

Foraging Ecology of a Mulga Bird Community

Harry F. Recher^A and William E. Davis, Jr^B

^ADepartment of Environmental Management, Edith Cowan University, Joondalup, WA 6027, Australia.

^BCollege of General Studies, Boston University, Boston, MA 02215, USA.

Abstract

Mulga is a distinctive woodland or shrub community with a wide distribution across the semi-arid zone of southern and central Australia. Mulga (*Acacia aneura*) is the dominant shrub and small tree, but other species of *Acacia* are common. Typical of Australian habitats in the arid zone, mulga has a core of resident bird species that is augmented by nomadic (opportunistic) species when conditions are favourable. This paper describes the foraging behaviour and habitat use of a mulga avifauna in the vicinity of Alice Springs during late winter, when many opportunistic species were present. Data were obtained for 24 species, of which 16 were confirmed as nesting. Many birds, regardless of their normal foraging habits, converged on a common food resource: a geometrid moth (Geometridae) that was abundant on mulga plants. Despite their use of a common food resource, species differed in their foraging behaviour, proportions of different substrates used, and foraging heights. Ground-foraging species dominated the avifauna, but in most respects the guild structure of the community was a scaled-down version of *Eucalyptus* forest avifaunas. Differences in guild structure between mulga and eucalypt forest are best explained by differences between the two habitats in the kinds of resources (e.g. foraging substrates, types of food) that are available.

Introduction

A single plant species, mulga (*Acacia aneura*), dominates shrublands and woodlands across a broad area of Australia's southern and central arid zone (Leeper 1970). Cody (1994) considered mulga a single, uniform plant community and described the avifauna of mulga habitats across its longitudinal distribution. He identified a core of 18 species that were resident in mulga throughout its distribution. An additional 28 species occurred less frequently and included a number of species that responded opportunistically to favourable conditions following rain. Cody attributed some of the variation in the distribution of birds within the mulga zone to interactions between species with similar foraging habits, but did not provide quantitative information on foraging.

In this paper we describe the foraging behaviour of mulga birds in central Australia near Alice Springs, Northern Territory, during late winter when most species are nesting. We use our data on foraging to review Cody's (1994) interpretations of the interactions between mulga bird species and to compare the guild structure of mulga avifaunas with those in the much richer eucalypt forests of eastern Australia.

Methodology

Study Location

Bird census and foraging data were collected between 23 July and 2 August 1995. Observations commenced shortly after sunrise and continued to dusk each day. Five sites were selected in mulga woodlands on Hamilton Downs Station along the Tanami Road 15–30 km west of the intersection with the Stuart Highway about 50 km north of Alice Springs. Two of the sites (1 and 3) were in the vicinity of Kunoth Well, while three others (Sites 2, 4 and 5) were spaced along the highway 6–15 km east of the well. The sites on Hamilton Downs were selected on appearance to represent the range of variation in the mulga communities in the area. The study area was selected after inspection of mulga-dominated woodlands within 100 km north and west of Alice Springs showed that Hamilton Downs had an abundant avifauna, while other places had few or no birds. Central Australia in the vicinity of Alice Springs had good rains in

late summer and autumn, and the vegetation throughout the region we inspected was in good condition and showed evidence of good winter growth and flowering.

Description of the Study Area

The study area was flat with evidence that extensive areas around Kunoth Well flooded after heavy rains. Kunoth Well is the low point in the landscape (J. Reid, personal communication). Mulga to a height of 6 m was the dominant shrub and small tree. Other acacias and shrubs that were abundant included dead finish (*A. tetragonophylla*), witchetty bush (*A. kempeana*) and umbrella bush (*A. ligulata*), cassias (*Cassia* spp.) and desert fuchsias (*Eremophila* spp.). Desert fuchsias, long-leaved corkwood (*Hakea suberea*) and Maiden's mistletoe (*Amyema maidenii*) were the main sources of nectar for birds. Berries eaten by birds were available on mistletoe (*Amyema preissii*), saltbush (*Einaadia nutans*) and *Rhagodia* sp.

Mulga and other tall plants tended to occur in thickets or stands separated by openings largely devoid of shrubs and trees. Over large areas, canopy cover was less than 20%. Mulga formed a small tree or shrub with foliage almost to ground level. In thickets, the lower branches were commonly dead. Near Kunoth Well, where cattle were abundant, a distinct browse line existed and the thickets were open with dead branches mainly broken off. Where cattle grazing was heaviest, openings between the mulga thickets had a sparse, low (< 30 cm) ground cover of grasses and forbs with extensive bare ground. In the thickets, ground vegetation under mulga tended to be taller and denser than that in the openings. Away from Kunoth Well, there was a uniformly dense ground cover across openings and under trees and shrubs. At the two sites near Kunoth Well, fresh water was available to birds at a cattle trough and a large dam; these were also the nearest sources of water for the other three sites.

Bird Counts

All birds seen and heard each day were recorded. Numbers of each species were counted, or, in the case of very abundant birds, such as zebra finches, estimated in orders of magnitude (i.e. tens, hundreds or thousands). Abundance data are presented as indicators of relative abundance and are not used to compare absolute abundances or densities among species. The census area covered each day was approximately 20 ha. With modifications for substantiated taxonomic revisions (see Christidis and Boles 1994), vernacular names and nomenclature follow CSIRO (1969). Vernacular and scientific names of birds referred to in the text and tables are presented in the Appendix.

Foraging Data

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, but it was not our intention to analyse the foraging behaviour of species in a statistical sense. Our objective was to describe the foraging ecology of the mulga avifauna within a short period and, as noted by Recher *et al.* (1985), multiple observations on individual birds increase the chance of recording infrequent or unusual behaviour. Recher and Gebski (1989) showed that no significant differences occurred in the proportions of the most important foraging behaviours between the first or second recorded observation and all recorded observations. However, a tendency existed for the first recorded foraging manoeuvre to be of birds in conspicuous locations (e.g. the end of a branch) or foraging actively (e.g. hawking). Hence, we ignored the first observed foraging action unless the bird was already under observation.

For each foraging manoeuvre in which the bird obtained or attempted to obtain a prey item, we recorded the species of bird, its sex if known, the substrate and height of the prey, and the attack behaviour used by the bird. Attack behaviours were defined as gleaning, snatching, pouncing, probing, hovering and hawking, following the terminology of Recher *et al.* (1985). For substrate, we recorded six categories: (1) ground [including ground, ground vegetation (i.e. grasses and forbs less than 30 cm tall) and litter and debris]; (2) bark (including small and large branches and main stem or trunk); (3) foliage (including twigs and leaves); (4) flowers (nectar); (5) fruit; and (6) air (for prey in flight). Sample sizes for dead substrates 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. Unidentified plants were mainly ground vegetation, small shrubs or scramblers, and were recorded only as ground vegetation or shrubs. Mulga was the only species of *Acacia* identified to species level.

