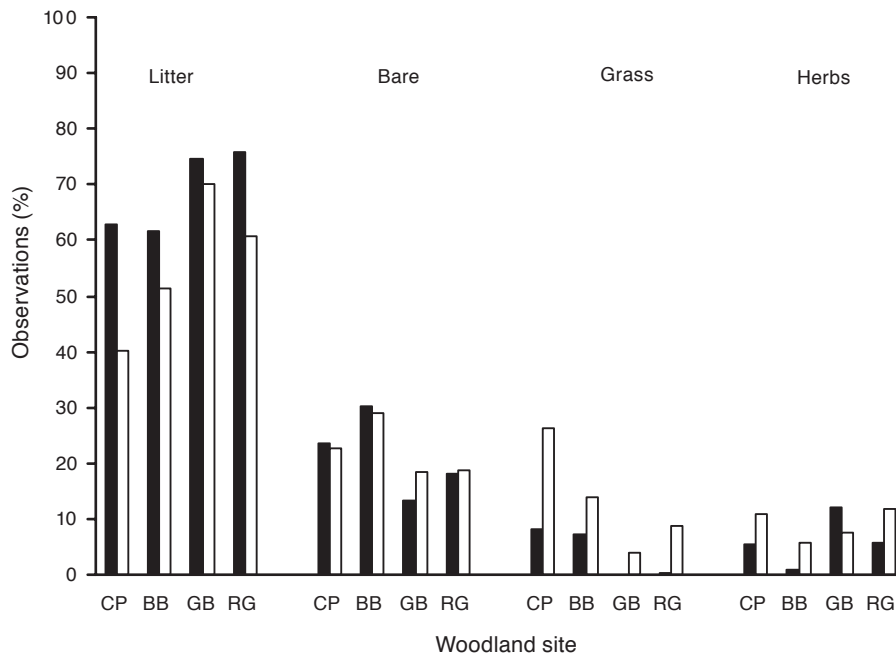


Fig. 2. Actual use of foraging substrates (% of observations) (black bars) by an assemblage of 13 species of ground-foraging birds compared with the availability (% ground cover) (white bars) of selected foraging substrates in four woodland sites. CP = White Cypress-pine ($n = 845$ foraging observations); BB = Black Box ($n = 688$); GB = Grey Box ($n = 770$); and RG = River Red Gum ($n = 446$). Availability of substrates was based on mean estimates of % cover in each woodland site by Antos and Bennett (2005).

only one, the White-winged Chough, appears to be a specialist ($J < 0.4$). The White-winged Chough used only two substrates frequently ($>5\%$ of observations; Table 4), with most (85%) foraging observations from leaf-litter. There was no significant difference between common and declining species in the evenness of use of foraging substrates ($t = 0.936$, d.f. = 11, $P = 0.369$).

Foraging actions

Six foraging actions were employed by the 13 species examined (Table 5). Gleaning and pouncing were the most frequently used, while snatching and wing-flushing were infrequently observed.

All species obtained food by gleaning to some extent. The Diamond Firetail, Southern Whiteface and Yellow-rumped Thornbill were observed to forage only by gleaning (Table 5). Other species that relied mainly on gleaning included Chestnut-rumped Thornbill (99% of observations), Superb Fairy-wren (99%) and Brown Treecreeper (77%). Four species employed pouncing as their primary foraging action: the Hooded Robin (95%), Scarlet Robin (87%), Red-capped Robin (79%) and Jacky Winter (66%). Probing was important for larger species such as the White-winged Chough (97%), White-browed Babbler (46%) and Brown Treecreeper (23%). Hawking was used by few species, and only the Willie Wagtail (16%) and Jacky Winter (14%) used it regularly. Few species ($n = 3$) used wing-flush foraging.

Table 3. Foraging substrates used by 13 species of ground-foraging birds in woodlands of the Northern Plains, Victoria
Values are the percentage of observations for each type of substrate, pooled across all seasons and woodland sites

| Species | <i>n</i> | Substrate | | | | | | | | | |
|---------------------------|----------|---------------|-------------|-------|-------|---------------|-------|----------|--------|--------|-----|
| | | Ground-litter | Bare ground | Grass | Herbs | Fallen timber | Trunk | Branches | Canopy | Shrubs | Air |
| Brown Treecreeper | 644 | 36 | 12 | 1 | 2 | 22 | 21 | 6 | 0 | 0 | 0 |
| Chestnut-rumped Thornbill | 116 | 29 | 5 | 3 | 20 | 19 | 3 | 5 | 4 | 11 | 0 |
| Diamond Firetail | 185 | 22 | 36 | 33 | 8 | 1 | 0 | 0 | 0 | 0 | 0 |
| Hooded Robin | 209 | 70 | 22 | 2 | 2 | 3 | 1 | 0 | 0 | 0 | 0 |
| Jacky Winter | 222 | 49 | 20 | 2 | 6 | 5 | 3 | 1 | 2 | 0 | 12 |
| Red-capped Robin | 479 | 67 | 16 | 1 | 5 | 5 | 3 | 0 | 0 | 0 | 3 |
| Scarlet Robin | 87 | 75 | 10 | 0 | 3 | 5 | 2 | 2 | 0 | 0 | 3 |
| Southern Whiteface | 125 | 41 | 22 | 2 | 22 | 6 | 2 | 2 | 3 | 0 | 0 |
| Superb Fairy-wren | 298 | 56 | 14 | 1 | 6 | 12 | 0 | 0 | 1 | 10 | 0 |
| White-browed Babbler | 158 | 61 | 8 | 1 | 6 | 14 | 6 | 4 | 0 | 0 | 0 |
| Willie Wagtail | 203 | 39 | 27 | 6 | 3 | 8 | 1 | 0 | 0 | 0 | 16 |
| White-winged Chough | 499 | 85 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Yellow-rumped Thornbill | 208 | 54 | 26 | 9 | 6 | 5 | 0 | 0 | 0 | 0 | 0 |

