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Foraging behaviour of mulga birds in Western Australia. II. Community structure and conservation

Harry F. Recher

School of Natural Sciences, Edith Cowan University, Joondalup, WA 6027, Australia *and*
Veterinary and Life Sciences, Murdoch University, Murdoch, WA 6150, Australia.
Email: hfrecher@gmail.com

Abstract. Mulga (*Acacia aneura*) woodlands dominate much of arid and semiarid Australia. Although mulga woodlands are floristically and structurally diverse, the composition of the mulga avifauna is consistent across the continent, with 50–70% of bird species shared between sites and a high proportion of migratory and nomadic species. A comparison of avian foraging guilds in mulga woodlands in the Murchison and Gascoyne Bioregions of Western Australia with those in the Northern Territory identified nine guilds. All guilds occurred at the three locations studied during wet years. The number of bird species, species' abundances, and the number of guilds declined on the Western Australian sites when there was less rain. Despite the commonality of guilds and species between sites, there were differences between sites and years in the grouping of species, with many species best associated with two or more guilds. These differences reflected differences between locations and wet and dry years in the food resources available to birds, which affected how species foraged. Particularly noticeable were the differences between sites and years in migratory and nomadic birds, which in Western Australia and the Northern Territory were the most abundant birds during wet conditions, but largely absent when conditions were drier.

Additional keywords: dispersive species, effects of rainfall, foraging guilds

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Introduction

Mulga (*Acacia aneura*) woodlands dominate 1.5 million km^2 (~20%) of the Australian continent and are 'keystone' habitats in arid and semiarid Australia (Johnson and Burrows 1994; Williams 2002; Maslin and Reid 2009). Maslin and Reid (2009) described mulga communities as 'resource hotspots', with high levels of productivity and the capacity to 'capture, retain, and cycle' sediments, nutrients, and water. Although the distribution of mulga is patchy, with pronounced spatial and temporal differences in vegetative structure and floristics (Johnson and Burrows 1994; Williams 2002; author's obs.), the species composition of its avifauna appears consistent across the continent (Cody 1994; Pavey and Nano 2009).

Recher and Davis (2018) studied the foraging behaviour of mulga birds in the Gascoyne and Murchison Bioregions of Western Australia (WA) in 1999 following a period of heavy rainfall. Recher revisited the study sites in 2002 when conditions were drier and made further observations on the foraging behaviour of mulga birds. An aim of those studies was to compare the foraging behaviour of birds in Western Australian mulga habitats with those studied by Recher and Davis (1997) in the Northern Territory (NT), also following a wet period. The two regions differed in vegetation structure and floristics, as well as land use: the WA sites were grazed by cattle, sheep, and goats, while those in the NT were grazed by cattle. In this paper I compare the mulga bird communities in WA and the NT as observed by Recher and Davis (1997, 2018) with those reported by Cody (1994) and test Cody's (1994) conclusion of a broadly consistent mulga avifauna. I then test the hypothesis that 'there is no difference in the foraging guilds of mulga birds between locations and seasons'.

Study locations

Birds were censused and foraging data collected between 23 July and 2 August 1995 on five sites on Hamilton Downs Station (23.7312°S, 133.8529°E; ~673 m above sea level) along the Tanami Road ~66 km north-west of Alice Springs in the NT, central Australia. Initial observations in WA in the Gascoyne Bioregion were made on 1–7 August and in the Murchison on 8–10 August 1999. In 2002, observations in the Gascoyne were made on 20–24 July and in the Murchison on 10–11 July. There was one study plot in the Gascoyne, on the Carnarvon/Mullewa Road 35 km west of Gascoyne Junction (25.05°S, 115.21°E; 144 m above sea level). Three study plots were located in the Murchison along the Geraldton/Mount Magnet Road near Mount Magnet (28.06°S, 117.85E; 426 m above sea level). Full details of locations and descriptions of the plots and their vegetation are given by Recher and Davis (1997, 2018).

Methods

Foraging behaviour

Details of the procedures used to record foraging behaviour are given in Recher and Davis (1997, 1998, 2002, 2018) but, briefly, the species of bird, the substrate and height of the food, the type (e.g. grass, shrub), species or genus of plant if identified, from which food was taken, and the foraging manoeuvre or method used by the bird to take food was recorded. For substrates and manoeuvres the terminology of Recher *et al.* (1985) and Recher and Davis (1998, 2002, 2018) was used. Observations commenced shortly after sunrise and, depending on weather conditions, continued to dusk. Foraging was recorded for all birds encountered. Following Recher and Gebski (1989), for each individual, up to five consecutive foraging manoeuvres commencing with the second observed manoeuvre were recorded.

In this paper, bark, dead wood, loose bark, and hanging bark are combined as 'bark'; twigs and petioles, and live and dead leaves as 'foliage'; and, bare ground, litter, logs, and coarse woody debris as 'ground'. 'Hover hawk' and 'hover glean' are combined with 'hover'. Rare behaviours (<0.1% of observations) were deleted from analyses.

Bird counts

Different procedures were used to count birds on plots in WA and the NT. Birds were not censused in 1999, but I kept a list of species and estimated numbers. In 2002, I counted the number of individuals of each species observed on each of the plots at Gascoyne Junction and Mount Magnet, with counts on the Mount Magnet plots combined to provide a single estimate of numbers for comparison with the Gascoyne Junction plot (see table 2 in Recher and Davis (2018) for abundances). In the NT, I recorded all birds seen and heard each day. Very abundant species (e.g. zebra finch) were recorded in orders of magnitude (i.e. 10–100, 100–1000, 1000+). For uncommon species the number of foraging observations recorded is used as a guide to their abundances.

Data analysis

In the analyses presented in this paper, only species for which 10 or more foraging observations were available at one or more locations or years were analysed. The percentage use of foraging manoeuvres and substrates used by mulga birds in WA are presented in Recher and Davis (2018) and those for the NT in Recher and Davis (1997). As the census procedures used provide relative abundances only and differed between locations and years, only species richness is compared between locations in this paper.