By covering as large an area of habitat as possible each day (approximately 20 ha), and by visiting a different location each day, we attempted to avoid recording data for the same individuals. Where groups of

birds were encountered, we ceased taking observations and moved when we lost track of individual birds. However, the movements of the birds themselves and the fact that we returned to the same sites during the period of study inevitably meant that data were recorded for the same individuals on more than one occasion. This was especially true for the less common species, such as inland and slate-backed thornbills.

Prey Abundance

To obtain an index of the abundance of geometrid larvae on mulga, we chose, from a distance of several metres, one branch between 1.5 and 2.0 m above the ground on an arbitrarily selected mature mulga (> 2 m tall). Between 75 and 160 plants were sampled at Sites 1, 3 and 5. Counts were made at two widely spaced locations within each site. All larvae on the outer 50 cm of the branch, a length that encompassed most of the terminal vegetation, were counted. At Sites 3 and 5, the number of larvae on the highest stem of a juvenile or sapling mulga (< 1.5 m tall) was also counted, for a sample of saplings. Such stems were generally about 30 cm long. Site 1 lacked sufficient saplings for sampling.

Data Analysis and Presentation

For each species, we present the total number of prey attacks observed, the number of separate foraging sequences, and an estimate of the total number of individuals from which data were obtained. Species for which we recorded fewer than 10 prey attacks are not considered. For the sexually colour-dimorphic rufous whistler, males and females are considered separately.

Results

Bird Species Richness and Abundance

In all, 51 species of birds were recorded during censuses (Table 1). The species composition of the mulga avifauna on the study area did not differ greatly from that reported by Cody (1994) for mulga habitats from Western Australia, Queensland and the Northern Territory. Cody (1994) identified a core of 18 species for mulga communities, 17 of which occurred on our sites (Table 1). This included 16 of the 24 species for which we obtained foraging data. Of 28 species classed by Cody (1994) as peripheral species, 16 occurred on Hamilton Downs (Table 1) with foraging data obtained for six. Of 35 casual species listed by Cody (1994), seven occurred on Hamilton Downs with foraging data obtained for two. In addition to raptors, which Cody (1994) did not list, we recorded only two species, the black honeyeater and Major Mitchell cockatoo, not reported by Cody.

The most abundant species on our plots were seed and ground foragers: the budgerigar, crimson chat, diamond dove, southern whiteface and zebra finch (Table 1). Also abundant were the black-faced cuckoo-shrike, black-faced woodswallow, little button quail, red-capped robin, splendid wren and rufous whistler (Table 1). Although we found rufous whistlers nesting, others appeared to be migrating through the region and numbers of whistlers differed greatly from day to day and between sites (Table 1).

Sites 4 and 5, in less-disturbed mulga away from Kunoth Well, had the fewest species (Table 1). Those species that were present, however, occurred in about the same abundances as they did on Sites 1 and 3, which were near the well and were most affected by grazing. The species absent from Sites 4 and 5 were mainly parrots and raptors, although the black-faced cuckoo-shrike, white-winged triller and black-faced woodswallow were among the more conspicuous and frequently encountered species also absent. The very abundant crimson chat was found only near Kunoth Well on Sites 1 and 3. Abundances of most species were similar on all the sites where they occurred. The southern whiteface was more abundant on Site 1, the most highly disturbed plot and the plot nearest Kunoth Well, than elsewhere, as was the crimson chat after the first census (Table 1). The budgerigar, diamond dove and zebra finch were most abundant on Site 3, which had the greatest area of sparse ground vegetation and bare ground. Little button quail were most abundant on Site 2, where the ground vegetation appeared the most continuous and luxuriant.

Several species were obviously uncommon or rare, including all the honeyeaters except the spiny-cheeked and singing honeyeaters, which were regular in their occurrence through the area

Table 1. Relative abundance of bird species in mulga woodlands on Hamilton Downs Station, Northern Territory

**, species confirmed nesting; *, species probably nesting. c, Cody's (1994) core species; p, Cody's (1994) peripheral species

Species	Site 1		Site 2		Site 3		Site 4		Site 5	
	24 July	29 July	25 July	27 July	1 Aug.	28 July	28 July	30 July	28 July	30 July
Black honeyeater**	0	1-10	0	1	1	0	0	0	0	0
Black-capped sittella **	0	0	0	0	1-10	1-10	1-10	0	0	0
Black-faced cuckoo-shrike (p)	1	10-100	10-100	10-100	1-10	0	0	0	0	0
Black-faced woodswallow (p)	10-100	10-100	0	10-100	10-100	0	0	0	0	0
Black kite*	0	1	1-10	0	0	0	0	0	0	0
Bourke's parrot	0	1-10	0	1-10	1-10	0	0	0	0	0
Brown falcon*	0	1	1	1	0	0	0	0	0	0
Brown goshawk*	1	1	1	1	0	0	0	0	0	0
Brown honeyeater* (p)	0	0	0	0	0	0	1-10	0	0	0
Budgerigar** (p)	10-100	0	100-1000	100-1000	100-1000	0	0	0	0	0
Chestnut-rumped thornbill** (c)	1-10	10-100	1	1-10	0	1	1	1-10	1	1-10
Common bronzewing pigeon* (p)	1	0	1	1	1	0	0	0	0	0
Crested bellbird** (c)	1	1-10	1	1-10	0	1-10	1	1	1	1
Crested pigeon* (p)	1	0	0	1-10	0	0	0	0	0	0
Crimson chat	1	1000+	0	100-1000	100-1000	0	0	0	0	0
Diamond dove** (c)	1	10-100	0	100-1000	10-100	1	1	1-10	1	1-10
Galah (c)	0	0	10-100	0	0	0	0	0	0	0
Grey fantail (p)	0	0	1-10	0	0	0	0	0	0	0
Grey-fronted honeyeater	0	1	0	0	0	0	0	0	0	0
Grey shrike-thrush* (c)	1	1	1-10	1-10	1	1-10	1	1-10	1	1-10
Hooded robin** (p)	1-10	0	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10
Horsfield bronze cuckoo* (p)	0	1-10	1-10	1	1	1	1	0	0	0
Inland thornbill** (c)	1-10	1-10	1-10	1-10	1	1	1	1	1	1-10
Little button quail	1	1-10	10-100	1-10	1	1-10	1	1-10	1	1-10
Little crow* (c)	1	1	0	0-10	0-10	0	0	0	0	0-10
Magpie-lark*	1	1	0	1-10	0	0	0	0	0	0
Major Mitchell cockatoo	0	1	0	0	0	0	0	0	0	0
Mistletoe bird** (p)	0	0	0	0	1	0	0	0	0	0
Mulga parrot (p)	0	0	0	1-10	1	0	0	0	0	0
Nankeen kestrel*	0	0	0	1	0	1-10	0	0	0	0
Pallid cuckoo** (p)	1-10	1-10	1-10	1-10	1-10	1-10	1	0	0	0
Pied butcherbird* (p)	0	0	1	0	0	0	0	0	0	0
Pipit**	1-10	0	1	0	0	0	0	0	0	0
Port Lincoln parrot	0	0	0	0	1	0	0	0	0	0
Red-capped robin** (c)	1-10	1-10	10-100	10-100	10-100	10-100	1-10	10-100	1-10	10-100
Rufous whistler** (c)	1-10	10-100	10-100	10-100	10-100	10-100	100-1000	10-100	10-100	10-100
Singing honeyeater (c)	1-10	1-10	0	1-10	0	1-10	0	0	0	10-100
Slate-backed thornbill** (p)	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10
Southern whiteface** (c)	100-1000	100-1000	10-100	10-100	10-100	10-100	10-100	10-100	10-100	10-100
Spiny-cheeked honeyeater (c)	1-10	1-10	1-10	10-100	1-10	1-10	1-10	1-10	1-10	1-10
Splendid wren** (c)	1-10	0	10-100	1-10	0	0	10-100	10-100	10-100	10-100
Wedge-tailed eagle	0	0	1	1	0	0	0	0	0	0
Western warbler** (c)	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10	1-10
Whistling kite	1	1-10	0	1	0	0	1-10	1-10	0	0
White-browed babbler* (c)	0	0	10-100	0	0	0	0	0	0	1-10
White-browed treecreeper* (p)	0	0	0	1-10	0	0	0	0	0	0