Table 4. Comparison of foraging niche breadth in relation to foraging substrates, foraging actions and foraging heights for 13 species of ground-foraging birds in woodlands of the Northern Plains, Victoria

Niche breadth is calculated using two measures: evenness (J) and the number of frequently used resource states (N) (see text for explanation); n = number of foraging observations

| Species | n | Foraging substrate | | Foraging action | | Foraging height | |
|---------------------------|-----|--------------------|------|-----------------|------|-----------------|------|
| | | N | J | N | J | N | J |
| Brown Treecreeper | 644 | 5 | 0.68 | 2 | 0.35 | 5 | 0.64 |
| Chestnut-rumped Thornbill | 116 | 6 | 0.82 | 1 | 0.03 | 4 | 0.48 |
| Diamond Firetail | 185 | 4 | 0.56 | 1 | | 1 | |
| Hooded Robin | 209 | 2 | 0.41 | 1 | 0.17 | 1 | 0.08 |
| Jacky Winter | 222 | 5 | 0.68 | 3 | 0.65 | 2 | 0.40 |
| Red-capped Robin | 479 | 4 | 0.50 | 3 | 0.51 | 1 | 0.19 |
| Scarlet Robin | 87 | 3 | 0.44 | 2 | 0.33 | 1 | 0.24 |
| Southern Whiteface | 125 | 4 | 0.69 | 1 | | 2 | 0.17 |
| Superb Fairy-wren | 198 | 5 | 0.60 | 1 | 0.04 | 2 | 0.31 |
| White-browed Babbler | 158 | 5 | 0.56 | 2 | 0.43 | 2 | 0.25 |
| Willie Wagtail | 203 | 5 | 0.69 | 4 | 0.88 | 2 | 0.39 |
| White-winged Chough | 499 | 2 | 0.19 | 1 | 0.08 | 1 | |
| Yellow-rumped Thornbill | 208 | 5 | 0.53 | 1 | | 1 | 0.04 |

Only two species were classed as generalists ($J \geq 0.6$) in their use of foraging actions (Jacky Winter, Willie Wagtail) (Table 4). On the other hand, six species were classed as specialists ($J \leq 0.4$). This included a broad grouping of gleaners (Chestnut-rumped Thornbill, Brown Treecreeper, Superb Fairy-wren), pouncers (Hooded Robin, Scarlet Robin) and a prober (White-winged Chough). The mean evenness index for foraging actions of common and declining species did not differ significantly ($t = 0.095$, d.f. = 8, $P = 0.926$).

Foraging heights

In general, birds foraged close to the ground (Table 5), but foraging heights nevertheless provide a useful indicator of foraging versatility. Note that foraging height is often influenced by foraging substrate – observations from substrates such as litter and bare ground will always have a height of 0 m.

Four species foraged almost exclusively on the ground: the Diamond Firetail (100% of observations), White-winged

Chough (100%), Yellow-rumped Thornbill (99%) and Hooded Robin (98%) (Table 5). Species foraging at ground level least frequently were the Brown Treecreeper (63%) and Chestnut-rumped Thornbill (73%). Additionally, the Jacky Winter, Superb Fairy-wren and Willie Wagtail also regularly foraged above ground (14–19% of observations), from substrates such as trunks, shrubs and the air.

Because all species examined were ground-foragers, nine were classed as specialists in relation to foraging heights (Table 4). Only the Brown Treecreeper was a generalist (Table 4). There was no significant difference in the mean evenness (J) of foraging heights for common and declining species ($t = 0.475$, d.f. = 9, $P = 0.646$).

Pouncing species

Five species, the Hooded Robin, Red-capped Robin, Scarlet Robin, Jacky Winter and Willie Wagtail, used pouncing, hawking and snatching actions frequently. These actions

Table 5. Foraging actions and heights used by 13 species of ground-foraging birds in woodlands of the Northern Plains, Victoria

Values are the percentage of observations for each action and height category, pooled across all seasons and woodland sites

| Species | n | Foraging action | | | | | | Foraging height (m) | | | | |
|---------------------------|-----|-----------------|--------|-------|------|--------|------------|---------------------|---------|-------|-------|-------|
| | | Glean | Pounce | Probe | Hawk | Snatch | Wing-flush | 0 | 0.1–0.5 | 0.6–1 | 1.1–3 | 3.1–8 |
| Brown Treecreeper | 644 | 77 | 0 | 23 | 0 | 0 | 0 | 63 | 13 | 7 | 6 | 11 |
| Chestnut-rumped Thornbill | 116 | 99 | 0 | 1 | 0 | 0 | 0 | 73 | 13 | 8 | 6 | 0 |
| Diamond Firetail | 185 | 100 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 |
| Hooded Robin | 209 | 3 | 95 | 0 | 0 | 2 | 0 | 98 | 1 | 1 | 0 | 0 |
| Jacky Winter | 222 | 2 | 66 | 1 | 14 | 15 | 2 | 81 | 9 | 2 | 4 | 4 |
| Red-capped Robin | 479 | 3 | 79 | 0 | 3 | 6 | 9 | 94 | 2 | 1 | 2 | 1 |
| Scarlet Robin | 87 | 2 | 87 | 0 | 3 | 8 | 0 | 92 | 2 | 2 | 2 | 2 |
| Southern Whiteface | 125 | 100 | 0 | 0 | 0 | 0 | 0 | 92 | 0 | 1 | 0 | 7 |
| Superb Fairy-wren | 298 | 99 | 1 | 0 | 0 | 0 | 0 | 86 | 10 | 3 | 0 | 1 |
| White-browed Babbler | 158 | 54 | 0 | 46 | 0 | 0 | 0 | 88 | 1 | 1 | 2 | 8 |
| Willie Wagtail | 203 | 47 | 15 | 0 | 16 | 4 | 18 | 83 | 8 | 3 | 3 | 3 |
| White-winged Chough | 499 | 3 | 0 | 97 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 |
| Yellow-rumped Thornbill | 208 | 100 | 0 | 0 | 0 | 0 | 0 | 99 | 1 | 0 | 0 | 0 |