Cluster analysis

Cluster Analyses (CA) based on the manoeuvre/substrate categories of bird species for which 10 or more foraging observations were available at each location and year were used to describe foraging guilds. Foraging relationships among birds can be described using CA whereby species are grouped according to the similarity of the manoeuvre/substrates each uses. The groups can then be used to define guilds, with a guild being a cluster of species using similar food resources and/or using similar foraging behaviours (Root 1967; Holmes and Recher 1986; Korňan *et al.* 2013).

Manoeuvre/substrate frequencies were log-transformed to reduce skewness and then standardised to bring the means to 0 and variances to 1.0. This weights all categories equally. Data were first tested incorporating species weight and foraging height distributions, but in no case were the results more informative and only analyses using manoeuvre/substrate foraging frequencies are presented. Results were selected that accounted for high levels of variance and, in the opinion of the author, best described the relationships among species as observed in the field.

A limitation of CA is that species are grouped with the species with which they are most similar. Thus, each species is placed in a single guild or grouping of species. To illustrate the variety of foraging behaviours used by different species and their association with multiple guilds I also grouped species into guilds based on their percentage use of different manoeuvre/substrate categories. My decisions on which guilds a species might belong to are useful to show the variety of foraging strategies mulga birds use and how species assemblages differ with location and environmental conditions through time.

All statistical analyses were done using the PAST statistical package available from http://palaeoelectronica.org/2001_1/past/issue1_01.htm (Hammer *et al.* 2001; Hammer and Harper 2006).

Results

Bird species

Cody (1994) censused mulga birds on 20 sites in three regions from western to eastern Australia. Of the 81 species recorded, Cody (1994) considered 14 to be 'core species', with >50% frequency of occurrence. That is, they were found on 10 or more of the sites censused. Four others qualified as core species in at least one region, while 28 species had a 15 to <50% frequency of occurrence and were listed by Cody (1994) as 'peripheral' to mulga. The remaining 35 species were recorded only once or twice and were considered 'casual' in occurrence. Core species accounted for 75% of individuals on Cody's (1994) plots.

Recher and Davis (1997) recorded 51 species on their mulga plots at Hamilton Downs. This included raptors (five species), which Cody did not count. Including raptors (seven species), 59 species were recorded in 1999 on the WA plots, 41 in the Gascoyne and 46 in the Murchison (Table 1). In 2002, 26 species were recorded on the Gascoyne site and 21 at Mount Magnet for a total of 35 species (Table 1). In total, 60 species were recorded on the WA plots. Excluding raptors, seven species in WA and four species at Hamilton Downs were not recorded by Cody. These were placed in Cody's 'casual' category (Table 1). Cody recorded 37 species not recorded on plots at Gascoyne Junction and Mount Magnet and 40 species not recorded at Hamilton Downs, but Cody (1994) included mulga habitats with eucalypts (*Eucalyptus* spp.) whereas the WA and Hamilton Downs plots lacked eucalypts. The WA plots shared 36 species with Hamilton Downs, with a total of 62 species recorded in the two regions. Excluding raptors (nine species), collectively 90 species were recorded by Recher and Davis (1997, 2018) and Cody (1994), of which 28 (31%) were recorded only by Cody.

Core species, as identified by Cody (1994) and excluding raptors, comprised 37–39% of WA species in 1999 and 42–52%

Table 1. Number of bird species recorded on plots at Gascoyne Junction (GJ) and Mount Magnet (MM), in Western Australia in 1999 and 2002 (Recher and Davis 2018), at Hamilton Downs (HD) in the Northern Territory in 1997 (Recher and Davis 1997), and Cody's (1994) counts and classification of mulga bird species

Percentages are given in parentheses. Cody's species are those he ranked in terms of frequency of occurrence on mulga (*Acacia aneura*) plots from Western Australia to Queensland, with core species occurring on more than 50% of the plots he censused, peripheral species in 15–50% of plots, with casual species recorded only once or twice (Cody 1994). Following Cody (1994), raptors are excluded from calculations, but the number of species recorded at each site is given. Species recorded in WA or the NT, but not recorded by Cody (1994) were grouped in the Casual category

	GJ 1999	MM 1999	GJ 2002	MM 2002	HD 1997	Cody 1994
Cody's Classification (%)						
Core	13 (37)	16 (39)	10 (42)	11 (52)	17 (38)	18 (22)
Peripheral	12 (34)	11 (27)	8 (33)	5 (24)	16 (36)	28 (35)
Casual[A]	10 (29)	14 (34)	6(25)	5(24)	12(26)	35 (43)
Total	35	41	24	21	45	81
Raptors	6	5	2	0	6	–
Total species	41	46	26	21	51	81

[A]Includes species not recorded by Cody (1994).

in 2002 compared with 38% at Hamilton Downs and 22% of Cody's counts (Table 1). Peripheral species in WA comprised 27–34% of species in 1999 and 24–33% in 2002 compared with 36% at Hamilton Downs and 35% for on Cody's sites (Table 1).

Unlike Cody (1994), where core species accounted for 75% of total bird numbers, the most abundant birds at Gascoyne Junction and Mount Magnet in 1999 were species listed by Cody as peripheral or casual: black-faced woodswallow, budgerigar, crimson chat, white-winged triller, and zebra finch (see Appendix 1 for scientific names). Each of these species numbered in the hundreds at Gascoyne Junction and formed large mixed foraging flocks (Davis and Recher 2002). All are dispersive (migratory and/or nomadic) *sensu* Gilmore *et al.* (2007). Of Cody's core species, the most abundant in 1999 at Gascoyne Junction and Mount Magnet were chestnut-rumped thornbill, red-capped robin, rufous whistler, southern whiteface, splendid wren, and white-browed babbler. Birds were less abundant in 2002 at Gascoyne Junction and Mount Magnet and there were fewer species (see table 1 in Recher and Davis 2018 for details).

At Hamilton Downs, the most abundant species (100–1000 individuals), as on the WA sites in 1999, were dispersive: budgerigar, crimson chat, diamond dove, rufous whistler, southern whiteface, and zebra finch (adapted from Recher and Davis 1997). These were followed in abundance (10–100 individuals) by black-faced cuckoo-shrike, black-faced woodswallow, red-capped robin, and splendid wren, of which the cuckoo-shrike and woodswallow are nomadic. Only diamond dove, red-capped robin, rufous whistler, and southern whiteface were among Cody's core species. At Hamilton Downs, the rufous whistler was migratory, with large numbers of individuals passing through (author's obs.).