Table 1. continued

Species	Site 1		Site 2	Site 3		Site 4	Site 5
	24 July	29 July		25 July	27 July		
White-plumed honeyeater	1	0	0	0	0	0	0
White-winged triller	1-10	0	1-10	1-10	0	0	0
Willie wagtail* (c)	1	1	0	1-10	0	1	0
Yellow-rumped thornbill** (c)	1-10	1-10	1-10	1-10	1-10	1-10	1-10
Zebra finch** (p)	100-1000	100-1000	100-1000	1000++	1000++	10-100	100-1000
Total No. of species	31	31	30	37	27	24	19

surveyed. The small number of honeyeaters reflected the paucity of blossoms available for nectar. Corkwood, which had large and nectar-rich blossoms, was uncommon, as were the various *Eremophila* species. Most nectar was obtained from mistletoe. Only one pair of white-browed treecreepers was located and only two groups of black-capped sittellas. A single pair or perhaps a small flock of grey fantails was found on Site 2 in a dense patch of tall mulga where the ground appeared quite moist. Despite an apparent abundance of mistletoe, mistletoe birds were not common.

Breeding

Sixteen species of birds were found nesting (69 nests). Behavioural characteristics suggested that another 17 species were breeding (Table 1). Yellow-rumped, slate-backed, inland and chestnut-rumped thornbills were in various stages of nesting, with some pairs or groups building nests while others were feeding nestlings or runners. The southern whiteface, crested bellbird, red-capped robin, splendid wren and rufous whistler were either building or had eggs. The western warbler, black honeyeater, spiny-cheeked honeyeater and hooded robin were building nests, while the black-capped sittella and diamond dove had eggs. Although we found nests with eggs and young, zebra finches may have nested earlier than other species, as flocks had large numbers of juveniles and many recent nests were empty.

Caterpillar Abundance

The larvae of what appeared to be a single species of geometrid moth were exceptionally abundant on mulga (Table 2) with as many as 16 caterpillars counted on a single branch. On saplings, as many as nine caterpillars were recorded on a single stem. Other branches and saplings had even greater numbers, but were not sampled during surveys. Caterpillars were 4-6 cm long and were an important food for many birds during the course of this study.

Caterpillars were found on all mulga plants searched, but not on all branches sampled (Table 2). Densities differed between locations within a site, but the differences were not significant (χ^2 , all $P > 0.05$) and the data for each site were pooled (Table 2). The numbers of caterpillars were significantly greater on Site 1 than on Site 3 ($\chi^2 = 6.067$, $P = 0.048$), but did not differ between Sites 1 and 5 (χ^2 , $P = 0.9$), or between Sites 5 and 3 ($\chi^2 = 5.901$, $P = 0.052$).

Thirty of 45 saplings in one sample and two of 25 saplings in a second had no larvae anywhere on the plant. Larvae were absent on 38 of the 45 stems scored in the first instance and 8 of 25 in the second (Table 2). Larvae were significantly more abundant on the saplings sampled on Site 5 than on Site 3 ($\chi^2 = 29.1$, $P < 0.001$). Numbers of larvae were greatest on new foliage, which explains the large variation in numbers of caterpillars. Saplings with the most new foliage appeared to have been browsed by cattle.

Table 2. Abundance of caterpillars (Geometridae) on mulga at Hamilton Downs Station, Northern Territory

Data are presented as the number of branches with 0, 1, 2, ..., n larvae, with mean, standard error and maximum number of larvae per branch. Sample size is in parentheses. Two samples of mature shrubs were taken at different locations within each site surveyed

Site No. (<i>n</i>)	No. of caterpillars per branch								Mean No. of caterpillars per branch (\pm s.e.)	Maximum No. of caterpillars per branch
	0	1	2	3	4	5	6	>6		
Mature shrubs (> 1.5 m)										
Site 1 (156)	120	18	6	5	4	1	0	2	0.6 ± 1.9	16
Site 3 (80)	64	14	1	1	0	0	0	0	0.2 ± 0.5	3
Site 5 (100)	75	13	4	6	0	0	1	1	0.5 ± 1.2	7
Sapling (< 1.5 m)										
Site 3 (45)	38	7	0	0	0	0	0	0	0.2 ± 0.4	1
Site 5 (25)	8	3	2	5	5	0	0	2	2.3 ± 2.3	9

Seventeen of the 24 species of birds for which foraging data were obtained took caterpillars from mulga. Mulga caterpillars also appeared to be a major source for the black-faced cuckoo-shrike and Horsfield bronze cuckoo, two species for which we obtained few foraging observations. Geometrid larvae were the major food fed to nestlings and runners by thornbills. Because of the abundance of geometrids, crimson chats and yellow-rumped and chestnut-rumped thornbills (species that we expected to forage more often on the ground and less often in shrubs and trees) took large numbers of caterpillars from mulga. Ground-foraging thornbills often forage in shrubs and trees when feeding young (Recher 1989) and this response of yellow-rumped and chestnut-rumped thornbills to an abundant prey is not unusual.