differ from others (such as gleaning, probing) because they require an additional substrate from which the action is launched. Six launch substrates were identified, from which pouncing, hawking and snatching manoeuvres were initiated (Fig. 3a). A further launch substrate (ground-litter) was used on a single occasion by the Red-capped Robin.

The proportional use of launch substrates differed between species ($\chi^2 = 75.83$, d.f. = 24, $P < 0.001$). Three substrates (air, canopy and shrubs) were infrequently used. Branches (especially dead branches) accounted for >60% of all launch substrates used by four of the five pouncing species. Fallen timber was also important (>20% of observations for four of the five species). The Scarlet Robin was the only species that used fallen timber as a launch substrate <20% of the time, but it also regularly used tree trunks (20% of observations).

Most of the launch substrates used were low to the ground, with all species launching foraging actions from <2 m on at least 70% of occasions. Launch substrates >4 m above ground were rarely used (Fig. 3b).

Differences in foraging between woodland sites

Significant differences in the use of foraging substrates between sites were observed for the Brown Treecreeper

($\chi^2 = 44.66$, d.f. = 15, $P < 0.001$), Diamond Firetail ($\chi^2 = 16.52$, d.f. = 2, $P < 0.001$), Southern Whiteface ($\chi^2 = 13.85$, d.f. = 3, $P = 0.003$), Superb Fairy-wren ($\chi^2 = 26.60$, d.f. = 8, $P = 0.001$), White-browed Babbler ($\chi^2 = 15.71$, d.f. = 4, $P = 0.003$), White-winged Chough ($\chi^2 = 28.98$, d.f. = 3, $P < 0.001$) and Yellow-rumped Thornbill ($\chi^2 = 20.43$, d.f. = 4, $P < 0.001$).

Relative differences in use of foraging substrates between sites were identified by comparing the number of observations for a particular substrate with that expected under the hypothesis of equal use in each woodland site. Thus, the Brown Treecreeper foraged 41% less frequently on bare ground at the River Red Gum site than expected, but more frequently (16% and 18% respectively) on fallen timber in the River Red Gum and Grey Box sites.

The use of foraging actions was more uniform across woodland sites, with only the Willie Wagtail ($\chi^2 = 27.85$, d.f. = 9, $P = 0.001$) showing a significant difference. It gleaned more frequently than expected in Grey Box and River Red Gum sites (42% and 23% respectively) but less frequently in the White Cypress-pine and Black Box sites (35% and 20% respectively). Wing-flush foraging was used