Foraging guilds

Among the three locations (Hamilton Downs, Gascoyne Junction, and Mount Magnet) there were 34 species with sufficient

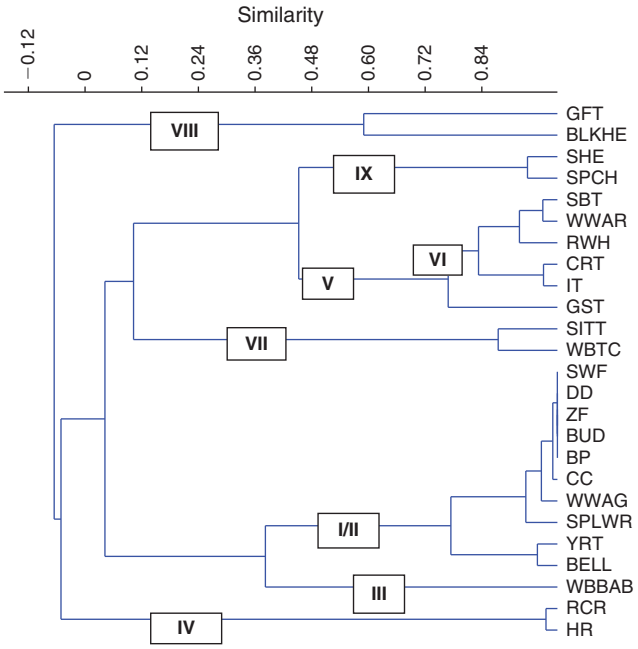

Fig. 1. Foraging guilds of mulga birds at Hamilton Downs Station, Northern Territory, in 1995 (adapted from Recher and Davis 1997), based on percentage of manoeuvre/substrate categories using Correlation Analysis (cophenetic correlation coefficient (coph. corr.) = 0.9243). Guilds are numbered (I–IX) following those presented in Table 2. Species abbreviations are also given in Table 2.

foraging observations for analysis; data for five species (diamond dove, black-capped sittella, grey shrike-thrush, inland thornbill, and white-browed treecreeper) were restricted to Hamilton Downs; three species (pied butcherbird, redthroat, and variegated wren) were restricted to Gascoyne Junction, and three species (black-faced cuckoo-shrike, grey butcherbird, and Port Lincoln parrot) to Mount Magnet. In addition to the species found only at Gascoyne Junction or Mount Magnet, black-faced woodswallow, white-winged triller, and yellow-throated miner were not present at Hamilton Downs.

Cluster analyses of the foraging data from Hamilton Downs and WA identified nine guilds based on manoeuvres and substrates (Figs 1–5). The guilds identified by CA were used to construct Table 2, in which species are placed in guilds based on the proportions of the different foraging manoeuvres and substrates used at each location and year.

All nine guilds were represented at Hamilton Downs in 1995 and at Gascoyne Junction and Mount Magnet in 1999 (Table 2; Figs 1–3). Six guilds were represented at Gascoyne Junction in 2002 and seven at Mount Magnet (Table 2; Figs 4–5). Of the 23 species common to two or more locations, singing honeyeater, western warbler, and willie wagtail were placed in a different guild at Hamilton Downs from either Gascoyne Junction or Mount Magnet (Table 2). Of the 16 species common to Gascoyne Junction and Mount Magnet in either 1999 or 2002, seven species (grey-crowned babbler, red-capped robin, spiny-cheeked honeyeater, splendid wren, white-winged triller, willie wagtail, and yellow-throated miner) were placed in one or more guilds that differed between locations (Table 2).

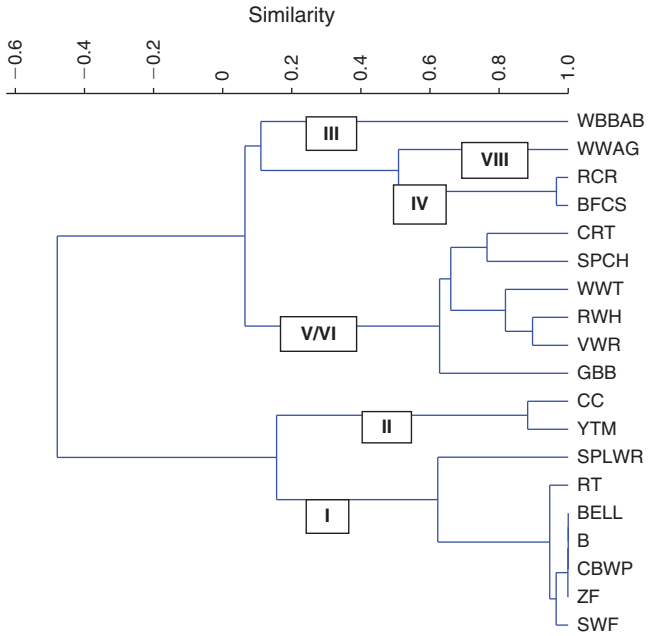

Fig. 2. Foraging guilds of mulga birds at Gascoyne Junction in 1999 based on percentage of manoeuvre/substrate categories using Correlation Analysis (coph. corr. = 0.9014). Guilds are numbered (I–IX) following those presented in Table 2. Species abbreviations are also given in Table 2.