Foraging Biology

Substrate and food

Thirteen species, or more than half of the avifauna, foraged predominantly on the ground (> 45 % of foraging manoeuvres) (Table 3). Diamond doves, budgerigars, Bourke's parrots and zebra finches foraged exclusively on the ground, where they took seeds from the ground and low (< 6 cm) vegetation. In all, 99% of observations of southern whitefaces were also of ground-foraging individuals, but birds foraged occasionally in mulga and other shrubs, where they took caterpillars and other arthropods. Southern whitefaces that foraged on the ground were probably taking seeds (Serventy and Whittell 1967) and in this report are considered to be seed eaters.

Hooded robins, willie wagtails, crimson chats and red-capped robins took 80% or more of their prey from the ground (Table 3). Willie wagtails took 18% of their prey from the air, while the other three species took 14–19% of prey from the foliage and bark of shrubs and rarely took flying insects. With the exception of the crimson chat, which may have taken seeds on the ground, arthropods were the primary prey of these species. Prey taken from bark and foliage were invariably geometrid moth larvae taken from mulga.

Splendid wrens, crested bellbirds and yellow-rumped thornbills foraged less often on the ground and more often in shrubs than did the previous species. When foraging in shrubs, most prey was taken from foliage (Table 3). All identified prey were arthropods, with geometrid caterpillars taken from mulga a major item. White-browed babblers also foraged in low vegetation, but 33% of their food was taken from bark (branches and main stems). Babblers also visited flowers, mainly corkwood (*Hakea* spp.), where they could have taken either nectar or insects.

Black-capped sittellas and white-browed treecreepers foraged predominantly on bark (> 80% of observations), sittellas on branches and treecreepers on main stems (Table 3). For

Table 3. Substrate of prey taken by bird species in mulga woodland at Hamilton Downs Station, Northern Territory

Numbers are the percentage of prey attacks. Numbers of observations are in parentheses

Guild, species (n)	Ground	Bark		Foliage	Air	Nectar or fruit
		Branches	Main stem			
Ground foragers						
Diamond dove (83)	100					
Budgerigar (1415)	100					
Bourke's parrot (25)	100					
Zebra finch (934)	100					
Southern whiteface (128)	99			1		
Hooded robin (58)	84		2	12	2	
Willie wagtail (44)	82				18	
Crimson chat (259)	82			17	1	
Red-capped robin (100)	78	3	3	13	3	
Splendid wren (160)	69		1	29	1	
Crested bellbird (16)	50			50		
Yellow-rumped thornbill (93)	45	5	2	38	8	2
White-browed babbler (69)	45	30	3	7		15
Bark foragers						
Black-capped sittella (43)	2	63	19	16		
White-browed treecreeper (24)	17	4	79			
Foliage foragers						
Rufous whistler (male) (32)		6		94		
Inland thornbill (60)		2		92	6	
Western warbler (85)			5	89	6	
Slate-backed thornbill (133)		14		86		
Grey shrike-thrush (16)	6	12		82		
Rufous whistler (female) (62)	13	8	2	77		
Chestnut-rumped thornbill (117)		11	7	73	9	
Aerial foragers						
Grey fantail (12)				16	84	
Nectar and fruit eaters						
Spiny-cheeked honeyeater (53)		1		49		50
Singing honeyeater (74)		4		34		62

sittellas, 16% of foraging manoeuvres were birds taking caterpillars from mulga foliage, while 17% of treecreeper observations were of birds foraging on the ground.

Six species took more than 70% of their prey from foliage (Table 3). All were insectivorous, and geometrid larvae were a major item. Male rufous whistlers took 94% of their prey from foliage and the remainder from branches. Female rufous whistlers took 87% of their prey from foliage and branches with the remainder taken from the ground, ground vegetation (< 10 cm tall), and debris or litter (Table 3). Inland thornbills, western warblers and chestnut-rumped thornbills took more than 5% of their prey from the air. Slate-backed thornbills, grey shrike-thrushes and chestnut-rumped thornbills took 12% or more of their prey from bark (Table 3). Shrike-thrushes also foraged on the ground, where they took prey from ground vegetation and litter.

Although we made few observations, grey fantails took more than 80% of their prey from the air and the remainder from foliage (Table 3). This conforms closely to the way grey fantails feed throughout their distribution (e.g. Recher *et al.* 1985; Ford *et al.* 1986) and is the reason we have included data for this species from mulga despite the small sample size.

Spiny-cheeked and singing honeyeaters fed on nectar and fruit (50 and 62% of foraging observations, respectively), and took insects, mainly geometrid larvae, from foliage (Table 3). Nectar was taken from mistletoe, corkwood and native fuchsias. Mistletoe berries and the fruit of *Rhagodia* were also eaten or the berries punctured and the juice extracted. Yellow-rumped thornbills were also observed to extract juice from these berries.

Plant species and arthropod prey

Mulga was the most commonly visited plant species from which arthropod prey were taken (Table 4). More than 80% of foraging records for each of 10 species of insectivorous birds were of prey taken from the foliage and bark of mulga.

One hundred individual prey were identified as they were taken by birds: 97 were geometrid larvae, two were moths, and one a beetle. While the large size and distinctive shape of the caterpillars facilitated identification, in our experience it is unusual for such a large proportion of identified prey to be of a single type and apparently the same species.

Table 4. Use of plant species by insectivorous birds in mulga woodland at Kunoth Well, Northern Territory

Numbers are the percentage of prey attacks. Number of observations that involved foraging on plants are in parentheses

Bird species (n)	Plant species	
	Mulga	Other
Black-capped sittella (42)	100	0
Chestnut-rumped thornbill (103)	84	16
Crimson chat (41)	95	5
Grey shrike-thrush (15)	100	0
Inland thornbill (56)	84	16
Rufous whistler (96)	92	8
Slate-backed thornbill (135)	97	3
Splendid wren (50)	82	18
Western warbler (77)	88	12
White-browed treecreeper (19)	100	0

Foraging behaviour

Gleaning or pecking was the principal foraging behaviour (> 65% of prey attacks) for 18 species (Table 5). Red-capped and hooded robins were pouncers, while grey fantails took mainly aerial prey by hawking. Male and female rufous whistlers, slate-backed thornbills and western warblers took 78% or more of their prey by gleaning or snatching. Western warblers (16% of prey attacks) and slate-backed thornbills (13%) took prey by hovering, with the warbler also taking prey by hawking (6% of prey attacks) (Table 5). Among the gleaners, chestnut-rumped thornbills also took prey by hovering (17% of prey attacks), snatching (9%) and hawking (9%). These active foraging behaviours were also used by inland (17% of prey attacks) and yellow-rumped (16%) thornbills (Table 5). Grey shrike-thrushes took 13% of prey by snatching, while splendid wrens snatched prey on 7% of foraging manoeuvres.

