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Assessment of avian site fidelity in arid *Acacia* shrubland based on a ten-year mark-recapture study in central Australia

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Mark-recapture surveys of bird communities were conducted at five *Acacia* shrubland sites near Alice Springs, central Australia, between 2001 and 2011. The primary objective was to examine the levels of site fidelity displayed by individuals to provide insight into local bird community dynamics that cannot be ascertained by visual surveying. Approximately 1800 birds from 50 species were banded and over 150 individuals were recaptured. Results for the 27 species whose members were captured and banded 10 or more times are reported and assessed for evidence of site fidelity. Eleven species were classified as sedentary based on relatively high recapture rates and individuals being recaptured over long time periods. Species with the highest rates of recapture and with individuals persisting at sites for many years included the Splendid Fairy-wren *Malurus splendens*, Redthroat *Pyrrolaemus brunneus* and Chestnut-rumped Thornbill *Acanthiza uropygialis*. The results provide new evidence of high site fidelity for a suite of species associated with *Acacia* shrubland habitat in central Australia. Conclusions about which species are sedentary and which are mobile are broadly consistent with those of previous studies in this habitat based on visual surveys and with banding data from other regions, but with some new insights being gained.

INTRODUCTION

Rainfall is a dominant driver of arid ecosystems (Noy-Meir 1973; Morton *et a*l. 2011) and in the central Australian arid-zone the amount and timing of rain that falls in a year varies to a much greater extent than in many other environments (Chesson *et al*. 2004; Van Etten 2009). The availability of water is a major influence on primary productivity in this system and can determine flowering, new growth and seeding of the standing vegetation at a particular time (Bailey *et al*. 2004), thereby directly influencing the availability of food resources for nectarivorous and granivorous birds. The increase in plant-based resources also leads to increased local abundance and richness of invertebrate populations, increasing the food resources available for insectivores. The timing of high rainfall 'boom' periods is variable, and overlayed on background seasonal weather patterns which, to varying degrees, stimulate cycles of growth and senescence and flowering and fruiting in plants, and determine the life cycles and activity of invertebrates. Furthermore, the spatial distribution of rainfall can be patchy at both small and large scales, stimulating high levels of productivity in local areas while other nearby areas remain dry. This spatial variability in the resources is, in turn, overlayed on a background of distinct vegetation communities which provide a suite of distinctive habitats and are therefore associated with characteristic faunal assemblages.

In the Australian arid-zone, abundance and species richness of bird assemblages can change markedly in response to rainfall (Paltridge and Southgate 2001; Burbidge and Fuller 2007), whilst foraging assemblages also vary spatially with the dominant vegetation type (Davis and Recher 2002). Mac Nally *et al*. (2004) suggest that there is a high level of dynamism and temporal variation in rangeland bird communities compared with those in higher rainfall areas because resources are less predictable. It follows that in an environment where food resources are highly variable in space and time, the majority of bird species should be nomadic to some extent at least, but this appears not to be the case (Shurcliff 1980).

Cody (1994) found that a stable and similar suite of bird species was regularly present in Mulga *Acacia aneura* woodland at sites across Australia, suggesting that the general resources available in this habitat can support relatively stable bird assemblages. Casual or peripheral species (i.e. those that are present sometimes or rarely), although making up a large proportion of the species present in this habitat at a given time, made up a very small component of the community in terms of density (Cody 1994). Pavey and Nano (2009), using a space-for-time approach, also found distinctive bird assemblages in the vegetation types present in the Finke bioregion of central Australia. Their study was carried out during a 'boom' period, but it still found structure in bird assemblages across vegetation types.

Current understanding of the dynamics of bird communities in the Australian arid zone and how they respond to temporal variation in resource availability is based mainly on visual survey data, and surveys are often restricted to a few days at any location. These types of surveys are generally limited to identifying species composition and estimates of relative abundance, and it is not possible to determine whether the same individuals are present from one survey to the next. In contrast, mark-recapture methods provide an opportunity to establish directly whether individual birds remain resident in particular areas, and for how long, hence providing valuable information about whether birds are resident or nomadic that is complementary to the findings of visual surveys (Leishman 2000).

The degree to which individuals can remain in an area over a long period of time (i.e. the level of site fidelity) indicates the extent to which an animal is able to survive using the resources in a limited area, rendering it unnecessary to move to another part of a landscape (Giuggioli and Bartumeus 2012). Banding, like any mark-recapture technique, has limitations; a territorial shift by an individual of mere metres may result in it never being caught again. Nevertheless, long-term banding studies can identify species that display a high level of site fidelity and, conversely, those that do not appear to be sedentary (e.g. Leishman 2000; Frith and Frith 2005).

The primary aim of this study was to gather evidence through mark-recapture surveys, specifically the rate of recapture of individuals and the length of time between recaptures, to support or refute current knowledge about site fidelity of bird species associated with *Acacia* shrubland communities in central Australia.

METHODS

Data were collected at two locations in two distinct time periods. During the first period from 2001 to 2003, banding was undertaken at three sites in the Alice Valley between the Hugh River and Ellery Creek, within the Tjoritja (West MacDonnell) National Park, approximately 60 to 90 km west of Alice Springs. Sites were named after nearby topographical or man-made features: Cummings Yard (23º42'38.32"S; 133º03'38.32"E), Ryan's Dam (23º46'33.97"S; 133º 11'43.5"E) and Hugh River (23º46'33.97"S; 133º19'35.44"E). During the second period from 2008 to 2011, birds were banded at two sites on the western and eastern sides of the Alice Springs Desert Park: Alice Springs Desert Park West (23º42'22.21"S; 133º49'40.75"E.) and Alice Springs Desert Park East (23º42'34.11"S; 133º50'25.21"E.), approximately 5 km apart. All sites were within the broader area of the West MacDonnell Ranges.