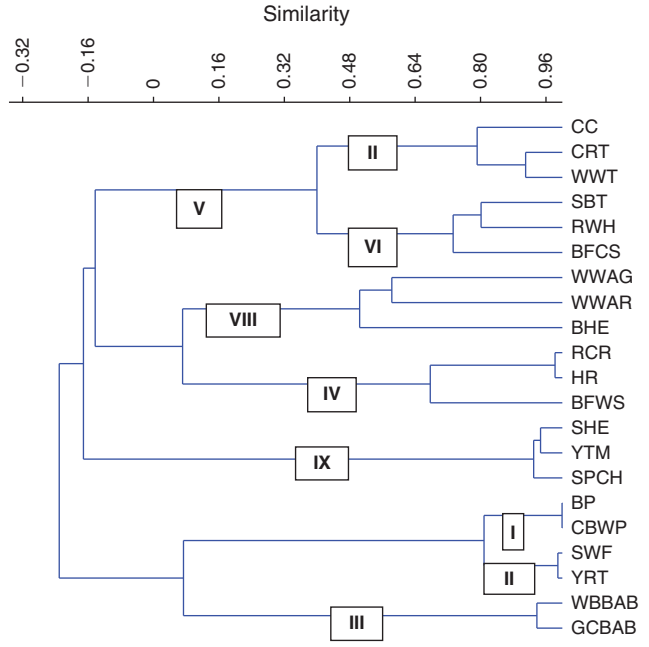

Fig. 3. Foraging guilds of mulga birds at Mount Magnet in 1999 based on percentage of manoeuvre/substrate categories using Correlation Analysis (coph. corr. = 0.8502). Guilds are numbered (I–IX) following those presented in Table 2. Species abbreviations are also given in Table 2.

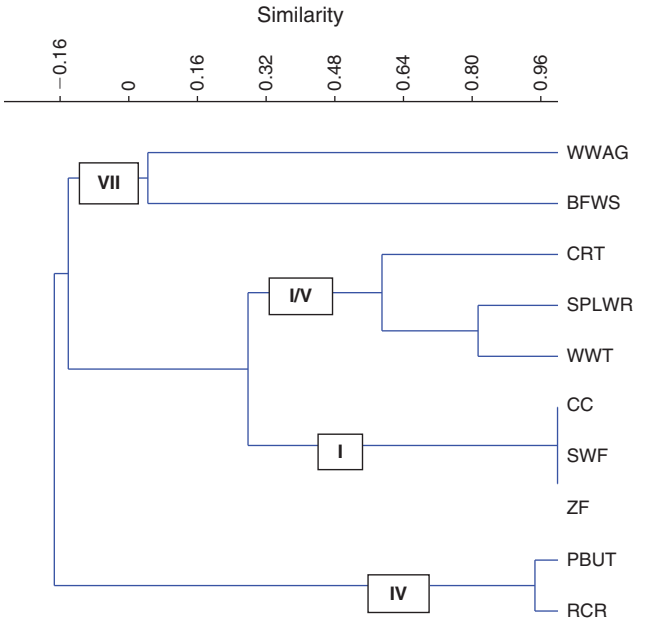

Fig. 4. Foraging guilds of mulga birds at Gascoyne Junction in 2002 based on percentage of manoeuvre/substrate categories using Correlation Analysis (coph. corr. = 0.8941). Guilds are numbered (I–IX) following those presented in Table 2. Species abbreviations are also given in Table 2.

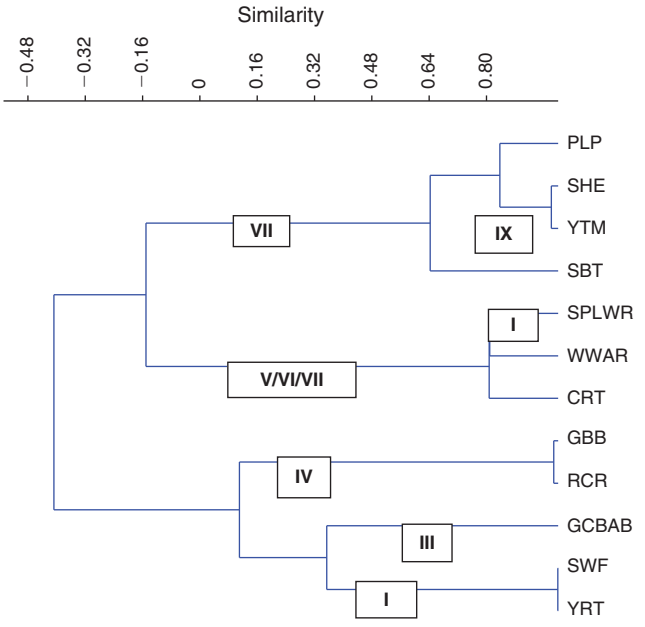

Fig. 5. Foraging guilds of mulga birds at Mount Magnet in 2002 based on percentage of manoeuvre/substrate categories using Correlation Analysis (coph. corr. = 0.9195). Guilds are numbered (I–IX) following those presented in Table 2. Species abbreviations are also given in Table 2.

Most species used a broad range of foraging manoeuvres and substrates and were best assigned to two or more guilds. At Hamilton Downs, 13 of the 25 species for which there were adequate data for analysis were assigned to multiple guilds (Table 2). In 1999, 11 of 19 species at Gascoyne Junction were placed in multiple guilds and 10 of 21 at Mount Magnet. In 2002, four of 10 species at Gascoyne Junction and four of 13 at Mount Magnet were placed in multiple guilds. At Gascoyne Junction in

Table 2. Foraging guilds at Hamilton Downs in the Northern Territory in 1995 (adapted from Recher and Davis 1997), and in Western Australia at Gascoyne Junction and Mount Magnet in 1999 and 2002

Guilds are based on cluster analysis using combined manoeuvre/substrate observations. Species may be assigned to two or more guilds depending on the percentage of different manoeuvre/substrate observations. Species are black honeyeater (BHE), black-capped sittella (BCSITT), black-faced cuckoo-shrike (BFCS), black-faced woodswallow (BFWS), Bourke's parrot (BP), budgerigar (BUD), chestnut-rumped thornbill (CRT), common bronzewing pigeon (CBWP), crested bellbird (BELL), crimson chat (CC), diamond dove (DD), grey butcherbird (GBB), grey fantail (GFT), grey-crowned babbler (GCBAB), grey shrike-thrush (GST), hooded robin (HR), inland thornbill (IT), pied butcherbird (PBB), Port Lincoln parrot (PLP), red-capped robin (RCR), redthroat (RT), rufous whistler (RWH), singing honeyeater (SHE), slaty-backed thornbill (SBT), southern whiteface (SWF), splendid wren (SPLWR), spiny-cheeked honeyeater (SPCHE), variegated wren (VWR), western warbler (WWAR), white-browed babbler (WBBAB), white-browed treecreeper (WBTC), willie wagtail (WWAG), yellow-throated miner (YTM), yellow-rumped thornbill (YRT), zebra finch (ZF). Species shown in bold are those found in multiple guilds for that location and year, and those with an asterisk (*) are species represented in a different guild from previous years