While the willie wagtail is listed as a 'gleaner' or 'pecker' (Table 5), its foraging behaviour is more active than this implies. The wagtail can be viewed as a terrestrial equivalent of the grey fantail, moving actively, searching for prey at relatively long distances, and then pursuing it. Because most of the prey taken by wagtails were terrestrial or on low ground vegetation, the

Table 5. Prey attack manoeuvres by bird species in mulga woodland at Hamilton Downs Station, Northern Territory

Numbers are the percentage of prey attacks. Numbers of observations are in parentheses

Guild, species (n)	Manoeuvre				
	Pouncing	Gleaning/pecking	Hovering	Snatching	Hawking
Pouncers					
Red-capped robin (100)	78	3	8	8	3
Hooded robin (58)	70	14	2	12	2
Gleaners/peckers					
Black-capped sittella (43)		100			
Bourke's parrot (25)		100			
Budgerigar (1415)		100			
Crested bellbird (16)		100			
Diamond dove (83)		100			
Southern whiteface (128)		100			
White-browed babbler (69)		100			
White-browed treecreeper (24)		100			
Zebra finch (934)		100			
Singing honeyeater (74)		99		1	
Spiny-cheeked honeyeater (53)		99		1	
Crimson chat (259)		94	3	2	1
Splendid wren (160)		92		7	1
Grey shrike-thrush (16)		87		13	
Yellow-rumped thornbill (93)		84	4	4	8
Inland thornbill (60)		83	7	3	7
Willie wagtail (44)		82			18
Chestnut-rumped thornbill (117)		65	17	9	9
Snatchers/gleaners					
Rufous whistler (male) (32)		41	9	50	
Rufous whistler (female) (62)	5	58	3	34	
Slate-backed thornbill (133)		54	13	33	
Western warbler (85)		58	16	20	6
Hawkers					
Grey fantail (12)			8	8	84

actual movement to capture the prey was a glean or peck, a description that hides the rapid running and short chases these birds performed.

Foraging height

Seven species foraged on or within 50 cm of the ground (Table 6), including both robins, willie wagtails and all seed-eaters. Female rufous whistlers and four other species foraged on the ground or in low shrubs and debris. Although foraging near or on the ground, female rufous whistlers took most of their prey from foliage, including grasses and forbs. Four species foraged mainly in low shrubs or in the lower parts of the taller mulga and other plants. White-browed treecreepers foraged on the ground and the main stem of the largest mulga plants. Male rufous whistlers and seven other species foraged mainly in the canopy, although most also visited lower vegetation and fed close to the ground. Black-capped sittellas mainly foraged on large branches (Table 3) in the tallest shrubs. The main source of flowers for singing and spiny-cheeked honeyeaters were either in tall, mature corkwoods, or mistletoes that were most abundant in the largest and tallest mulga.

Table 6. Foraging heights for birds in mulga habitats at Kunoth Well, Northern Territory

Guild, species	Mean foraging height (m) \pm s.d.	No. of observations
Ground foragers		
Zebra finch	0.0 \pm 0.0	190
Budgerigar	0.0 \pm 0.0	283
Diamond dove	0.0 \pm 0.0	82
Southern whiteface	0.0 \pm 0.2	130
Hooded robin	0.2 \pm 0.5	53
Willie wagtail	0.2 \pm 0.9	44
Red-capped robin	0.4 \pm 0.8	90
Ground-and-low-shrub foragers		
Rufous whistler (female)	0.5 \pm 1.0	61
Crimson chat	0.5 \pm 1.3	260
Blue-breasted wren	0.9 \pm 1.1	66
White-browed babbler	1.2 \pm 1.2	70
Yellow-rumped thornbill	1.3 \pm 1.4	93
Shrub-and-lower-canopy foragers		
White-browed treecreeper	1.4 \pm 1.3	22
Crested bellbird	1.6 \pm 2.4	16
Inland thornbill	1.9 \pm 0.9	59
Chestnut-rumped thornbill	2.1 \pm 1.2	117
Canopy foragers		
Western warbler	2.3 \pm 0.9	86
Black-capped sittella	2.4 \pm 0.5	42
Slate-backed thornbill	2.4 \pm 1.0	109
Rufous whistler (male)	2.9 \pm 1.1	32
Singing honeyeater	3.1 \pm 1.0	63
Grey fantail	3.5 \pm 1.0	12
Spiny-cheeked honeyeater	4.1 \pm 1.6	52
Grey shrike-thrush	4.1 \pm 2.4	16

Guild Structure

The foraging guild structure of the mulga avifauna (Fig. 1) summarises the main divisions and groupings among species according to their use of substrates, type of food, and prey-attack behaviour, which are described above in more detail.

Data on habitat segregation were not collected, but there were several conspicuous examples of habitat and size separation within guilds. Among ground pouncers, the red-capped robin is smaller than the hooded robin and may forage more often within the shelter of vegetation than does the hooded robin. Among foliage gleaners, the grey shrike-thrush is much larger than the inland thornbill, while among foliage snatchers, the rufous whistler is larger than either the western warbler or slate-backed thornbill. The slate-backed thornbill foraged more on the inner vegetation of mulga, while the western warbler foraged more in the outer vegetation.