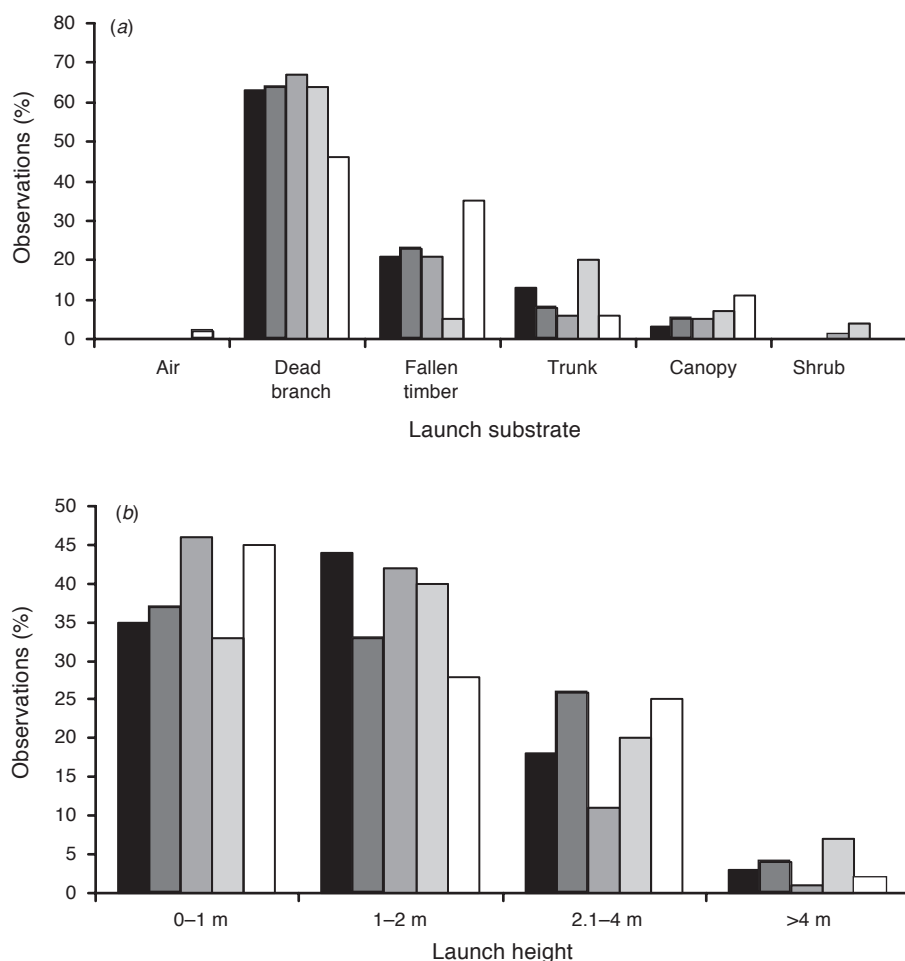


Fig. 3. Observations of launch substrates (Fig. 3a) and heights (Fig. 3b) from which foraging actions were initiated by five species of pouncing or hawking ground-foraging birds in the Northern Plains, Victoria. Values are the percentage of observations pooled across all seasons and woodland sites. Black bar = Hooded Robin ($n = 202$ observations); dark-grey bar = Jacky Winter ($n = 207$); mid-grey bar = Red-capped Robin ($n = 419$); light-grey bar = Scarlet Robin ($n = 85$); and white bar = Willie Wagtail ($n = 65$).

27% more frequently in the Black Box site but 60% less than expected in the River Red Gum site.

The White-browed Babbler was the only species that differed significantly in foraging heights among woodland sites ($\chi^2 = 7.167$, d.f. = 1, $P = 0.007$). It spent more time foraging above the ground and in trees in the White Cypress-pine site than in the Grey Box site.

Differences in foraging between seasons

Fewer species showed significant differences in foraging behaviour between seasons than was seen between woodland sites. Seasonal use of foraging substrates differed for the Brown Treecreeper ($\chi^2 = 19.41$, d.f. = 5, $P = 0.002$), Southern Whiteface ($\chi^2 = 19.31$, d.f. = 2, $P < 0.001$) and Superb Fairy-wren ($\chi^2 = 13.71$, d.f. = 4, $P = 0.008$). Brown Treecreepers used bare ground more frequently (25%) than expected during the breeding season and less (34%) during the non-breeding season. This coincided with more frequent use of tree trunks and branches during the non-breeding season. The Southern Whiteface foraged on litter more (17%) than expected and on bare ground less frequently (47%) during the breeding season. A reverse pattern occurred during the non-breeding season. Superb Fairy-wrens foraged more frequently (31%) than expected on herbs and grass during the breeding season and 27% more frequently on bare ground during the non-breeding season.

The use of foraging actions differed between seasons for the Brown Treecreeper ($\chi^2 = 45.64$, d.f. = 1, $P < 0.001$), and the Treecreeper and Jacky Winter were the only species that showed seasonal differences in the heights at which they foraged ($\chi^2 = 30.22$, d.f. = 4, $P < 0.001$ and $\chi^2 = 9.776$, d.f. = 1, $P = 0.002$, respectively). The Brown Treecreeper gleaned more frequently during the breeding season and probed less frequently, and foraged closer to the ground during the breeding season. Of the 13 species examined, only the Brown Treecreeper showed significant seasonal variation in all three foraging parameters measured.

Similarities and overlaps in foraging methods

There were no significant differences between common and declining species in overall use of foraging substrates (ANOSIM Global $R = -0.151$, $P = 0.918$) or foraging actions (ANOSIM Global $R = -0.026$, $P = 0.477$). Both groups include species with a wide range of foraging ecologies.

A comparison was also made between the subsets of declining and common species, based on evenness indices for each species for foraging substrates, actions and heights (Table 4). No significant difference was evident between declining and common species in their use of foraging niche states (ANOSIM Global $R = 0.128$, $P = 0.224$).

Ordination of foraging substrates, actions and heights used by each species by using multi-dimensional scaling produced a two-dimensional solution (stress = 0.07) that grouped species into five broad groups (Fig. 4). The small

ground-gleaning and pouncing species each formed distinct groups in the ordination space. CLUSTER analysis revealed that the small ground gleaners shared > 75% similarity in their foraging ecology while the pouncers shared nearly 80% similarity. This group also contained the two species with greatest foraging overlap, the Red-capped and Scarlet Robins (92% similarity). The Willie Wagtail (a generalist) and White-winged Chough (a specialist) were clearly separated from other groups in the ordination space. The Brown Treecreeper and White-browed Babbler were grouped loosely (Fig. 4) but shared >70% similarity according to CLUSTER analysis.

The horizontal axis of the ordination (MDS 1) represents foraging actions. It was strongly positively correlated (Spearman rank correlation, $r_s > 0.5$) with the frequency of pouncing, hawking and snatching actions and negatively correlated ($r_s < -0.5$) with frequency of gleaning. The vertical axis (MDS 2) represents differences in foraging substrates and, to a lesser extent, actions. It was strongly positively correlated ($r_s > 0.5$) with the frequency of use of grass, herbs, air and hawking and negatively correlated ($r_s < -0.5$) with the use of litter as a substrate and with probing actions.