Study site habitat

The habitat at all sites was *Acacia* shrubland dominated by Mulga and Witchetty Bush *A. kempeana*. Scattered trees at the banding sites included Bloodwood *Corymbia opaca* and Long-leafed and Fork-leafed Corkwoods *Hakea longifolia* and *divaricata*, and *Eremophila* and *Senna* species were occasionally present in the understorey. The ground cover was composed primarily of native and introduced grasses, with introduced Buffel Grass *Cenchrus ciliaris* being present at all sites. Specific banding sites were chosen for apparent uniformity of habitat and ease of access for equipment. To our knowledge there were no sources of water close to any of the banding sites, except for the Ryan's dam site which was approximately 200m from an old farm dam that occasionally held water.

Climatic conditions at all sites were similar, with mean maximum daily temperatures ranging between 19.7^{o}C and 22.7^{o}C in winter and 35.1^{o}C and 36.3^{o}C in summer. Mean minimum temperatures were between 4^{o}C and 6^{o}C in winter and 20.3^{o}C and 21.5^{o}C in summer. Most banding was conducted in the cooler months of the year. The average annual rainfall in the area is 283mm, and occurs mainly in summer, although it can occur at any time. During the period prior to and during this study, the area received well above average rainfall in 2000 and 2001 (664 and 741 mm) and then again in 2010 and 2011 (770 and 340 mm).

Mist netting

Mist nets used to capture birds were approximately 3m high by either 12 or 18m long. They were erected in areas that were thought to be potential flyways and out of sunlight as much as possible. Nets were opened at dawn on banding days and checked every 20-30 min (Faaborg *et al*. 2004). Sex and age of captured birds were recorded if known, and Australian Bird and Bat Banding Scheme (ABBBS) bands were applied on the right leg.

The number of nets opened at any one time varied between 6 and 12, depending on the number and experience of volunteers available. Therefore, the area within which mist nets were set up was generally between 3 and 5ha. Banding was not conducted if ambient temperature rose above 33^{o}C or in strong winds or rain. Length of time that nets were open also depended on the availability of volunteers and the capture rate of birds, which decreased over time as birds in the area became aware of the nets. Nets were usually operated twice at each site, but not always on consecutive days. Each day's banding was regarded as an individual sample (referred to as a 'banding event'). The timing and number of banding events at each location are outlined in Table 1.

Data Analysis

Analysis of recaptures was designed to identify degrees of site-fidelity and two recapture measures were calculated. One was the percentage of banded individuals of each species that were recaptured. The second percentage calculated (referred to as 'recapture rate') included every recapture for each species (i.e. including multiple recaptures of the same individual). Other measures used to assess site-fidelity were the time-intervals between captures of the same individual, and the frequency at which species occurred at the different sites. As the number of individuals banded varied among species and the likelihood of recapturing individuals depends partly on the number of individuals banded initially, we conducted additional analyses to account for these effects. We first tested whether the predicted positive relationship between the number of individuals banded and the number of recaptures made was significant, and described this relationship using linear regression. We also examined how species deviated from the expected relationship by examining the residual values from the regression for each species.

Activities were undertaken with approval from the Charles Darwin University Animal Ethics Committee (project # A08007) and under Scientific Permit (# 39155) issued by the Parks and Wildlife Commission of the Northern Territory. The project had ABBBS approval (Authority 2392 Project 1).

RESULTS

Between 2001 and 2011, 1803 individual birds of 50 species were captured and banded. In addition, 169 individual birds were recaptured, some on multiple occasions, resulting in a

Table 1

Dates and locations of mark-recapture activities. Numbers of banding events are shown in parentheses.

Year	Cummings Yard (8)	Ryans Dam (9)	Hugh River (9)	Desert Park E (37)	Desert Park W (20)
2001	Oct (1)	Oct (1)	Oct (1)	Sep (2) Dec (2)	
2002	Feb (1) May (2) Sep (2)	Feb (1) May (2) Sep (2)	Feb (1) May (2) Sep (2)	Mar (2) Jul (2) Aug (2)	Jul (1)
2003	Jan (2)	Jan (2) Sep (1)	Jan (2) Sep (1)	Jan (2) Mar (3) Jun (1) Jul (1)	Sep (1)
2004	–	–	–	Jun (2)	–
2005	–	–	–	–	–
2006	–	–	–	–	–
2007	–	–	–	May (1)	–
2008	–	–	–	Jun (2) Dec (2)	Jun (2)
2009	–	–	–	May (2) Aug (2) Nov (1) Dec (1)	Apr (2) Jul (2) Sep (2)
2010	–	–	–	May (2) Oct (1) Nov (2)	Mar (2) Apr (2) Aug (2) Nov (2)
2011	–	–	–	Apr (2)	Mar (2)

total of 222 recaptures (10% recapture rate). Six hundred and twenty-one individuals of 37 species were caught in the Alice Valley and 1182 individuals of 45 species near the Alice Springs Desert Park.

Our focus was on the 27 species in which ten or more individuals were banded during the project (Table 2), because the likelihood of recapturing species in which very few individuals are banded is very low (even if the species is highly sedentary), and therefore not informative with respect to our research question. Data for the 28 species in which fewer than ten individuals were banded are provided in Appendix 1. Of the 27 most commonly banded species, 20 included individuals that were recaptured (Table 2). The 7 species with no recaptures all had relatively low (<30) numbers of individuals that were banded; however, other species with similarly low numbers of banded individuals, such as the Redthroat *Pyrrolaemus brunneus*, White-plumed Honeyeater *Lichenostomus penicilatus* and Southern Whiteface *Aphelocephala leucopsis*, had high recapture rates (Table 2). In some species, such as Splendid Fairy-wren *Malurus splendens* and Redthroat, individuals were caught on multiple occasions. Although only a small number of Redthroats were caught, they were proportionally the most recaptured species, with over 50% of trapped individuals being re-trapped at the initial point of capture (Table 2).

The time between original trapping and recapture provides an indication of the level of site fidelity for a species, with the maximum time between recaptures representing the minimum time that an individual is present at the site. When compared among species, the maximum time between recaptures for any individual and the mean maximum time between recaptures of individuals provide information about relative levels of site fidelity (Table 3). It is important to consider when interpreting these data that the number of days between recaptures is partly dependent on the time between banding events and that data suggesting long-term site fidelity will be biased toward longer-lived species (Table 3).