Alternative descriptions of the guild structure of birds at Kunoth Well are conceivable, but all would show the preponderance of ground foragers and the broad overlap among species using the same substrates and taking similar kinds of food during the period of abundant food when we made our observations. We predict that as conditions deteriorate over summer the opportunistic species will depart and the birds that remain will diverge further in their use of resources. Chestnut-rumped thornbills, for example, should forage more frequently on the

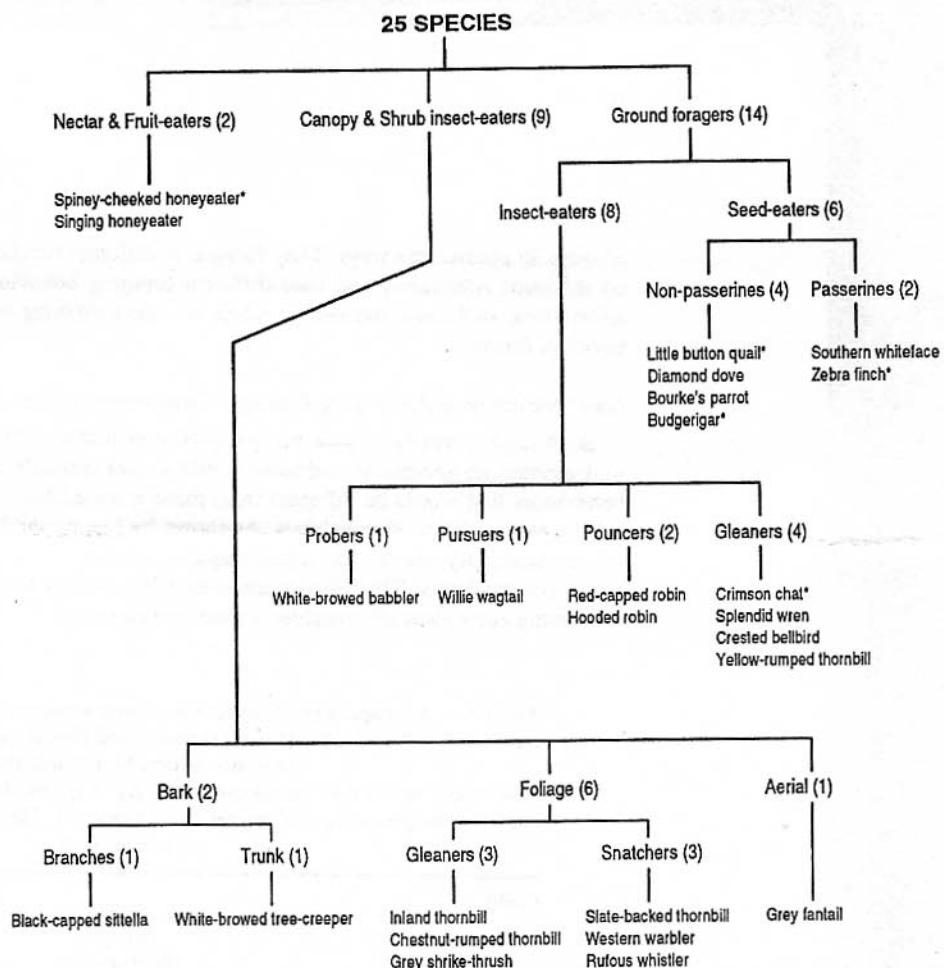


Fig. 1. A schematic diagram of the foraging guilds at Kunoth Well, Northern Territory, during late winter in 1995. Opportunistic or nomadic species have been marked with an asterisk (*) and are expected to leave the area as conditions deteriorate over summer. The number in parentheses is the number of species in each guild. Alternative presentations of guild structure for this avifauna are possible, and could include species for which foraging data were not recorded (e.g. the pallid cuckoo). However, this schema is intended only to highlight major divisions among species and to illustrate the dominance of ground foragers and opportunistic species.

ground, while inland thornbills should continue to forage mainly on the foliage of shrubs. Greater use may be made of plant species other than mulga once the number of geometrid larvae declines.

Discussion

The avifauna at Hamilton Downs was typical of the mulga bird communities described by Cody (1993, 1994). It was composed of a core of resident species augmented by a number of nomadic or opportunistic species that had moved into the area in response to favourable conditions following rain earlier in the year. Although there was an outbreak of geometrid larvae on mulga, with many birds using them as food, bird species differed in their foraging

ecology in predictable ways. They foraged at different heights in the vegetation, exploited prey on different substrates, and used different foraging behaviours. This extended to intersexual differences, with male and female rufous whistlers showing the same separation as they show in eucalypt forest.

Guild Structure and Foraging Ecology: Comparison with Eucalypt Forest

Although a study of the mulga avifauna under different conditions (e.g. drought, midsummer, no geometrid outbreak) would almost certainly include fewer species and foraging behaviours that would be different from those reported here, it is useful to compare our data to similar studies from other habitats. As shown by Holmes and Recher (1986), such comparisons, while necessarily coarse, can signal major differences or similarities in the foraging ecology of avian communities. This allows more-detailed studies to focus on what might be the most interesting ecological relationships within an ecosystem.

Table 7. A comparison of the foraging guild structure between the mulga avifauna on Hamilton Downs, Northern Territory, and that in eucalypt forest and woodland in south-eastern New South Wales

New South Wales data are adapted from fig. 6 (p. 94) in Recher and Holmes (1985). Numbers are percentages of species in each category. Because of rounding, numbers do not sum to 100%

Guild	Habitat	
	Mulga (% of species)	Eucalypt forest and woodland (% of species)
Ground foragers	54	32
Seed eaters	21	0
Insectivores	33	32
Pouncers	8	7
Above-ground foragers	46	68
Bark foragers	8	15
Foliage foragers	25	32
Gleaners	13	20
Snatchers	13	12
Aerial foragers	4	10
Seed eaters	0	5
Nectar feeders	8	7
Total No. of species	24	41

Using the same procedures employed in this study, Recher and his colleagues (Recher *et al.* 1985; Recher and Holmes 1985; Holmes and Recher 1986) described the foraging guild structure of a eucalypt forest avifauna in south-eastern New South Wales during the breeding season. Despite a much richer avifauna (41 species cf. 23), the foraging guilds described for eucalypt forest are broadly similar to those described for the mulga avifauna in Fig. 1. We compare the foraging guild structure of the two avifaunas in Table 7. The guilds described by Recher and Holmes (1985, fig. 6, p. 94) have been modified in this comparison by placing four species [the silvereye (*Zosterops lateralis*), brown-headed honeyeater (*Melithreptus brevirostris*), white-naped honeyeater (*M. lunatus*), and yellow-faced honeyeater (*Meliphaga chrysops*)] of the nectar-feeding guild in the above-ground, foliage-foraging guild, and putting a

fifth honeyeater, the white-eared honeyeater (*M. leucotis*), in the bark-foraging guild. While these five species will take nectar, they rely on alternative carbohydrates (e.g. lerp, honeydew) produced by insects. The three honeyeaters remaining in the nectar-feeding guild of Recher and Holmes (1985) are dependent on nectar obtained from flowers.