Discussion

In total, 89 species of birds were recorded from the four woodland sites (Antos and Bennett 2005) of which 40 (45%) foraged, at least in part, on the ground. Of these, 15 were non-passerines (e.g. parrots, cuckoos) and two were intro-

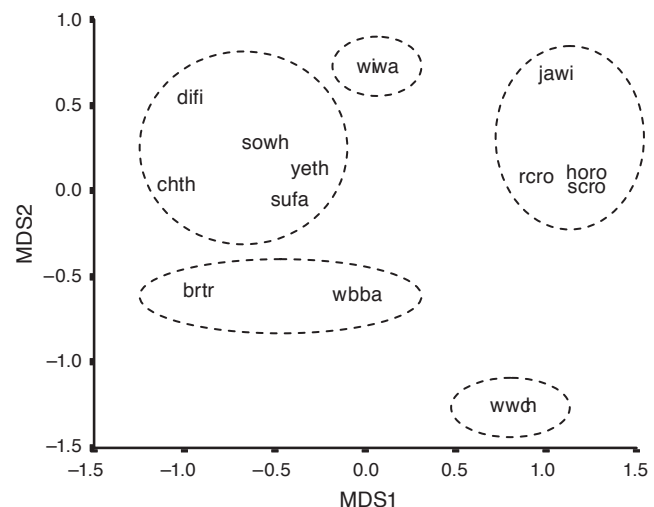


Fig. 4. Ordination (MDS) of ground-foraging species based on Bray–Curtis measures of similarity of foraging substrates, actions and heights (stress = 0.07). Species are denoted as follows: brtr = Brown Treecreeper, chth = Chestnut-rumped Thornbill, difi = Diamond Firetail, hcro = Hooded Robin, jawi = Jacky Winter, rcro = Red-capped Robin, scro = Scarlet Robin, sowh = Southern Whiteface, sufa = Superb Fairy-wren, wbba = White-browed Babbler, wiwa = Willie Wagtail, wwch = White-winged Chough, and yeth = Yellow-rumped Thornbill. Dashed lines enclose groups of species with similar foraging ecology, as identified by CLUSTER analysis.

duced. Of the remaining 23 species, adequate numbers of foraging observations were obtained for 13 species. Some species regarded nationally as declining, such as the Brown Treecreeper and Red-capped Robin, were relatively common and many observations were obtained (e.g. 644 and 479 respectively); others such as the Painted Button-quail and Gilbert's Whistler were scarce and it was difficult to obtain observations. Other species, such as the Sacred Kingfisher and Pallid Cuckoo were present only at particular times of the year and were excluded from observations.

Foraging substrates, actions and heights

Leaf-litter was most frequently used by the overall assemblage (54% of pooled observations) followed by bare ground (17%). There are several possible reasons for the importance of leaf-litter and bare ground as foraging substrates. First, these were the most widespread substrates, with leaf-litter accounting for 40–70% of ground cover, and bare ground 15–27% of ground cover in the four woodland sites (Antos and Bennett 2005). However, litter was used more frequently than expected based on its proportional cover (Fig. 2), indicating preferential use. Second, these substrates are amenable to most foraging actions. Prey can be taken from leaf-litter and bare ground by gleaning, probing, pouncing, snatching or wing-flushing. Third, food items such as seeds and arthropods may be more visible and accessible. Other substrates such grass and herbs may provide more cover for prey or be difficult to move through. Last, the litter layer may host a substantial proportion of the energy flow in woodland habitats and serve as the main location for nutrient cycling, thus providing a productive environment for invertebrates (McIntyre *et al.* 2002).

Most species used a wide range of substrates, and we classified six as being generalists and only one as a specialist. Recher *et al.* (2002) suggested that the use of ground substrates is unlikely to be an important separator of co-existing ground-foraging species. The use of foraging actions was more specialised than use of substrates, and six species were classified as specialists. They consisted of a range of gleaners (Chestnut-rumped Thornbill, Brown Treecreeper, Superb Fairy-wren), pouncers (Hooded Robin, Scarlet Robin) and a prober (White-winged Chough). Only two species could be regarded as generalists in their use of foraging actions: the Willie Wagtail and Jacky Winter. Both species had a greater number of frequently used foraging actions (e.g. gleaning, hawking, pouncing and snatching) in their repertoire than most other species.

Nearly all species were specialists in relation to foraging height, with most, or all, foraging actions conducted on the ground. The Brown Treecreeper was the only species classified as a foraging height generalist. Its habit of frequently foraging on the trunks of trees (Ford *et al.* 1986) enables it to forage at a wide range of heights.

Variation in foraging ecology between woodland sites

The four woodland sites differed significantly in many aspects of habitat structure, including the size and density of trees, composition of the ground layer, and density and size of fallen timber (Antos and Bennett 2005). It was not surprising that the main difference in the foraging ecology of species between woodland sites was in the use of foraging substrates, rather than variation in foraging actions and heights. The use of foraging actions by bird species appeared to be relatively fixed, with limited plasticity between sites and seasons. In contrast, Wheeler and Calver (1996) suggested that all aspects of foraging habits, including actions and heights, of an insectivorous bird community were plastic and changed from month to month. Recher *et al.* (2002) concluded that the foraging behaviours of ground-pouncing species were relatively broad and suggested that habitat characteristics and prey availability were likely to be the main determinants of foraging behaviour, a result consistent with this study.

Variation in foraging ecology between woodland sites may simply reflect differences in the availability of substrates in each woodland habitat. For instance, greater use of fallen timber by the Brown Treecreeper in the Grey Box and River Red Gum woodlands corresponds with the greater abundance of these substrates in those woodlands. However, this is not true of all substrates: some, such as leaf-litter, were used more frequently than their availability would suggest, while others, such as grass, were used less frequently (Fig. 2). Variation in foraging ecology between woodlands may also relate to the differing composition of their bird assemblages (Antos and Bennett 2005). Species such as the Jacky Winter, White-browed Babbler and Scarlet Robin, for example, did not occur in all woodland sites. The foraging behaviour of a species may be influenced by the presence and abundance of sympatric species (e.g. Bell 1985). Overall, most ground-foraging species were versatile in their use of substrates between woodland sites. Provided they are equipped with the foraging modes and capabilities to exploit them, most species can use a wide range of substrates.