	Manoeuvre/Substrate								
	Ground				Foliage		Bark/Wood	Aerial	Nectar
	Glean		Probe	Pounce	Glean	Snatch/Hover	Glean/Probe	Hawk/Sweep	Probe
Guilds	Ground I	Foliage/Seed II	III	IV	V	VI	VII	VIII	IX
Hamilton Downs	**BELL, WWAG CC, SPLWR YRT** ZF, SWF BP, DD	**BELL CC, SPLWR** BUD	**WBBAB**	RCR HR	**RWH, SBT CRT, IT SHE, SPCHE YRT** WWAR, GST	**RWH, SBT CRT, IT**	**CRT, WBBAB** BCSITT, WBTC	**BHE, WWAG** GFT	**BHE, SHE SPCHE**
Gascoyne Junction 1999	**CC** ZF, SWF CBWP, RT BELL	**CC, SPLWR YTM, WWT** GCBAB, BUD	**WBBAB**	**BFWS**, **GBB** RCR	**CRT, VWR GBB, RWH SPLWR, YTM SPCHE**	**CRT, VWR GBB, RWH WWT**	**SPCHE, WBBAB**	**BFWS** WWAG	**SPCHE**
Gascoyne Junction 2002	**WWT*, SPLWR*** CC, ZF SWF	**WWT**		**RCR** PBUT	**CRT SPLWR**	**CRT, RCR***		WWAG, BFWS	
Mount Magnet 1999	**SWF, YRT WBBAB** CBWP, BP CC	**SWF, YRT WWT** CRT	**WBBAB** GCBAB	**BFWS, WWT** RCR, HR	**SBT, RWH WWAG** BFCS	**RWH, WWAR SBT**	**RWH, WWAR** WWT	**BHE, WWAG BFWS** YTM	**BHE** SHE, SPCHE
Mount Magnet 2002	**SPLWR** YRT, SWF		**GCBAB**	RCR, GBB	**SPLWR**	WWAR	**SHE*, YTM* GCBAB*** SBT*, CRT* PLP		**SHE, YTM***

2002, three species were assigned to guilds different from 1999 and at Mount Magnet five species were placed in different guilds (Table 2).

Ground-foraging guilds had the greatest number of species (and individuals) at Hamilton Downs and in WA in 1999 (Table 2; Figs 1–3). The most abundant and species-rich ground-foraging guild at all sites and years was ground gleaners. Ground foliage gleaners and seed eaters were also abundant at Hamilton Downs and at Gascoyne Junction and Mount Magnet in 1999. Seed-eaters were abundant at Gascoyne Junction in 1999, but absent (e.g. budgerigar, little button quail) or present in reduced numbers (e.g. diamond dove, zebra finch) in 2002 (Table 2). The only ground foliage gleaner at Gascoyne Junction in 2002 was the white-winged triller; the guild was absent at Mount Magnet in 2002. Babblers represented ground probers at all locations and years; white-browed babblers were found at Hamilton Downs, and at Gascoyne Junction and Mount Magnet in 1999, but absent from Gascoyne Junction and Mount Magnet in 2002. In 1999, white-browed babblers were part of the ground gleaner and prober guilds (Table 2). Grey-crowned babblers were present both years at Mount Magnet, but absent from Gascoyne Junction in 2002. In 1999, at Gascoyne Junction they were ground foliage gleaners. Babblers were also prominent as bark and wood probers, with white-browed babblers included in this guild at Hamilton Downs and at Gascoyne Junction in 1999. Grey-crowned babblers were ground and bark/wood probers at Mount Magnet in 2002 and ground probers in 1999 (Table 2).

In WA, five species of ground pouncers were recorded between the sites; red-capped robin was ubiquitous. Black-faced woodswallows at Gascoyne Junction and Mount Magnet in 1999 were included in the ground-pouncing guild, but also formed part of the aerial foraging guild at both locations as hawkers (Table 2). Black-faced woodswallows were found at both locations in 2002, but were uncommon at Mount Magnet and insufficient data were obtained for analysis. In 2002, woodswallows were aerial sweepers at Gascoyne Junction (Table 2). Hooded robins were present at Hamilton Downs and at Mount Magnet in 1999 and included in the ground pouncing guild. They were not observed at Gascoyne Junction in either year and were absent from Mount Magnet in 2002. Grey butcherbirds formed part of the ground-pouncing, foliage gleaning, and foliage snatching/hovering guilds at Gascoyne Junction in 1999. They were absent at Mount Magnet in 1999, but were ground pouncers in 2002 (Table 2). Pied butcherbirds were present at Gascoyne Junction in 2002 as ground pouncers, but were otherwise absent. Woodswallows and butcherbirds were not recorded at Hamilton Downs.

The second most species-rich and abundant guilds were foliage foragers (Table 2). Foliage gleaners, including chestnut-rumped, inland and slaty-backed thornbills, and splendid and variegated wrens, were also part of the foliage snatcher/hover guild (Table 2). The wrens were also ground gleaners. Black-capped sittella and white-browed treecreeper are specialised bark/wood gleaners and probers and were found only at Hamilton Downs. Other bark and wood foragers were primarily foliage gleaners and snatchers (chestnut-rumped thornbill, rufous whistler, white-winged triller) or ground foragers (grey-crowned and white-browed babblers) (Table 2).

Within the aerial-foraging guild the grey fantail was a specialised aerial forager at Hamilton Downs, although the black honeyeater, a nectar-feeder, took arthropods from the air, as did black-faced woodswallow and willie wagtail, which were otherwise grouped within the ground-foraging guild (Table 2). Western warbler was a foliage-gleaner at Hamilton Downs and a foliage-snatcher/hoverer at Mount Magnet in 1999 and 2002, but was also included in the aerial-foraging guild at Mount Magnet in 1999 (Table 2).