Closely related and morphologically similar species differed in their use of resources in the same ways and to about the same extent as among related species in other habitats. For example, the foliage-foraging inland and slate-backed thornbills appeared to maintain mutually exclusive territories, with the inland thornbill dominating (Recher and Davis, personal observations). Although both species took more than 85% of their prey from foliage and took large numbers of geometrid caterpillars, they differed in prey-attack behaviour, use of plant species, and foraging height. We did not measure the habitat attributes of the nesting territories we found, but our impression was that the slate-backed thornbill was more of a mulga specialist than was the inland thornbill and was found only in reasonably dense and tall thickets of mulga. The slate-backed thornbill foraged almost exclusively on mulga, while the inland thornbill used a greater range of plants and often foraged in low shrubs or among piles of debris. The inland thornbill appeared to require an abundance of low shrubs in the territories where it nested. These differences are similar to those reported between other species of thornbills in other habitats (e.g. Recher *et al.* 1987; Recher 1989).

Although the same guilds can be identified in both habitats, ground foragers (13 species) dominate the mulga avifauna, while above-ground foragers (28 species) dominate the eucalypt avifauna (Table 7). The difference in the number of species in the ground-foraging guilds results from the presence of five species of ground-foraging seed eaters in the mulga community and none in the eucalypt forest. The proportions of ground-foraging insectivores are the same (33 and 32% respectively) in the two avifaunas. Woinarski and Fisher (1995) also report a higher incidence of ground-foraging birds in woodlands of lancewood (*Acacia shirleyi*) than in nearby eucalypt woodlands in the Northern Territory. They attributed this difference to the absence of a dense grass cover and the presence of a dense mat of litter in the lancewood woodland.

Among the birds that forage predominantly above the ground, the proportions of bark, foliage and aerial foragers, as well as of seed eaters, are greater in the eucalypt community than in the mulga (Table 7). In the eucalypt forest, the proportion of foliage gleaners is greater than that of foliage snatchers, whereas in mulga the two are equal. The difference is attributable to a group of foliage-gleaning forest birds that feed mainly on lerp and other carbohydrates [e.g. the striated thornbill (*Acanthiza lineata*) and white-naped honeyeater] and that are absent from mulga. The proportions of nectar feeders are the same in the two communities. In contrast, the lancewood woodlands studied by Woinarski and Fisher (1995) had more bark-foraging birds than did the nearby eucalypt woodlands, a difference attributed to the higher density of woody stems in the lancewood habitat.

The differences in guild structure between mulga and the eucalypt forest studied by Recher and his colleagues reflect the different resources in the two habitats, as do differences in forest guild structure between North America and Australia (Holmes and Recher 1986). The bark-foraging birds that obtain food by probing under or tearing loose and decorticating bark from eucalypts [e.g. the crested shrike-tit (*Falcunculus frontatus*)] are absent from mulga, as are species that forage on seeds in the canopy [e.g. the crimson rosella (*Platycercus elegans*)], and birds that feed on lerp and other carbohydrates gleaned from the foliage of eucalypts (e.g. the striated thornbill). The food resources required by these birds are absent in mulga. Mulga also lacks aerial foragers that take relatively large flying insects by sallying [e.g. the satin flycatcher (*Myiagra cyanoleuca*)]. As the vertical structure of mulga appears suitable for such sallying species, we presume that mulga lacks sufficient flying insects in the necessary size range. The eucalypt forest lacks seed-eating birds that foraged on the ground (e.g. the diamond dove and little button quail) and does not have plants to produce seeds in the necessary abundance for such species.

It appears that the mulga avifauna is a scaled-down version of the eucalypt forest avifauna because there are fewer kinds of foraging resources in the mulga. For the food resources that are

common to the two habitats (i.e. non-psyllid foliage arthropods, ground arthropods, non-decorticating bark arthropods and nectar), each habitat has about the same number of species. That is, the species-packing along each common resource dimension is the same. Each habitat, for example, has a sittella and a treecreeper that respectively exploit branches and tree trunks (main stems) regardless of whether the substrate has loose, decorticating bark or not. Each has two species of ground-pouncing robins and a ground-pouncing cuckoo that specialises in hairy lepidopteran larvae. In New South Wales, there were three robins, but scarlet and flame (*Petroica multicolor* and *P. phoenicea*) robins maintained mutually exclusive territories, and yellow robins (*Eopsaltria australis*) occupied a different habitat within the study areas (Recher, unpublished data). At Hamilton Downs, pallid cuckoos were common, but we failed to obtain sufficient foraging data for analysis. The observations we did make on foraging pallid cuckoos showed that they foraged by pouncing to the ground and taking large hairy caterpillars, as they do in other habitats where we have studied their foraging behaviour (Recher, unpublished data). We suggest that species are added to each habitat as new resources are added (see Holmes and Recher 1986). It does not appear that as habitats become more productive or structurally diverse, species narrow the range of resources used and pack together more closely, but this hypothesis should be treated with caution until tested more widely.

Species that occurred in both eucalypt forest and mulga, such as the rufous whistler, grey fantail and yellow-rumped thornbill, foraged similarly in the two habitats. The same is true for ecological replacements, such as the black-capped sittella and orange-winged sittella (*Daphoenositta chrysopera*), the inland thornbill and brown thornbill (*Acanthiza pusilla*), and the splendid wren and superb blue wren (*Malurus cyaneus*). In both the eucalypt forest (Recher and Holmes, unpublished data) and mulga, male rufous whistlers foraged higher than females, but used the same foraging behaviours and exploited the same substrates.

Species Interactions

Cody (1994) used presumed differences and similarities in the way species foraged to account for some of the variance in bird species composition and abundances between plots. He considered that the six species of *Acanthiza* he recorded were 'broadly similar in foraging ecology' and similar to two other acanthizids, the redthroat (*Sericornis brunneus*) and southern whiteface, which he recorded in mulga. Cody placed these eight species in a single guild, whereas we found that the four *Acanthiza* species and the southern whiteface differed in the way they foraged and placed them in different guilds (Fig. 1). This difference in interpretation is a consequence of our more detailed consideration of the species' foraging behaviours; Cody (1994) took a broader view in his analysis.

However, we disagree with Cody's (1994) description of the western (white-tailed) warbler and weebill (*Smicromyias brevirostris*) as ecological replacements. The western warbler is a canopy forager that takes most of its prey from foliage and small branches. Gleaning is its major foraging behaviour, but it takes large numbers of prey by snatching, hovering and hawking. Its foraging behaviour on Hamilton Downs was the same as the behaviour we have recorded for this species in a variety of habitats in Western Australia (Keast and Recher, in press; Recher and Davis, personal observations). The warbler has a wide habitat distribution, and near Alice Springs it occurred in mulga, acacia woodlands and riparian eucalypt habitats (authors' personal observations). The weebill did not occur in mulga where eucalypts were lacking, but was present in the nearby West MacDonnell Ranges where eucalypts were common.