Seasonal variation in foraging ecology

Seasonal variation in foraging behaviour was less pronounced than variation between woodland sites. No changes in foraging actions or heights were detected between the breeding and non-breeding seasons, except for the Brown Treecreeper (actions, height) and Jacky Winter (height). Most seasonal variation detected was in the use of foraging substrates, especially bare ground and leaf-litter, but these patterns were not consistent between species. We cannot relate these differences to the availability of arthropods because no measures of potential prey were made in this study.

The apparent low level of seasonal variation may be because the species studied are largely adapted to terrestrial foraging and some, such as the White-winged Chough and White-browed Babbler, are unlikely to adopt different foraging behaviours to take advantage of seasonally varying resources, such as aerial insects. Further, birds with a narrow range of foraging actions, such as ground gleaners, are less likely to show changes in foraging techniques than species with a broader range of foraging techniques (Unno 2002). Alternatively, the limited seasonal variation in foraging ecology may be a consequence of relatively stable food resources between seasons in these woodlands, but to test this requires an assessment of food availability. It is likely that inter-year variation in the foraging ecology of species occurs owing to different environmental cues and climatic conditions (Petit *et al.* 1990; Kleintjes and Dahlsten 1995; Blendinger 2005) and this may be greater than inter-seasonal variation (Wagner 1981).

Comparison of common and declining woodland birds

A primary objective of this study was to compare the foraging ecology of declining and common ground-foraging birds to determine whether declining species use a distinctive set of foraging behaviours, or are more specialised in their foraging ecology. No systematic differences were evident between common and declining species in relation to use of foraging substrates, actions or heights. Likewise, there was no evidence that declining species, as a group, were more specialised in their foraging ecology. Both groups included species with widely varying foraging ecologies, and which ranged from generalists to specialists. For instance, the groups representing ground-probing and ground-gleaning foragers included declining species (e.g. White-browed Babbler and Diamond Firetail respectively) as well as common species (e.g. White-winged Chough and Superb Fairy-wren respectively). The ground-pouncing species, however, were all declining species.

We note that analyses in this study were limited to species for which sufficient observations could be made. Consequently, even the declining species were relatively numerous in this study area. It is possible that declining species that occurred in low abundance, such as Gilbert's Whistler or Painted Button-quail, may show more pronounced differences from common species in their foraging behaviour.

When all foraging niche dimensions were considered (substrate, action and height), there was considerable overlap between some species. Most studies examining co-existing species within a foraging guild have concluded that broad overlaps occur in the foraging ecologies of species (e.g. Wooller and Calver 1981; Robinson 1992), and major foraging substrates are typically exploited by ecologically similar species (Ford 1985). The Diamond Firetail and Yellow-rumped Thornbill, for instance, showed > 80% similarity in foraging ecology. Both foraged by gleaning from the ground

on substrates such as leaf-litter and bare ground, although the Firetail foraged more frequently on grass. One of these species is experiencing severe decline throughout much of its range (Diamond Firetail) while the other (Yellow-rumped Thornbill) is proliferating.

This study provides no evidence that declining ground-foraging species are characterised by a distinctive set of foraging attributes, but rather they consist of species with a range of foraging behaviours and habitat requirements. Factors other than foraging behaviour *per se* need to be considered to distinguish declining ground-foragers from common ground-foragers.

Implications for conservation

A number of foraging substrates were identified as important to ground-foraging birds. Overall, leaf-litter and bare ground were most commonly used, but individual species also relied on others, such as grass, herbs, fallen timber and tree trunks. Litter was used in greater frequency than expected from its availability, which suggests it is particularly important for the overall ground-foraging assemblage. Our results suggest that ground mosaics that contain large areas of leaf-litter interspersed with bare ground offer suitable foraging opportunities for many species. However, other substrates also need to be well represented to provide foraging opportunities for the full complement of declining woodland birds (e.g. native grass cover for the Diamond Firetail; low, native herbs for the Chestnut-rumped Thornbill and Southern Whiteface; fallen timber for the Brown Treecreeper and White-browed Babbler).

Declining woodland birds used a wide range of foraging substrates, actions and heights. Consequently, woodlands that have a heterogeneous ground layer that offers a diversity of foraging substrates are likely better to accommodate rich assemblages of such ground-foraging species. The importance of diverse substrates is particularly pertinent for ground-pouncing species. Not only do they require suitable substrates on which to pounce, but they also require other microhabitats, such as dead branches and fallen timber in appropriate locations and at appropriate heights, from which to launch pouncing actions (Recher *et al.* 2002; Fitri and Ford 2003; Cousin 2004).

Many ground substrates are vulnerable to degradation. Inappropriate burning regimes may eliminate leaf-litter, fallen timber, shrubs and invertebrates (Gill *et al.* 1999), overgrazing can simplify or otherwise alter plant and invertebrate communities (Arnold and Weeldenburg 1998; Bromham *et al.* 1999; Abensperg-Traun *et al.* 2000a, 2000b; Martin and Possingham 2005) and weed invasion can reduce heterogeneity of the ground layer by replacing native plants with exotics, by covering bare ground and litter, and reducing access to the ground layer (Robinson 1994).

Maintaining a diverse ground layer suitable for a large suite of ground-foraging species presents a major challenge

to woodland managers. It requires a careful balance between excluding some damaging processes while allowing other disturbance processes to maintain structural diversity and provide new foraging opportunities (Robinson 1994; McIntyre *et al.* 2002; Recher *et al.* 2002; Martin and Possingham 2005). Substrates used for foraging cannot be viewed in isolation. For example, although leaf-litter and bare ground are important, surrounding elements such as grass, herbs and fallen timber all contribute to the productivity of local sites. In the case of pouncing species, a lack of appropriate perches may render large areas of otherwise suitable foraging substrates difficult to exploit.