In 1999, the nectar-feeder guild was represented at Gascoyne Junction by the spiny-cheeked honeyeater, which was not abundant (12 foraging observations). In 1999, the nectar-feeding guild at Mount Magnet was represented by three species, all of which were relatively abundant (35–70 observations). There were three species of nectar-feeders at Hamilton Downs, with spiny-cheeked and singing honeyeaters relatively abundant (53 and 73 observations respectively: Recher and Davis 1997). Among the nectar-feeders, singing and spiny-cheeked honeyeaters and yellow-throated miners took arthropods by gleaning from foliage and bark, and were grouped in those guilds, with the black honeyeater in the aerial-foraging guild.

In 2002, nectar-feeding, ground probing, and bark/wood gleaning/probing guilds were absent at Gascoyne Junction, and there were fewer ground and foliage-foragers (Table 2; Figs 4, 5). There were fewer ground-, foliage-, and nectar-foragers and no aerial-foragers at Mount Magnet in 2002. The only guild to increase in abundance and richness in 2002 was the bark/wood gleaner/prober guild at Mount Magnet.

Changes in foraging behaviour and foraging substrates between 1999 and 2002 at Gascoyne Junction and Mount Magnet resulted in species being assigned to different guilds. At Gascoyne Junction, black-faced woodswallow shifted from ground-pouncing in 1999 to aerial-foraging in 2002, while white-winged triller moved from being a foliage snatcher/hoverer to gleaning ground vegetation. Red-capped robin continued to ground pounce in 2002, but did more foliage foraging (Table 2). In 2002 at Mount Magnet, chestnut-rumped and slaty-backed thornbills did more bark-foraging, as did grey-crowned babbler, singing honeyeater, and yellow-throated miner.

Discussion

The large number of species in common between Cody's (1994) plots and those in WA and Hamilton Downs supports Cody's (1994) conclusion of a broad consistency in mulga bird communities across Australia. Pavey and Nano (2009) reached similar conclusions. They surveyed birds on 197 sites in arid Australia, with 40 sites described as mulga. Using CA, Pavey and Nano (2009) identified nine species as diagnostic of mulga. Of these, seven were listed by Cody (1994) as core species and two as peripheral to mulga. All nine species were recorded on the Gascoyne Junction plot, eight on the Mount Magnet plots, and seven at Hamilton Downs in the NT (Recher and Davis 1997, 2018).

Of the 90 species of non-raptors recorded in mulga habitats by Recher and Davis (1997, 2018) and Cody (1994), 52 were in common. This includes 39 of the 46 species that Cody (1994) considered to be core or peripheral to mulga. Excluding from Cody's counts 14 species dependent on eucalypts (e.g. weebill, striated pardalote, brown-headed and white-eared honeyeater: Recher and Davis 1997, 1998, 2002) or the nectar-rich flora

associated with eucalypts (e.g. little and noisy friarbirds, brown honeyeater: author's obs.) the percentage of species in common increases from 58% to 68%.

Despite the apparent consistency of mulga bird communities, species assemblages differ between locations and seasons with rainfall, vegetative structure, floristics, and time since fire (Burbidge and Fuller 2007; Leavesley 2008; Tischler *et al.* 2013; Bell *et al.* 2014; Turpin and Johnstone 2017). Additionally, the composition of mulga bird communities is strongly influenced by resource pulses driven by rainfall (Mac Nally *et al.* 2004; Burbidge and Fuller 2007; Recher and Davis 2018). Confirming Cody's (1994) findings, Pavey and Nano (2009) found predictable assemblages of bird species in mulga and other semiarid habitats in inland Australia. They attributed this to the consistency within habitats of vegetation structure and floristics. Their interpretation was that structure and specific plant species provided the nesting and foraging resources required by birds so that species segregated by habitat creating unique assemblages in each vegetation type. These separate observations and conclusions are not contradictory, but reinforce observations on the variability of arid-zone and mulga bird communities across habitats and in space and time as determined by stochastic environmental factors, such as rainfall and disturbance history.

On her study area in arid north-western New South Wales, Smith (2015) also found distinct assemblages of bird species in different habitats, and over the four years of her study she recorded temporal differences in assemblages related to rainfall and the availability of food resources. The differences in species assemblages at Gascoyne Junction and Mount Magnet between 1999 and 2002 and those recorded by Smith (2015) are correlated with rainfall and can largely, but not entirely, be attributed to the movements of migrants and food nomads. Throughout arid and semiarid Australia the abundances and number of bird species are affected by rainfall, with numbers of resident and dispersive species increasing after rain and decreasing with drought (Keast 1968; Davies 1983; Paltridge and Southgate 2001; Burbidge and Fuller 2007; Tischler *et al.* 2013; Recher and Davis 2014, 2018; Smith 2015). As noted by Tischler *et al.* (2013), arid-zone bird communities are temporally dynamic assemblages, with a high proportion of dispersive species.

The number of species in mulga that are migratory or food nomads is substantial and these include species, such as budgerigar, crimson chat, white-winged triller, and zebra finch, that are frequently the most abundant birds when conditions are favourable (author's obs.). Chan (2001) estimated that ~40% of Australian land birds are migratory, with many of these being 'partial migrants' having both migrant and resident individuals. Smith (2015) classified 35% of the birds on her plots as nomads and 13% as migrants. Of the 60 species recorded on the WA plots, 24 (40%), including the seven raptors, were dispersive (author's obs.). At Hamilton Downs, 25 of 51 (49%) species were dispersive. The presence of food nomads at Gascoyne Junction and Mount Magnet during drought in 2002 when there were few birds relative to the same plots in 1999 suggests that nomads, like migratory species (Chan 2001), include individuals that respond differently to conditions or move independently of other individuals within the population.

Foraging behaviour and guilds

I tested the hypotheses that 'there are no differences in the foraging behaviour and guilds of mulga birds between locations and seasons'. It is important to test these hypotheses as details of the foraging resources required by birds and how these differ through space and time are important in the formulation of plans for conservation management and evaluating the adequacy of Australia's conservation reserve system.