The weebill is a eucalypt-dependent species that feeds extensively on lerp produced by psyllid insects. It takes large amounts of prey while hovering at the outer foliage where branches are too small to support other species (Recher 1989; Recher and Davis, unpublished data). Its foraging differs significantly from those of the western warbler and the two species cannot be considered ecological analogues.

Cody (1994) concluded that the western warbler and weebill were ecological replacements because the warbler was absent from his Western Australia and Queensland sites where the

weebill was common. The weebill occurred less frequently on the Northern Territory sites while the warbler was present on all of Cody's sites in the Northern Territory. Differences in vegetation structure could not account for these differences; hence, Cody (1994) concluded that the western warbler and weebill are ecological replacements. However, Cody used measurements of foliage structure to describe his sites and did not consider floristic differences, such as the presence or absence of eucalypts. Around Alice Springs and on our plots in Western Australia, the two species occur together wherever there are eucalypts (Recher and Davis, unpublished data). Cody (1993) described his mulga sites in Queensland as having a eucalypt overstorey, which explains the presence of the weebill on those sites. We do not know why Cody failed to find western warblers on his mulga plots in Western Australia and Queensland within the species' range, but we do not think that it was a consequence of it being replaced by the much smaller and ecologically different weebill.

Patterns of Species Abundance

A large proportion of the birds typical of mulga habitats in Australia have either increased or decreased in abundance following the introduction of domestic stock and other non-Australian herbivores (Reid and Fleming 1992). These changes must in part be due to changes in habitat (Burbidge and McKenzie 1989; Morton 1990). The abundance of birds near Kunoth Well where habitat degradation was most evident therefore requires explanation. Since other areas of mulga with apparently similar levels of degradation (i.e. a browse line, bare soil, trampled thickets, few saplings) lacked the richness and abundance of birds found near the well, it may be that the presence of water caused birds to congregate in the area.

It is also possible that the area around Kunoth Well has elevated nutrient levels and that the abundance of birds at the well is an instance of the relationship between soil nutrient levels, elevated food resources for birds, and an abundant and diverse avifauna (Recher 1985; Recher *et al.* 1991, 1996). As pointed out by Julian Reid (personal communication), Kunoth Well is the low point in the surrounding landscape and may be naturally enriched by drainage to the site. In this case, it may be an example of the 'hot spots' characterised by higher levels of productivity that Morton (1990) postulated were critical refuges for arid-zone fauna during drought. Additionally, the bare soil and sparse vegetation caused by the concentration of cattle near the well, as well as the availability of water, may have facilitated foraging by seed-eating birds. If the area around Kunoth Well has elevated nutrient levels, this did not appear to result in more-abundant food for insectivorous birds, nor was the abundance of resident insectivores any greater near the well than on sites further away (Table 1). Although some of the highest densities of mulga caterpillars occurred on the highly degraded Site 1, the lowest densities occurred on the equally degraded Site 3, which was about the same distance from the well and topographically similar. Numbers of caterpillars on Site 5, a less degraded area and 6 km from the well, were similar to those on Site 1. Understanding the relationships between habitat degradation and species richness and abundances of birds will require more-detailed studies, but if Kunoth Well is an example of one of Morton's (1990) 'hot spots', it graphically illustrates how important such areas may be for the future survival of the arid-zone avifauna.

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Appendix. Index of common and scientific names of birds found in this study

Common name	Scientific name
Black honeyeater	<i>Certhionyx niger</i>
Black-capped sittella	<i>Daphoenositta pileata</i>
Black-faced cuckoo-shrike	<i>Coracina novaehollandiae</i>
Black-faced woodswallow	<i>Artamus cinereus</i>
Black kite	<i>Milvus migrans</i>
Bourke's parrot	<i>Neopsephotus bourkii</i>
Brown falcon	<i>Falco berigora</i>
Brown goshawk	<i>Accipiter fasciatus</i>
Brown honeyeater	<i>Lichmera indistincta</i>
Budgerigar	<i>Melopsittacus undulatus</i>
Chestnut-rumped thornbill	<i>Acanthiza uropygialis</i>
Common bronzewing pigeon	<i>Phaps chalcoptera</i>
Crested bellbird	<i>Oreoica gutturalis</i>
Crested pigeon	<i>Ocyphaps lophotes</i>
Crimson chat	<i>Epthianura tricolor</i>
Diamond dove	<i>Geopelia cuneata</i>
Galah	<i>Cacatua roseicapilla</i>
Grey fantail	<i>Rhipidura fuliginosa</i>
Grey-fronted honeyeater	<i>Meliphaga keartlandi</i>
Grey shrike-thrush	<i>Colluricinclla harmonica</i>
Hooded robin	<i>Melanodrya cucullata</i>
Horsfield bronze cuckoo	<i>Chrysococcyx basalis</i>
Inland thornbill	<i>Acanthiza apicalis</i>
Little button quail	<i>Turnix velox</i>
Little crow	<i>Corvus bennetti</i>
Magpie-lark	<i>Grallina cyanoleuca</i>
Major Mitchell cockatoo	<i>Cacatua leadbeateri</i>
Mistletoe bird	<i>Dicaeum hirundinaceum</i>
Mulga parrot	<i>Psephotus varius</i>
Nankeen kestral	<i>Falco cenchroides</i>
Pallid cuckoo	<i>Cuculus pallidus</i>
Pied butcherbird	<i>Cracticus nigrogularis</i>
Pipit	<i>Anthus novaeseelandiae</i>
Port Lincoln parrot	<i>Barnardius zonarius</i>
Red-capped robin	<i>Petroica goodenovii</i>
Rufous whistler	<i>Pachycephala rufiventris</i>
Singing honeyeater	<i>Meliphaga virescens</i>
Slate-backed thornbill	<i>Acanthiza robustirostris</i>
Southern whiteface	<i>Aphelocephala leucopsis</i>
Spiny-cheeked honeyeater	<i>Acanthagenys rufogularis</i>
Splendid wren	<i>Malurus splendens</i>
Wedge-tailed eagle	<i>Aquila audax</i>
Western warbler	<i>Gerygone fusca</i>
Whistling kite	<i>Haliastur sphenurus</i>
White-browed babbler	<i>Pomatostomus superciliosus</i>
White-browed tree creeper	<i>Climacteris affinis</i>
White-plumed honeyeater	<i>Meliphaga penicillatus</i>
White-winged triller	<i>Lalage sueurii</i>
Willie wagtail	<i>Rhipidura leucophrys</i>
Yellow-rumped thornbill	<i>Acanthiza chrysorrhoa</i>
Zebra finch	<i>Taeniopygia guttata</i>