Acknowledgments

Logistical and financial support for this research was provided by the School of Ecology and Environment, Deakin University. We are also grateful for financial support provided by the Holsworth Wildlife Research Endowment, the Stuart Leslie Research Fund and Birds Australia's VicGroup Research Fund. Three anonymous referees provided comments that improved this manuscript. Dr John White provided useful advice throughout the course of this research.

References

- Abensperg-Traun, M., Smith, G. T., and Main, B. Y. (2000a). Terrestrial arthropods in a fragmented landscape: a review of ecological research in the western Australian central wheatbelt. *Pacific Conservation Biology* **6**, 102–119.
- Abensperg-Traun, M., Smith, G. T., Steven, D. E., and Atkins, L. (2000b). Different woodland types, different grazing effects? Plants and soil and litter arthropods in remnant woodlands in the Western Australian wheatbelt. In 'Temperate Eucalypt Woodlands in Australia'. (Eds R. J. Hobbs and C. J. Yates.) pp. 225–234. (Surrey Beatty: Sydney.)
- Antos, M. J., and Bennett, A. F. (2005). How important are different types of temperate woodlands for ground-foraging birds? *Wildlife Research* **32**, 557–572. doi:10.1071/WR04118
- Arnold, G., and Weeldenburg, J. (1998). The effects of isolation, habitat fragmentation and degradation by livestock grazing on the use by birds of patches of gimlet *Eucalyptus salubris* woodland in the wheatbelt of Western Australia. *Pacific Conservation Biology* **4**, 155–163.
- Bell, H. L. (1985). The social organization and foraging behaviour of three syntopic thornbills *Acanthiza* spp. In 'Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 151–163. (Surrey Beatty: Sydney.)
- Bennett, A. F., and Ford, L. A. (1997). Land use, habitat change and the conservation of birds in fragmented rural environments: a landscape perspective from the Northern Plains, Victoria, Australia. *Pacific Conservation Biology* **3**, 244–261.
- Blendinger, P. G. (2005). Foraging behaviour of birds in an arid sand-dune scrubland in Argentina. *Emu* **105**, 67–79. doi:10.1071/MU03050
- Bromham, L., Cardillo, M., Bennett, A. F., and Elgar, M. (1999). Effects of stock grazing on the ground invertebrate fauna of woodland remnants. *Australian Journal of Ecology* **24**, 199–207. doi:10.1046/j.1442-9993.1999.00963.x
- Clarke, K. R., and Warwick, R. M. (1994). 'Change in Marine Communities: An Approach to Statistical Analysis and Interpretation.' (Plymouth Marine Laboratory: Plymouth, UK.)
- Cousin, J. A. (2004). Pounce site characteristics of the Western Yellow Robin *Eopsaltria griseogularis*: the importance of assessing foraging microhabitat. *Pacific Conservation Biology* **10**, 21–27.
- Crome, F. H. J. (1978). Foraging ecology of an assemblage of birds in lowland rainforest in northern Queensland. *Australian Journal of Ecology* **3**, 195–212.
- DNRE (Department of Natural Resources and Environment) (2001). 'Mid-Murray Forest Management Area Proposed Forest Management Plan.' (Department of Natural Resources and Environment: Melbourne.)
- Fitri, L., and Ford, H. A. (2003). Foraging behaviour of Hooded Robins *Melanodryas cucullata* in the northern tablelands of New South Wales. *Corrella* **27**, 61–67.
- Ford, H. A. (1985). A synthesis of the foraging ecology and behaviour of birds in eucalypt forests and woodlands. In 'Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management'. (Eds A. Keast, H. F. Recher, H. Ford and D. Saunders.) pp. 323–331. (Surrey Beatty: Sydney.)
- Ford, H. A., Noske, S., and Bridges, L. (1986). Foraging of birds in eucalypt woodlands in north-eastern New South Wales. *Emu* **86**, 168–179.
- Ford, H. A., Huddy, L., and Bell, H. (1990). Seasonal changes in foraging behaviour of three passerines in Australian eucalyptus woodland. *Studies in Avian Biology* **13**, 245–253.
- Ford, H. A., Barrett, G. W., Saunders, D. A., and Recher, H. F. (2001). Why have birds in the woodlands of southern Australia declined? *Biological Conservation* **97**, 71–88. doi:10.1016/S0006-3207(00)00101-4
- Frith, D. W. (1984). Foraging ecology of birds in an upland tropical rainforest in north Queensland. *Australian Wildlife Research* **11**, 325–347. doi:10.1071/WR9840325
- Garnett, S. T., and Crowley, G. M. (2000). 'The Action Plan For Australian Birds 2000.' (Environment Australia: Canberra.)
- Gill, A. M., Woinarski, J. C. Z., and York, A. (1999). Australia's Biodiversity – Responses to Fire. Biodiversity Technical Paper No. 1, Environment Australia, Canberra.
- Kleintjes, P. K., and Dahlsten, D. L. (1995). Within-season trends in the foraging behaviour of the Mountain Chickadee. *Wilson Bulletin* **107**, 655–666.
- Krebs, C. J. (1999). 'Ecological Methodology.' (Addison Wesley Longman: Menlo Park, CA.)
- LCC (Land Conservation Council) (1983). 'Report on the Murray Valley Area.' (Land Conservation Council: Melbourne.)
- Luck, G., Charmantier, A., and Ezanno, P. (2001). Seasonal landscape differences in the foraging behaviour of the rufous tree creeper *Climacteris rufa*. *Pacific Conservation Biology* **7**, 9–20.
- Mac Nally, R. C. (1995). 'Ecological Versatility and Community Ecology.' (Cambridge University Press: Cambridge, UK.)
- Mac Nally, R. (2000). Coexistence of a locally undifferentiated foraging guild: avian snatchers in a southeastern Australian forest. *Austral Ecology* **25**, 69–82. doi:10.1046/j.1442-9993.2000.01013.x
- Martin, T. G., and Possingham, H. P. (2005). Predicting the impact of livestock grazing on birds using foraging height data. *Journal of Applied Ecology* **42**, 400–408. doi:10.1111/j.1365-2664.2005.01012.x
- McIntyre, S., McIvor, J. G., and Heard, K. M. (Eds) (2002). 'Managing and Conserving Grassy Woodlands.' (CSIRO Publishing: Melbourne.)
- Morrison, M. L. (1984). Influence of sample size and sampling design on analysis of avian foraging behaviour. *Condor* **86**, 146–150.