Species such as the Yellow-rumped Thornbill *Acanthiza chrysorrhoa* and Diamond Dove *Geopelea cuneata* (near the bottom of Table 3) were only ever recaptured within a few days of their initial capture when there were multiple banding events within a month, whereas individuals of other species (near the top of Table 3), such as the Splendid Fairy-wren, Spiny-cheeked Honeyeater *Acanthagenys rufogularis* and Chestnut-rumped Thornbill *Acanthiza uropygialis*, were caught at the same location years after initial capture (Table 3).

As predicted, for each species the number of individuals recaptured depended partially on the number of individuals banded. Thus, recaptures were more likely for species in which many individuals were banded and less likely in species in which very few individuals were banded ($R^2 = 29.2\%$; df = 1.25; $P = 0.004$) (Fig. 1). The regression line in Figure 1 is described by the equation *Recaptures = 2.6 + 0.08 Birds Banded*. This equation predicts the number of recaptures that could be expected based on the number of birds banded at our sites, assuming no differences in site fidelity. The residual values from the regression for each species (Table 4) represent the position and distance of each species in Figure 1 relative to the fitted regression line. Species with positive residuals are those that were recaptured more than expected (i.e. evidence of relatively high site fidelity), whilst those with negative residuals (points below the line) were recaptured fewer times than expected based on the number of individuals banded (i.e. evidence of relatively low site fidelity). From these analyses, the species with the strongest evidence of site fidelity were the Splendid Fairy-wren, Redthroat, Singing Honeyeater *Lichenostomus virescens* and Spiny-cheeked Honeyeater; species with the weakest evidence of site fidelity, suggesting high mobility, were the Diamond Dove and Zebra Finch *Taeniopygia guttata*.

There was variation in the regularity with which species were captured among the study sites. Some species were not captured at every study site or on every sampling occasion, but others were regularly caught at all sites. Table 5 illustrates the rate at which species were encountered in both spatial and temporal terms in the study sites. Notably, some species with relatively low recapture rates (e.g. Zebra Finch) were encountered very regularly at all sites, whereas other less abundant species with low recapture rates (e.g. Willie Wagtail *Rhipidura leucophrys*) or that were never recaptured (e.g. Mistletoe Bird *Dicaeum hirundinaceum*) were still encountered across all sites.

Table 2

Capture and recapture data for species with 10 or more individuals banded. Species are ordered according to percentage of banded individuals that were recaptured, from highest to lowest.

Species		No. banded (No. recaptures)	No. individuals recaptured	% Banded individuals recaptured	% Recapture rate
Redthroat	*Pyrrholaemus brunneus*	17 (12)	9	52.9	70.5
Chestnut-rumped Thornbill	*Acanthiza uropygialis*	33 (10)	9	27.2	30.3
White-browed Babbler	*Pomatostomus superciliosus*	38 (11)	9	23.6	28.9
Splendid Fairy-wren	*Malurus splendens*	198 (63)	41	20.7	31.8
White-plumed Honeyeater	*Lichenostomus penicillatus*	21 (4)	4	19.0	19.0
Southern Whiteface	*Aphelocephala leucopsis*	16 (3)	3	18.7	18.7
Grey-crowned Babbler	*Pomatostomus temporalis*	38 (7)	7	18.4	16.6
Singing Honeyeater	*Lichenostomus virescens*	113 (19)	16	14.1	16.8
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	136 (21)	19	13.9	15.4
Rufous Whistler	*Pachycephala rufiventris*	87 (13)	12	13.7	14.9
Western Bowerbird	*Ptilonorhynchus guttata*	16 (2)	2	12.5	12.5
Inland Thornbill	*Acanthiza apicalis*	51 (8)	6	11.7	15.6
Red-capped Robin	*Petroica goodenovii*	78 (9)	7	8.9	11.5
Yellow-throated Miner	*Manorina flavigula*	24 (2)	2	8.3	8.3
Hooded Robin	*Melanodryas cucullata*	30 (2)	2	6.6	6.6
Brown Honeyeater	*Lichmera indistincta*	97 (4)	4	4.1	9.7
Willie Wagtail	*Rhipidura leucophrys*	26 (1)	1	3.8	3.8
Zebra Finch	*Taeniopygia guttata*	425 (15)	12	2.8	3.5
Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	40 (1)	1	2.5	2.5
Diamond Dove	*Geopelia cuneata*	93 (2)	2	2.1	2.1
Budgerigar	*Melopsittacus undulatus*	29 (0)	0	0	0
Western Gerygone	*Gerygone fusca*	14 (0)	0	0	0
Pied Honeyeater	*Certhionyx variegatus*	23 (0)	0	0	0
Grey-headed Honeyeater	*Lichenostomus keartlandi*	22 (0)	0	0	0
Crimson Chat	*Epthianura tricolor*	12 (0)	0	0	0
White-winged Triller	*Lalage sueurii*	24 (0)	0	0	0
Mistletoebird	*Dicaeum hirundinaceum*	26 (0)	0	0	0

Table 3

Data on the times between recaptures, with species ordered by the longest time between banding and recapture of any individual.

Species	Mean maximum time between recaptures of individuals (days)	% of recaptures >180 days	% of recaptures >360 days	% of recaptures >730 days	Longest time between recapture of any individual (days)
Splendid Fairy-wren	292	14.0	8.3	1.5	2151
Spiny-cheeked Honeyeater	369	6.9	5.7	3.2	1947
Singing Honeyeater	271	6.1	2.3	0.7	1825
Chestnut-rumped Thornbill	378	13.3	11.1	2.2	1521
Rufous Whistler	319	7.2	3.1	2.1	1338
Grey-crowned Babbler	319	4.5	4.5	4.5	1125
Redthroat	333	29.6	11.1	7.4	882
Inland Thornbill	331	10.3	5.2	3.4	852
Red-capped Robin	246	7.1	3.5	0.0	608
Western Bowerbird	324	5.9	5.9	0.0	547
White-browed Babbler	276	12.2	12.2	0.0	517
Southern Whiteface	155	5.3	5.3	0.0	456
Hooded Robin	229	6.3	0.0	0.0	336
Yellow-throated Miner	370	3.8	0.0	0.0	334
Zebra Finch	73	0.2	0.0	0.0	213
Brown Honeyeater	77	0.0	0.0	0.0	168
White-plumed Honeyeater	93	0.0	0.0	0.0	122
Diamond Dove	11	0.0	0.0	0.0	13
Willie Wagtail	4	0.0	0.0	0.0	4
Yellow-rumped Thornbill	1	0.0	0.0	0.0	1