The foraging behaviour and guilds of birds at Hamilton Downs, Gascoyne Junction, and Mount Magnet were broadly similar, but differed between locations and years according to habitat structure, floristics, and the kinds and abundances of food resources (Recher and Davis 2018). The same nine guilds described the three locations, with differences in the numbers of guilds appearing only with less rainfall at Gascoyne Junction and Mount Magnet. Apart from some ground-foragers (mainly ground-gleaners) most birds have a wide repertoire of foraging behaviours using different foraging manoeuvres and exploiting different plant species, foraging substrates and foraging at different heights according to the food resources available (Recher *et al.* 1985, 2016; Recher 1989*a*, 1989*b*; Recher and Majer 1994; Recher and Davis 1997, 1998, 2002, 2018; Wilson and Recher 2001). A result is that it is difficult to consistently assign species to specific foraging guilds, as illustrated by Table 2. Although the same species occurred in the same guilds at Hamilton Downs, Gascoyne Junction, and Mount Magnet, some species were grouped in multiple guilds and/or were placed in different guilds as food resources, and consequently foraging behaviour, changed between locations and years.

Conservation

Although there is a core similarity to mulga habitats and the mulga avifauna across Australia (Cody 1994; Pavey and Nano 2009), the dependence of nomadic and migratory mulga birds on a complex mosaic of habitats within which food resources change in type and abundance seasonally and between years emphasises the importance of a new approach to Australia's conservation reserve system (Runge *et al.* 2015; Runge and Tulloch 2017).

Despite the extensive movements in tracking food resources and their variable distribution in time, dispersive species have specific habitat requirements tied to their food resource requirements (Pavey and Nano 2009; Tischler *et al.* 2013; Smith 2015). The complexity of the resource requirements of dispersive species argues against relying on the traditional system of static conservation reserves for their conservation (Woinarski *et al.* 2014; Runge *et al.* 2015; Runge and Tulloch 2017). In an era of accelerating climate change, it is not acceptable to set aside areas of habitat as reserves and assume the biota will persist in the long term. The conservation of dispersive species and mulga birds requires a whole-of-landscape approach, including the establishment of conservation reserves, and the adoption of sustainable pastoral management. Current pastoral management practices coupled with the proliferation of feral herbivores (e.g. goats, camels, donkeys) are continuing the degradation of Australia's arid and semiarid lands across the continent begun with the arrival of Europeans and their sheep and cattle. A core requirement to reverse this process of degradation and the loss of

biodiversity is the creation of defined linkages across the continent such as envisioned in the American Wildlands Project and the Australian concept of WildCountry (Recher 2003). The conservation of Australia's flora and fauna demands integrated management of the landscape on a continental scale irrespective of land tenure. Anything less will see the continuing decline of the continent's biota and the loss of mulga as a keystone habitat.

Conflicts of interest

The author declares no conflicts of interest.

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Appendix 1. Mulga birds recorded in the Gascoyne (GJ) and Murchison (MM) Bioregions in 1999 and 2002, on Hamilton Downs Station, NT (HD) in 1997, and by Cody (1994) on 20 sites in mulga woodlands

Species are ordered according to Cody's (1994) categories based on frequency of occurrence in his counts. Species not recorded by Cody are shown, along with raptors, which Cody did not record. The presence of a species is shown by 1, its absence by 0

		GJ 1999	MM 1999	GJ 2002	MM 2002	HD	Cody
Core species							
Australian raven	*Corvus coronoides*	0	1	0	0	0	1
Chestnut-rumped thornbill	*Acanthiza uropygialis*	1	1	1	1	1	1
Crested bellbird	*Oreoica gutturalis*	1	1	1	1	1	1
Diamond dove	*Geopelia cuneata*	1	1	1	0	1	1
Galah	*Eolophus roseicapillus*	1	1	0	0	1	1
Grey shrike-thrush	*Colluricincla harmonica*	1	1	1	1	1	1
Inland thornbill	*Acanthiza apicalis*	0	0	0	0	1	1
Little crow	*Corvus bennetti*	1	1	0	1	1	1
Red-capped robin	*Petroica goodenovii*	1	1	1	1	1	1
Rufous whistler	*Pachycephala rufiventris*	1	1	1	1	1	1
Singing honeyeater	*Lichenostomus virescens*	0	1	0	1	1	1
Southern whiteface	*Aphelocephala leucopsis*	1	1	1	1	1	1
Spiny-cheeked honeyeater	*Acanthagenys rufogularis*	1	1	1	1	1	1
Splendid wren	*Malurus splendens*	1	1	1	0	1	1
Western warbler	*Gerygone fusca*	0	1	0	1	1	1
White-browed babbler	*Pomatostomus superciliosus*	1	1	0	0	1	1
Willie wagtail	*Rhipidura leucophrys*	1	1	1	0	1	1
Yellow-rumped thornbill	*Acanthiza chrysorrhoa*	0	0	0	1	1	1
Total		13	16	10	11	17	18
Peripheral species							
Apostlebird	*Struthidea cinerea*	0	0	0	0	0	1
Black-faced cuckooshrike	*Coracina novaehollandiae*	1	1	1	0	1	1
Black-faced woodswallow	*Artamus cinereus*	1	1	1	1	1	1
Brown honeyeater	*Lichmera indistincia*	0	0	0	0	1	1
Budgerigar	*Melopsittacus undulatus*	1	1	0	0	1	1
Buff-rumped thornbill	*Acanthiza reguloides*	0	0	0	0	0	1
Common bronzewing pigeon	*Phaps chalcoptera*	1	0	0	0	1	1
Crested pigeon	*Ocyphaps lophotes*	1	1	0	0	1	1
Grey butcherbird	*Cracticus torquatus*	1	1	0	1	0	1
Grey fantail	*Rhipidura fuliginosa*	0	0	0	0	1	1
Hooded robin	*Melanodryas cucullata*	0	1	0	0	1	1
Horsfield bronze cuckoo	*Chrysococcyx basalis*	1	1	1	0	1	1
Jacky winter	*Microeca leucophaea*	0	0	0	0	0	1
Laughing kookaburra	*Dacelo gigas*	0	0	0	0	0	1
Mistletoe bird	*Dicaeum hirundinaceum*	0	0	0	0	1	1
Mulga parrot	*Psephotus varius*	0	1	0	0	1	1
Pallid cuckoo	*Cuculus pallidus*	0	1	1	0	1	1
Pied butcherbird	*Cracticus nigrogularis*	0	1	1	1	1	1
Rainbow bee-eater	*Merops ornatus*	1	0	0	0	0	1
Redthroat	*Pyrrholaemus brunneus*	1	0	0	0	0	1
Slaty-backed thornbill	*Acanthiza robustirostris*	0	0	0	1	1	1
Striated pardalote	*Pardalotus striatus*	0	0	0	0	0	1
Striped honeyeater	*Plectorhyncha lanceolata*	0	0	0	0	0	1
Weebill	*Smicrornis brevirostris*	0	0	0	0	0	1
White-browed treecreeper	*Climacteris affinis*	0	0	0	0	1	1
White-fronted honeyeater	*Purnella albifrons*	1	0	1	0	0	1
Yellow-throated miner	*Manorina flavigula*	1	1	1	1	0	1
Zebra finch	*Taeniopygia guttata*	1	0	1	0	1	1
Total		12	11	8	5	16	28
Casual species							
Australian magpie	*Cracticus tibicen*	0	1	0	1	0	1
Bar-shouldered dove	*Geopelia humeralis*	0	0	0	0	0	1
Black-capped sittella	*Neositta pileata*	0	0	0	0	1	1
Bourke's parrot	*Neopsephotus bourkii*	0	1	0	0	1	1
Brown-headed honeyeater	*Melithreptus brevirostris*	0	0	0	0	0	1
Chestnut-crowned babbler	*Pomatostomus ruficeps*	0	0	0	0	0	1