- Parks Victoria (2002). 'Terrick Terrick National Park Management Plan.' (Parks Victoria: Melbourne.)
- Petit, L. J., Petit, D. R., Petit, K. E., and Fleming, J. W. (1990). Annual variation in foraging ecology of Prothonotary Warblers during the breeding season. *Auk* **107**, 146–152.
- Recher, H. F. (1989). Foraging segregation of Australian warblers (Acanthizidae) in open forest near Sydney, New South Wales. *Emu* **89**, 204–215.
- Recher, H. F., and Davis, W. E. (1997). Foraging ecology of a mulga bird community. *Wildlife Research* **24**, 27–43. doi:10.1071/WR96052
- 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 Gebbski, V. (1990). Analysis of the foraging ecology of eucalypt forest birds: sequential versus single-point observations. *Studies in Avian Biology* **13**, 174–180.
- Recher, H. F., Holmes, R. T., Schulz, M., Shields, J., and Kavanagh, R. (1985). Foraging patterns of birds in eucalypt forest and woodland on the tablelands of south-eastern Australia. *Australian Journal of Ecology* **10**, 399–419.
- Recher, H. F., Davis, W. E., and Calver, M. C. (2002). Comparative foraging ecology of five species of ground-pouncing birds in western Australian woodlands with comments on species decline. *Ornithological Science* **1**, 29–40. doi:10.2326/osj.1.29
- Reid, J. R. W. (1999). Threatened and declining birds in the New South Wales sheep–wheat belt: 1. Diagnosis, characteristics and management. Consultancy report to NSW National Parks and Wildlife Service, CSIRO Wildlife and Ecology, Canberra.
- Robinson, D. (1992). Habitat use and foraging behaviour of the Scarlet Robin and the flame robin at a site of breeding-season sympatry. *Wildlife Research* **19**, 377–395. doi:10.1071/WR9920377
- Robinson, D. (1994). Research plan for threatened woodland birds of southeastern Australia. Arthur Rylah Institute for Environmental Research Technical Report Series No. 133, Department of Conservation and Natural Resources, Melbourne.
- Robinson, D., and Traill, B. J. (1996). Conserving woodland birds in the wheat and sheep belts of southern Australia. *Wingspan* **6**, 1–16. Supplement
- Sabo, S. R., and Holmes, R. T. (1983). Foraging niches and the structure of forest bird communities in contrasting montane habitats. *Condor* **85**, 121–138.
- Salewski, V., Bairlein, F., and Leisler, B. (2003). Niche partitioning of two Palearctic passerine migrants with Afrotropical residents in their West African winter quarters. *Behavioral Ecology* **14**, 493–502. doi:10.1093/beheco/arg021
- Sierro, A., Arlettaz, R., Naef-Daenzer, B., Strebel, S., and Zbinden, N. (2001). Habitat use and foraging ecology of the nightjar (*Caprimulgus europaeus*) in the Swiss Alps: towards a conservation scheme. *Biological Conservation* **98**, 325–331. doi:10.1016/S0006-3207(00)00175-0
- Timewell, C. A. R., and Mac Nally, R. (2004). Diurnal foraging-mode shifts and food availability in nectarivore assemblages during winter. *Austral Ecology* **29**, 264–277. doi:10.1111/j.1442-9993.2004.01344.x
- Unno, A. (2002). Tree species preferences of insectivorous birds in a Japanese deciduous forest: the effect of different foraging techniques and seasonal change of food resources. *Ornithological Science* **1**, 133–142. doi:10.2326/osj.1.133
- Wagner, J. L. (1981). Seasonal change in guild structure: oak woodland insectivorous birds. *Ecology* **62**, 973–981.
- Weikel, J. M., and Hayes, J. P. (1999). The foraging ecology of cavity-nesting birds in young forests of the northern Coast Range of Oregon. *Condor* **101**, 58–66.
- Wheeler, A. G., and Calver, M. C. (1996). Resource partitioning in an island community of insectivorous birds during winter. *Emu* **96**, 23–31.
- Wiens, J. A. (1994). 'The Ecology of Bird Communities. Vol. 1, Foundations and Patterns.' (Cambridge University Press: Cambridge, UK.)
- Wooller, R. D., and Calver, M. C. (1981). Feeding segregation within an assemblage of small birds in the Karri forest understorey. *Australian Wildlife Research* **8**, 401–410. doi:10.1071/WR9810401
- Yates, C. J., and Hobbs, R. J. (2000). Temperate eucalypt woodlands in Australia – an overview. In 'Temperate Eucalypt Woodlands in Australia'. (Eds R. J. Hobbs and C. J. Yates.) pp. 1–5. (Surrey Beatty: Sydney.)
- Zanette, L., Doyle, P., and Tremont, S. M. (2000). Food shortage in small fragments: evidence from an area sensitive passerine. *Ecology* **81**, 1654–1666.

Manuscript received 3 August 2005, accepted 2 December 2005