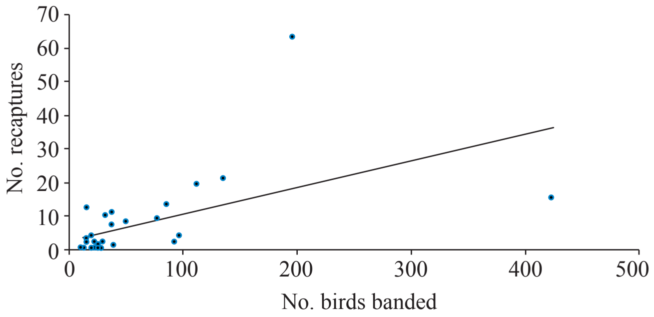

Figure 1. *Regression plot showing the relationship between the number of individuals banded and the number recaptured. Recaptures = 2.6 + 0.08 Birds Banded (R^2 = 29.2%, P = 0.004).*

DISCUSSION AND SYNTHESIS

Classification of species as sedentary or mobile based on mist netting

The capture and recapture rates and times between recapture of individuals that we have presented can be used to draw conclusions about the level of site fidelity of species. For example, some species, such as Splendid Fairy-wren and Chestnut-rumped Thornbill, had high recapture rates and long intervals between recaptures. These patterns of recapture are compelling indicators of site fidelity and sedentary behaviour (Leishman 2000; Frith and Frith 2005). These species were also regularly encountered at several sites throughout the year, indicating that they can be regarded as sedentary in *Acacia* shrubland. Other species exhibited a contrasting pattern; they were captured irregularly and some were never recaptured. It is impossible to draw conclusions for some species because few individuals were banded. However, for species in which many individuals were banded, low rates of recapture and short intervals between recaptures indicate that they are mobile and that individuals do not stay at a site for long. Such species may still be strongly associated with *Acacia* shrubland and occur predictably at many sites and times, but there is no evidence that they exhibit sedentary behaviour within this habitat. Based on the results of 10-years of banding surveys that we have presented, we have assigned the species trapped into three categories: sedentary, mobile and unclassifiable (insufficient data, the results are inconclusive) (Table 6). Our classification is compared to those of other authors who have presented data on the status of birds in Mulga communities, and to reported ABBBS recapture rates in Table 6.

Sedentary species

Of the 21 species encountered in >10 % of our banding events (see Table 6), 13 were among the 18 species listed by Cody (1994) as 'core' to *Acacia* habitat, four were considered peripheral, three casual, and one was unlisted by Cody. Eighteen of our 21 commonly encountered species were considered resident in *Acacia* shrubland in the Finke bioregion in central Australia by Pavey and Nano (2009). Our data for encounter rates therefore generally support the findings of Cody (1994) and Pavey and Nano (2009) with respect to species that are strongly associated with *Acacia* shrubland habitat. Notable

Table 4

Residual values for each species from the regression: Recaptures = 2.63 + 0.08 Birds Banded. Positive residuals indicate that more individuals than expected were recaptured and negative residuals that fewer individuals than expected were recaptured, when accounting for the number of birds of each species that were banded.

Species	Residual
Splendid Fairy-wren	44.12
Singing Honeyeater	8.28
Redthroat	8.00
Spiny-cheeked Honeyeater	7.27
White-browed Babbler	5.31
Chestnut-rumped Thornbill	4.55
Rufous Whistler	3.37
Grey-crowned Babbler	1.31
Inland Thornbill	1.19
Red-capped Robin	0.10
White-plumed Honeyeater	-0.32
Southern Whiteface	-0.92
Western Bowerbird	-1.92
Yellow-throated Miner	-2.56
Hooded Robin	-3.04
Crimson Chat	-3.60
Willie Wagtail	-3.72
Western Gerygone	-3.76
Grey-headed Honeyeater	-4.40
Pied Honeyeater	-4.48
White-winged Triller	-4.56
Mistletoebird	-4.72
Budgerigar	-4.96
Yellow-rumped Thornbill	-5.01
Brown Honeyeater	-5.59
Diamond Dove	-8.11
Zebra Finch	-21.81

exceptions are the Brown Honeyeater *Lichmera indistincta* and Redthroat, which we encountered relatively commonly but which were not recorded in Pavey and Nano's (2009) surveys and were classified as peripheral species by Cody (1994).

Among the commonly occurring species, we identified 11 for which there was clear evidence of high site fidelity. We classified these species as sedentary on the following basis: individuals were regularly encountered and (a) demonstrated fidelity to a site as indicated by a recapture rate >10% and (b) a maximum mean time between recaptures that was >240 days (8 months) or longer than a migratory cycle. Of the 11 species that we classified as sedentary, all except three were listed as a 'core' Mulga species by Cody (1994); this author listed the Redthroat as a peripheral species, Grey-crowned Babbler *Pomatostomus temporalis* as a casual species and did not list the Western Bowerbird *Ptilonorynchus guttata*. Below we discuss these three species first and then some of the other species that were classified as sedentary.

Although Cody (1994) listed the Grey-crowned Babbler as a casual Mulga species, he notes that babblers as a group rank as 'core' to Mulga, with the babbler species present differing

Table 5

Frequency of occurrence (expressed as the percentage of banding events) of species at different banding sites and over the entire study area.