(*Continued*)

Appendix 1. (Continued)

		GJ 1999	MM 1999	GJ 2002	MM 2002	HD	Cody
Cinnamon quailthrush	*Cinclosoma cinnamomeum*	0	0	0	0	0	1
Cockatiel	*Nymphicus hollandicus*	0	1	0	0	0	1
Crimson chat	*Epthianura tricolor*	1	1	1	0	1	1
Emu	*Dromaius novaehollandiae*	1	1	1	0	0	1
Grey-crowned babbler	*Pomatostomus temporalis*	0	1	0	1	0	1
Grey-fronted honeyeater	*Lichenostomus keartlandi*	0	0	0	0	1	1
Hall's babbler	*Pomatostomus halli*	0	0	0	0	0	1
Little button quail	*Turnix velox*	1	0	0	0	1	1
Little friarbird	*Philemon citreogularis*	0	0	0	0	0	1
Mallee ringneck	*Barnardius barnardi*	0	0	0	0	0	1
Noisy friarbird	*Philemon corniculatus*	0	0	0	0	0	1
Noisy miner	*Manorina melanocephala*	0	0	0	0	0	1
Olive-backed oriole	*Oriolus sagitattus*	0	0	0	0	0	1
Painted honeyeater	*Grantiella picta*	0	0	0	0	0	1
Port Lincoln parrot	*Barnardius zonarius*	1	0	0	1	1	1
Red-backed kingfisher	*Todiramphus pyrrhopygius*	0	1	0	0	0	1
Red-winged parrot	*Aproscmictus erythropterus*	0	0	0	0	0	1
Rufous songlark	*Cinclorahamphus mathewsi*	0	0	0	0	0	1
Sacred kingfisher	*Halcyon sancta*	0	0	0	0	0	1
Silvereye	*Zosterops lateralis*	0	0	0	0	0	1
Southern scrubrobin	*Drymodes brunneopygia*	0	0	0	0	0	1
Variegated wren	*Malurus lamberti*	1	0	1	0	0	1
Wedgebill	*Psophodes cristatus*	0	0	0	0	0	1
White-browed woodswallow	*Artamus superciliosus*	0	0	0	0	0	1
White-eared honeyeater	*Lichenostomus leucotis*	0	0	0	0	0	1
White-plumed honeyeater	*Meliphaga penicillatus*	0	0	0	0	1	1
White-winged chough	*Corcorax melanorhamphos*	0	0	0	0	0	1
White-winged triller	*Lalage sueurii*	1	1	1	0	1	1
Yellow thornbill	*Acanthiza nana*	0	0	0	0	0	1
Total		6	8	4	3	8	35
Species not recorded by Cody (1994)							
Australasian pipit	*Anthus novaeseelandiae*	0	1	0	0	1	0
Australian bustard	*Ardeotis australis*	1	0	0	0	0	0
Black honeyeater	*Sugomel niger*	0	1	0	0	1	0
Black-eared cuckoo	*Chrysococcyx osculens*	1	1	1	1	0	0
Little corella	*Cacatua sanguinea*	1	0	0	0	0	0
Magpie lark	*Grallina cyanoleuca*	0	1	0	0	1	0
Major Mitchell cockatoo	*Cacatua leadbeateri*	0	0	0	0	1	0
Pied honeyeater	*Certhionyx variegatus*	0	1	1	0	0	0
Torresian crow	*Corvus orru*	1	1	0	1	0	0
Total		4	6	2	2	4	0
Raptors							
Brown falcon	*Falco berigora*	1	1	1	0	1	0
Brown goshawk	*Accipter fasciatus*	0	1	0	0	1	0
Black kite	*Milvus migrans*	0	0	0	0	1	0
Collared sparrowhawk	*Accipiter cirrocephalus*	1	0	0	0	0	0
Little eagle	*Hieraaetus morphnoides*	1	1	1	0	0	0
Little falcon	*Falco longipennis*	1	0	0	0	0	0
Nankeen kestrel	*Falco cenchroides*	1	1	0	0	1	0
Wedge-tailed eagle	*Aquila audax*	1	1	0	0	1	0
Whistling kite	*Haliastur sphenurus*	0	0	0	0	1	0
Total		6	5	2	0	6	0
Total species		41	46	26	21	51	81