Species	Frequency of occurrence (%)					
	Cummings (n = 8)	Ryans (n = 9)	Hugh (n = 9)	Desert Park E (n = 37)	Desert Park W (n = 20)	% of all sites and all trips
Splendid Fairy-wren	75.0	66.7	33.3	75.0	75.0	69.4
Singing Honeyeater	62.5	75.0	77.8	61.1	80.0	69.4
Zebra Finch	50.0	50.0	66.7	58.3	65.0	58.8
Rufous Whistler	37.5	83.3	77.8	52.8	50.0	57.7
Spiny-cheeked Honeyeater	50.0	33.3	55.6	63.9	50.0	54.1
Red-capped Robin	62.5	58.3	11.1	50.0	75.0	54.1
Inland Thornbill	37.5	58.3	44.4	27.8	55.0	40.0
Brown Honeyeater	25.0	25.0	11.1	50.0	15.0	31.8
Chestnut-rumped Thornbill	75.0	50.0	55.6	13.9	20.0	30.6
Diamond Dove	0.0	33.3	11.1	22.2	40.0	24.7
Yellow-rumped Thornbill	50.0	50.0	22.2	13.9	20.0	24.7
Hooded Robin	50.0	41.7	55.6	2.8	5.0	21.2
Willie Wagtail	37.5	8.3	22.2	16.7	15.0	17.7
Redthroat	0.0	33.3	0.0	11.1	30.0	16.5
Western Gerygone	0.0	25.0	11.1	11.1	25.0	15.3
White-browed Babbler	12.5	37.5	0.0	19.4	10.0	15.3
Western Bowerbird	25.0	0.0	0.0	27.8	0.0	14.2
Grey-headed Honeyeater	25.0	33.3	33.3	8.3	5.0	14.1
Mistletoebird	25.0	8.3	11.1	11.1	15.0	12.9
Southern Whiteface	12.5	41.7	0.0	2.8	10.0	10.6
Grey-crowned Babbler	12.5	16.7	33.3	11.1	0.0	10.6
White-plumed Honeyeater	0.0	0.0	11.1	19.4	0.0	9.4
Yellow-throated Miner	37.5	8.3	44.4	0.0	0.0	9.4
White-winged Triller	0.0	0.0	11.1	11.1	15.0	9.4
Pied Honeyeater	0.0	0.0	0.0	11.1	10.0	7.1
Crimson Chat	0.0	0.0	0.0	2.8	25.0	7.1
Budgerigar	0.0	0.0	11.1	2.8	5.0	3.5

with location. Both White-browed *Pomatostomus superciliosus* and Grey-crowned Babblers were encountered at most sites throughout the year in our study, but were only present in approximately 15% (White-browed) and 10% (Grey-crowned) of banding events, which may indicate they are less common residents of Mulga or that they are not easily trapped in mist nets. Our recapture data (numbers of recaptures and time between recaptures) indicate moderate site fidelity for these species. This is consistent with Higgins and Peter (2002) who describe both species as sedentary.

The absence of the Western Bowerbird in Cody's (1994) lists of *Acacia* shrubland birds may be partly explained by the limited distribution of this species in relation to his sites. The Western Bowerbird was considered a resident species of *Acacia* woodlands in the Finke bioregion by Pavey and Nano (2009). There are no ABBBS data on recapture rates for this species because of the limited number of banding studies in central Australia. Our recapture data suggest moderate site fidelity for this species.

Redthroats were not caught at every site and were only caught in small numbers. However, they exhibited the highest recapture rate of any species in our study, with over 50% of individuals banded being recaptured. They were caught in most months of the year at three out of five sites. This information suggests that they may have more specialised habitat requirements and live in larger territories compared to, for example, the Splendid Fairy-wren (which was commonly encountered at all sites in large numbers). The low numbers of Redthroats captured may also be the result of territorial instead of colonial habits. Higgins and Peter (2002) indicate a 20% recovery rate of banded individuals of this species; it is thought to be sedentary, with recoveries mainly occurring within 10km of the banding site, and this is supported by our data. The Redthroat's social organisation is poorly known, but it is thought to live in pairs or small family groups (Higgins and Peter 2002). The shy, cryptic nature of this species may limit sightings in observational surveys and probably accounts for it being described as peripheral to *Acacia* shrubland habitat by Cody (1994), and also why it was not recorded during the Finke Bioregion study (Pavey and Nano 2009). Based on our results, and contrary to Cody (1994), we suggest that the Redthroat is a 'core' species of some Mulga habitats; it was not found at every banding site, but where it occurred it was recaptured regularly.

Table 6

Classifications (sedentary vs. mobile) of species based on our mark-recapture results for species with >10 individuals banded compared with classifications of species from previous studies in arid Acacia habitat. A summary of the main variables from which our assessments were made is provided, along with recapture data from ABBBS (Higgins *et al.* 2001) for comparison.

Species	Our Classification	% Occurence (n = 83 banding events)	Mean days between recaptures	% Rate of recapture	% Rate of recapture (ABBBS)	Cody (1994)	Pavey and Nano (2009)
Splendid Fairy-wren	Sedentary	69.4	290	31.8	29.9	Core	Resident
Singing Honeyeater	Sedentary	69.4	268	16.8	21.6	Core	Resident
Zebra Finch	Mobile	58.8	74	3.5	23.8	Casual	Resident
Rufous Whistler	Sedentary	57.6	319	14.9	17.1	Core	Resident
Spiny-cheeked Honeyeater	Sedentary	54.1	369	15.4	6.4	Core	Resident
Red-capped Robin	Sedentary	54.1	247	11.5	11.7	Core	Resident
Inland Thornbill	Sedentary	40.0	331	15.6	24.8	Core	Resident
Brown Honeyeater	Mobile	31.8	78	4.1	9.7	Peripheral	n/a
Chestnut-rumped Thornbill	Sedentary	30.6	379	30.3	13.0	Core	Resident
Diamond Dove	Mobile	24.7	11	2.1	3.9	Core	Nomadic
Yellow-rumped Thornbill	Insufficient data	24.7	1	2.5	10.8	Core	Resident
Hooded Robin	Insufficient data	21.2	230	6.6	19.3	Peripheral	Resident
Willie Wagtail	Insufficient data	17.7	4	3.8	7.0	Core	Resident
Redthroat	Sedentary	16.5	334	70.5	19.4	Peripheral	n/a
Western Gerygone	Insufficient data	15.3	0	0.0	6.5	Core	Resident
White-browed Babbler	Sedentary	15.3	277	28.9	35.7	Core	Resident
Western Bowerbird	Sedentary	14.1	324	12.5	n/a	n/a	Resident
Grey-headed Honeyeater	Mobile	14.1	0	0.0	7.7	Casual	Resident
Mistletoebird	Insufficient data	12.9	0	0.0	8.3	Peripheral	Resident
Southern Whiteface	Insufficient data	10.6	155	18.7	13.0	Core	Resident
Grey-crowned Babbler	Sedentary	10.6	320	18.4	16.6	Casual	Resident
White-winged Triller	Mobile	9.4	0	0.0	0.9	Casual	Nomadic
White-plumed Honeyeater	Insufficient data	9.4	86	19.0	20.2	Casual	Resident
Yellow-throated Miner	Insufficient data	9.4	371	8.3	15.7	Peripheral	Resident
Pied Honeyeater	Mobile	7.1	0	0.0	0.9	n/a	Nomadic
Crimson Chat	Mobile	7.1	0	0.0	5.6	Casual	Nomadic
Budgerigar	Mobile	3.5	0	0.0	4.2	Peripheral	Nomadic

The Splendid Fairy-wren was encountered in 69% of banding events in our study. For this species, 23.6% of all captures were recaptures, with a mean time elapsed between encounters of 290 days and a total recapture rate of 31.8%. Individuals were caught at all study sites throughout the year. Splendid Fairy-wrens are social birds that live in family groups in relatively small territories. The high capture rate for this species occurred even though it is likely to be under-represented in our study because its terrestrial foraging habits may often take individuals underneath mist nets or, in common with other small passerines, they may bounce out of nets and avoid capture. Data in Higgins *et al*. (2001) and from the ABBBS indicate a 30% recapture rate within 10km of point of capture for this species and recaptures in the area of original capture up to 11 years after banding. Our study supports existing evidence that this species displays high site fidelity and may be regarded as sedentary. Other authors have listed this species as 'core' to *Acacia* habitat (Cody 1994; Pavey and Nano 2009).

Yellow-rumped Thornbills were caught in moderate numbers, but their recapture rate (2.5%) was much lower than those of two other co-existing species, the Inland *Acanthiza apicalis* (15.6%) and Chestnut-rumped Thornbills (30.3%). Yellow-rumped Thornbills are more terrestrial in their foraging behaviour than the other central Australian thornbills, and so may be more likely to move beneath mist nets, which may limit the chance of capture. It is noted in ABBBS data that recapture rates for this species are substantially lower than for other thornbills, although individuals have been recaptured up to thirteen years after original capture. Higgins and Peter (2002) documented a 14% recapture rate for Yellow-rumped Thornbills in other parts of their range, measurably lower than that in other thornbill species with higher degrees of site fidelity. This species, as well as the Inland and Chestnut-rumped Thornbill, was listed as 'core' to *Acacia* shrubland habitat by Cody (1994) and as resident by Pavey and Nano (2009). It may be, therefore, that whilst the species frequently resides in Mulga, it does not display the same degree of site fidelity as other thornbill species or may occupy larger home ranges. We did not have sufficient information to definitively rank this species as sedentary or mobile. The other central Australian thornbill species are also probably under-represented in our study, mainly due to their tendency to bounce out of mist nets in even a light breeze. Nevertheless, Higgins and Peter (2002) classify both Inland (30% recapture rate) and Chestnut–rumped Thornbills

(18%) as sedentary, a conclusion supported by our results. The Slaty-backed Thornbill *A. robutirostris*, also present at our sites (Appendix 1), was not among the species that we trapped more than 10 times. When observed, it seemed to be foraging mainly in the upper strata of the shrubland above the mist nets, which probably accounts for our low capture rates.

Red-capped Robins *Petroica rutenovii* were caught at all sites in every month of the year. They exhibited a recapture rate >10% and individuals were caught at their original capture site up to 600 days after being banded, indicating a degree of site fidelity. Higgins and Peter (2002) describe Red-capped Robin movements as unclear; they are designated as sedentary in some parts of their range, but migratory or nomadic in others. In arid Australia, they are thought to be sedentary, with a 22% recapture rate (Higgins and Peter 2002), which is consistent with our classification. Hooded Robins *Melanodryas cuculatta* were encountered in similar numbers as Red-capped Robins in our study and several individuals were recaptured after a year, suggesting a level of site fidelity; however, we did not have enough information on the species to definitively categorise it as sedentary. Red-capped Robins were found at all sites and captures were dispersed over the months of the year, which is consistent with Pavey and Nano's classification of the species as resident in *Acacia* woodland. They were also described as sedentary by Higgins and Peter (2002); however, observations have suggested some movement in central Australia.

The Rufous Whistler *Pachycephala rufiventris* was one of the more commonly encountered species in our study. Individuals were caught at all sites in all months of the year, and 13% of banded individuals were recaptured at the site of initial capture, some up to three years after they were originally banded. The overall recapture rate was 14.9%. Their movements are poorly understood. They are thought to be resident in the inland and possibly seasonal migrants near the coast (Higgins and Peter 2002), and have a national recapture rate of 24%. Of the eighty-seven individuals caught and banded during our study, fifty-five had adult plumage on initial capture; of these, 11 were recaptured, sometimes some years after the initial encounter. Of the birds with sub-adult or juvenile plumage which made up approximately 30% of the sample, only one was recaptured, nine days after it was initially banded. This turnover of juvenile birds would be expected to some extent in all species in the study and has been documented in other studies (e.g. Debus 2006).

Spiny-cheeked and Singing Honeyeaters were caught at all banding sites in all months of the year. More than 10% of individuals of each species captured were recaptured, and they were among the species most commonly recaptured, when scaled for the initial number banded. Elapsed time between recaptures for both species indicates that some members of the populations displayed a high degree of site fidelity, remaining at a site for over five years. These medium-sized honeyeaters are readily caught in mist nets, as they fly low down and at speed through the shrubs. Higgins *et al.* (2001) documented these species as sedentary in some parts of their range, but more mobile in others. The documented recapture rate nationally for Spiny-cheeked Honeyeaters is 6.4% (substantially lower than in our study) and for Singing Honeyeaters 21% (higher than our study). There is clear evidence that both species were sedentary at our sites.

Small numbers of White-plumed Honeyeaters were caught throughout the year at two sites closest to their preferred riverine environments. A small number of recaptures was recorded, with the longest time between recaptures being 122 days. Higgins and Peter (2002) consider this species to be sedentary (20% recapture rate) and our limited data tentatively support this categorization, although we have insufficient information to draw definitive conclusions.

Species not displaying site fidelity

In contrast to the species discussed above, there were other commonly-encountered species that were rarely recaptured, and we suggest that this is clear evidence against long-term site fidelity. In addition to the honeyeaters already discussed, we banded more than ten Grey-headed Honeyeaters *Lichenostomus keartlandi*, Brown Honeyeaters and Pied Honeyeaters *Certhionyx variegatus*. These species were caught at all sites and captures were spread throughout the year, but there were few recaptures. Hence, we have classified these species as mobile, which is consistent with honeyeaters often being generally regarded as nomadic or locally nomadic in response to flowering. However, this contrasts with the high degree of site fidelity that was apparent in Singing and Spiny-cheeked Honeyeaters, which may be mobile only within smaller home ranges.

Diamond Doves were caught in most months of the year and were present at four out of five sites. However, there were just a few recaptures, within two weeks of initial banding, indicating low site fidelity for this species. Although this species is clearly regularly present in *Acacia* shrubland and can be considered 'core' to this habitat (Cody 1994), it appears to be highly mobile. Our data are consistent with previous knowledge of the species; ABBBS data also indicate a low rate of recapture for Diamond Doves and Pavey and Nano (2009) list them as nomadic. Like many granivores, Diamond Doves may need to move frequently to track seed resources stimulated by local rain. Most of the Diamond Doves captured in this study were caught over two days in May 2010 after a substantial rainfall event in the preceding three months. Resource-based movements of this species have previously been documented (Higgins and Davies 1996) and are the most likely explanation for low recapture rates in our study.

Budgerigars *Melopsittacus undulatus* are well-known to be nomadic (Wyndham 1982). Small numbers of individuals were caught on a few occasions in our study, but there were no recaptures. In other banding studies, local recaptures have occurred only in the days soon after initial banding. The species is described as nomadic and irruptive (Higgins 1999). Other parrot species found in central Australia are relatively large birds that are dispersed in pairs or small groups across the landscape. They do not commonly congregate in large flocks like Budgerigars. Whilst they spend time foraging in the lower strata and on the ground, their size makes them unlikely to be caught in mist nets, and if they fly into nets they often do not become tangled and hence find their own way out. Thus, the Budgerigar was the only parrot that we banded in sufficient numbers to assess levels of site fidelity.

The Zebra Finch was one of the most commonly encountered species in this study, with an encounter rate of close to 60%

across all sites in all months of the year. Zebra finches had a low recapture rate of 3%, with few longer-term recaptures; hence we have classified them as mobile. In other studies, Zebra Finch recaptures have been up to 23% (Higgins *et al*. 2006) and investigations based on visual observations have labelled them as resident (Pavey and Nano 2009). However, this species is known to be highly mobile within its extensive home range, with movements being strongly influenced by food and water availability (Zann *et al*. 1995). Our study was not conducted in grassland habitats favoured by Zebra Finches and was not near water. Nets set close to sources of available water would probably produce higher rates of recapture if finches return repeatedly to the same water source.

Species with insufficient data for categorization and the limitations of mist-netting

There are some species for which we had insufficient data to be able to make meaningful inferences about whether they remain resident at a local site for long periods, some of which have been mentioned above. Information on these species was often limited due to the small numbers captured and banded, which is partly due to the limitations of mist netting for capturing some species.

For example, Western Gerygones *Gerygone fusca* were not regularly caught in our study, even though they were observed at four out of five sites. Mist netting, as applied in our study, appears to be ineffective for sampling this species. Western Gerygones are upper strata foliage gleaners and tend to fly over the top of mist nets (Higgins and Peter 2002). Due to their small size, they may also tend to bounce out of mist nets. This species shows no sign of regular movements in central Australia (i.e. it seems to be sedentary), although there are thought to be seasonal movement in south-western Western Australia (Higgins and Peter 2002). Similarly, some species (e.g. Southern Whiteface *Aphelocephala leucopsis*) did not meet our criteria to be classified as having high site fidelity, but showed some clear evidence of sedentary behaviour. Thus, it is important to note that the exclusion of a species from being classified as sedentary based on our research does not imply mobility.

Banding studies offer the opportunity to gain information on bird communities that is difficult to obtain, or unobtainable, through other survey methods (Dunn and Ralph 2004); for example, through the capture of cryptic, non-singing species. However, mist-netting has its own set of challenges. Variation in the capture efficiency of mist nets is brought about by mesh size, vegetation height, weather (including wind velocity), net visibility (due to cloud cover and other influences) and body-size of the species, as well as aspects of the flight and territorial behaviour of each species (Lukas and Leuenberger 1996; Lovei *et al*. 2001). Weather conditions can play a role in biasing mist net capture, with small birds such as thornbills bouncing off or seeing and avoiding the net, especially if the nets have been open for long periods (Saffer 2001; Faaborg *et al*. 2004).

Pardiek and Wade (1992) found that small individuals (<20 g) escaped more frequently than large individuals from 36mm nets, with only approximately 50% being retained, and Lukas and Leuenberger (1996) felt that wind added a 7-16% probability of escape to this effect. Saffer (2001) stated that the retaining efficiency of 25mm mesh nets for sparrow-sized passerines was 63%. On several occasions individuals of both small (<15 g) and large (>100 g) species were observed escaping from our 31mm nets. Furthermore, foraging height must also be considered. Mist nets appear to be most effective in catching fast-flying, medium-sized birds (15-50g) that forage in low to medium strata. Hence, the proportion of the community sampled may decrease as canopy height increases. In summary, mist netting over-represents some species in the community and under-represents others (Hardy and Farrell 1990; Faaborg *et al*. 2004; Mallory *et al*. 2004). Just as care needs to be taken in drawing conclusions about population size and demography based on mist netting data alone (Ballard *et al*. 2004), conclusions drawn from our mist netting study about site fidelity need to take into account the limitations of the method. Whereas large numbers of recaptures and long intervals between recapture of individuals is irrefutable evidence for high levels of site fidelity, results for species which did not apparently demonstrate high site fidelity and for species captured in low numbers need to be treated more cautiously.

Differences among species in the rate of decline of recaptures with elapsed time from initial banding may reflect differences in mobility, but could also result from disparities in longevity, mortality or dispersal patterns. Data from ABBBS indicate that many birds in our study are long-lived, surviving more than ten years (Baker *et al*. 1999). Mortality rates in populations of small Australian passerines have been estimated at between 32% and 58% (Debus 2006) and the reproductive potential of most species in our study, and their ability to produce multiple clutches over an extended breeding season, suggest that high mortality rates may be a factor contributing to low recapture rates. Our interpretations of the data have attempted to take these considerations into account.

Comparisons with banding studies in other regions

Similar general patterns of site fidelity to those that we have reported have been found in other long-term banding studies in a variety of Australian locations and habitats, from tropical rainforests (Frith and Frith 2005) to sclerophyll woodlands and forests (Tidemann *et al*. 1988; Leishman 2000). Irrespective of habitat, there seems to be a group of small, primarily insectivorous species of the mid- to lower vegetation strata that are sedentary. The number of sedentary species found in North Queensland rainforest (Frith and Frith 2005) and high-altitude *Eucalyptus* forest in the Australian alpine region (Tidemann *et al*. 1998) was almost double the number identified in our study and may be correlated with higher rainfall and therefore productivity at these sites. In contrast, Leishman (2000) found evidence of a similar number of sedentary species in *Eucalyptus* forest in eastern Australia as in our *Acacia* sites. It appears that species such as fairy-wrens, scrubwrens, thornbills, robins and whistlers may be resident for long periods of time across these different habitats (Tidemann *et al*. 1988; Leishman 2000; Frith and Frith 2005). In each of these banding studies, newly-banded immature birds were recaptured less often than adults, suggesting that the sedentary individuals are older, territorial birds. Estimates of the number of sedentary species from all banding studies are necessarily conservative, as more species than suggested by mark-recapture may be sedentary: uncertainty exists due to factors such as ‘shyness’ of mist nets, inconsistent ease of trapping, use by the birds of habitat strata out of mist net range, or spatial movements within home ranges that are larger than the areas sampled by nets (Leishman 2000; Ballard *et al*. 2004; Frith and Frith 2005).

Conclusions

Our results are broadly consistent with Cody's (1994) classification of the birds of arid *Acacia* shrublands and Pavey and Nano's (2009) classification based on surveys in the Finke bioregion. Together, these studies indicate that a predictable suite of bird species occurs in arid *Acacia* shrubland habitats over different months of the year and among different years. By following individual birds through time, our study enabled additional conclusions to be drawn about the sedentary versus mobile behaviour of these species. It also raised some interesting points of difference with previous studies that have relied on purely visual methods. For example, our very high recapture rates for Redthroats across several sites suggest that the species is probably a sedentary resident, at least in our study region, although it was previously described as peripheral to *Acacia* shrublands (Cody 1994) or simply not recorded (Pavey and Nano 2009). Redthroats are cryptic when not calling and their presence in the community is easily underestimated in visual surveys. Our results demonstrate that mark-recapture studies conducted over a long time-span can provide important insights into bird communities that are not easily obtained through observational techniques.

Overall, a significant proportion of small passerines encountered in our study displayed sedentary behaviour, resembling that found among suites of birds in coastal areas (Marchant 1982; Frith and Frith 2005). Despite the high variability of rainfall-driven resources in space and time in central Australia, the degree of site fidelity found amongst the suite of species present in *Acacia* shrubland suggests that many of them can persist in a single location over long time periods and be sustained by the resources available in the local area even during periods of low rainfall.

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Appendix 1

Species for which fewer than ten individuals were banded, showing comparative capture rates. Species are ordered by the rate at which they were captured across all banding events, from highest to lowest.

Species		No. banded	No. sites captured (n = 5)	Capture rate (% of all banding events)
Crested Bellbird	*Oreoica gutturalis*	9	4	10.6
Slaty-backed Thornbill	*Acanthiza robutirostris*	7	3	7.1
Little Button Quail	*Turnix velox*	6	2	4.7
Variegated Fairy-wren	*Malurus lamberti*	4	2	4.7
Grey Shrike-thrush	*Colluricincla harmonica*	5	2	4.7
Rufous Songlark	*Cinclorhamphus mathewsi*	9	2	4.7
Mulga Parrot	*Psephotus varius*	4	2	3.5
Red-browed Pardalote	*Pardalotus rubricatus*	4	2	3.5
Black-faced Woodswallow	*Artamus cinereus*	5	2	3.5
Grey Butcherbird	*Cracticus torquatus*	3	2	3.5
Horsfield's Bronze Cuckoo	*Chalcites basalis*	2	2	2.4
White-fronted Honeyeater	*Pumella albifrons*	5	1	2.4
Pied Butcherbird	*Cracticus nigrogularis*	5	2	2.4
Common Bronzewing	*Phaps chalcoptera*	1	1	1.2
Crested Pigeon	*Ochyphaps lophotes*	3	2	1.2
Bourke's Parrot	*Neosephotus bourkii*	1	1	1.2
Weebill	*Smicromis brevirostris*	3	1	1.2
Striated Pardalote	*Pardalotus striatus*	1	1	1.2
Black Honeyeater	*Sugomel nigrum*	1	1	1.2
Varied Sittella	*Daphoenositta chrysoptera*	3	1	1.2
Magpie Lark	*Grallina cyanoleuca*	1	1	1.2
Painted Finch	*Emblema pictum*	1	1	1.2