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Dispersal of juvenile Southern Scrub-robins *Drymodes brunneopygia* in the Murray Mallee of South Australia

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A key to successful species conservation is knowledge of how an animal moves among habitats, especially in highly fragmented landscapes. The Southern Scrub-robin *Drymodes brunneopygia* is a sedentary, ground-foraging, insectivorous bird that inhabits shrubby Mallee habitat across the southern states of mainland Australia. Due to habitat loss and fragmentation in the Murray Mallee region of South Australia, the species is now largely restricted to four spatially separated patches of territories in this region. To study the species' movements in this area, juveniles individually recognisable by colour-bands or an attached radio-transmitter were intensively tracked at Short's Farm, Bakara, from 2008 to 2011. Chasing of juveniles by parents was observed on the natal territory, but juvenile males left their natal territory later (mean departure age 299 days) than juvenile females (mean 310 days). Juveniles of both sexes generally left natal territories earliest in 2010, the wettest year of the study, and some were observed to return to the natal territory after forays beyond its boundary. Juvenile females moved further from the natal territory (mean distance 1,832 m) than juvenile males (mean 604 m) and visited more territories than did males. Mean distance moved by scrub-robins differed among the four patches studied, and in one patch no birds left the natal territory. Female juveniles visited sites already occupied by scrub-robins, whereas males visited both occupied and unoccupied areas. Some juveniles were still present on their natal territory at one year of age, and these birds were predominantly on territories with more shrub cover in the high use areas of the territory. As females typically moved further from the natal territory, they may have been more affected by habitat fragmentation than were males. The results provide an insight into dispersal of Southern Scrub-robins in a fragmented environment that could be helpful in the species' management and conservation.

Keywords: Southern Scrub-robin; mallee; juveniles; ground foraging insectivore dispersal; habitat fragmentation; habitat corridor

INTRODUCTION

Howard (1960) defined breeding dispersal as "the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate". The ability of birds to successfully disperse between habitat patches is usually essential to the survival of both individuals and entire populations (Clobert *et al.* 2012). Dispersal also achieves other functions, particularly the avoidance of inbreeding and the relaxation of competition for local resources (Matthysen 2012). However, these movements have also been associated with an increased risk of predation (Yoder *et al.* 2004; Roedel *et al*. 2015; Silva *et al.* 2020). Habitat fragmentation increases the possibility of restricted gene flow among populations and the consequent loss of genetic diversity and fitness (Méndez *et al.* 2014; Stevens *et al*. 2016; Beckmann *et al.* 2021). For effective species management, it is important to know what habitat individuals can move through and eventually settle in (Ford 2011). For example, the failure of female Brown Treecreepers *Climacteris picumnus* to reach male territories due to their isolation is likely to be a factor contributing to the decline of this species in fragmented landscapes (Cooper and Walters 2002). The presence of suitable post-fledging habitat is particularly important for fledgling birds, given their high mortality in the first year of life (Anders *et al.* 1998; Streby and Andersen 2013).

Few studies have been conducted on the dispersal movements of Australian terrestrial birds (Kozakiewicz *et al*. 2017) and very little has been documented of scrub-robin (Petroicidae) movements. However, being territorial and not cooperative breeders, Southern Scrub-robins *Drymodes brunneopygia* (hereafter scrub-robins) are likely to undergo breeding dispersal (Higgins and Peter 2002). As in other birds inhabiting the Mallee, including the Shy Heathwren *Sericornis cautus*, Gilbert's Whistler *Pachycephala inornata* and the Inland Thornbill *Acanthiza apicalis*, all known recaptures of scrub-robins prior to 2002 occurred within 10 km of the original banding site (Higgins and Peter 2002). One study showed that scrub-robins are found relatively infrequently in anthropogenically-induced habitat edges (Luck *et al.* 1999), suggesting that they prefer extensive areas of intact vegetation. Brooker (1998) reported that at Point Peron, Western Australia, two scrub-robins were sighted at one year of age courting partners 100–200 m from their natal territories. This study also showed that males exhibited stronger site fidelity than females (Brooker 1998). A higher proportion of males than females being resighted in this study could indicate female-biased dispersal, male-biased philopatry, greater female crypticity and/or greater female mortality, characteristics typical of many other Australian passerines (Mulder 1995; Brooker 1998; Green and Cockburn 2001; Cooper and Walters 2002). Female scrub-robins probably leave the natal territory in their first year (Brooker 1998) and further studies of scrub-robin movements may well indicate a substantial level of dispersal.

The Southern Scrub-robin is of considerable conservation concern given recent population declines across its entire range

Figure 1. *Location of the South Australian Murray Mallee in South Australia. Bakara in red. Green areas indicate extant native vegetation.*

Figure 2. *The farm at Bakara, showing all scrub-robin observations (pink) and (in yellow) the perimeters of areas containing the key understorey species Acacia sclerophylla or Leptospermum coriaceum. Single yellow dots are isolated A. sclerophylla or L. coriaceum shrubs. The habitat patches (circled in red, from top left to lower right) are: The Northwest patch (NW), The Heritage Agreement (HA) (centre, top), the North patch (NTH) (centre right) and the South patch (STH)(lower right). Scale 1:20,000. Aerial photo taken in 2000 provided courtesy of DEWNR.*

and the disappearance of already small and isolated populations in the Murray Mallee region of South Australia (Brooker 1998; Cale and Mladovan 2007; Willoughby 2008; BirdLife International 2023). The aim of the present investigation was to document the extra-territorial movements of juvenile Southern Scrub-robins, explore the social or habitat factors that may explain these movements and determine whether there are differences in the dispersal patterns of male and female juvenile birds.

METHODS

Study population and marking

This study focuses on the scrub-robins inhabiting a privately owned 2,100 ha farm in Bakara ('Bakara farm') (34°39'27'S 139°46'50'E) in the Murray Mallee of South Australia (Fig. 1). The farm contains four patches of habitat inhabited by scrub-robins, with 5–17 territories in each patch (Fig. 2). 105 birds (72 adults and 33 juveniles) were mist-netted and individually colour-banded from all the patches studied. Radiotelemetry was also used to assist in finding and following eleven birds in dense, scrubby habitat. The feathers on the mid to lower back were trimmed and transmitters (88-day battery life, weighing 0.9 g and emitting 26 pulses per minute; Advanced Telemetry Systems, Isanti, MN) were affixed with superglue. After transmitter attachment, the birds were released and located using a three-element folding Yagi antenna and an Icom® R10 RX5 radio receiver. Transmitters eventually fell off. All captured birds were aged by checking for lighter coloured fringes on the primary covert feathers to determine if they were in their first year of life, and measured to determine their sex (males being larger than females) (Higgins and Peter 2002; pers. obs.).

Scrub-robin tracking commenced in August 2008 and finished in November 2011. It took place in the two hours after dawn (when birds are most vocal), with the observer visually searching for marked birds, listening for calls and recording observational data. In the absence of direct observations, call

playback was used to attract birds. All territories were visited fortnightly and searched for 1 – 3 hours. Observational data (GPS position, behaviour, habitat occupied and bird ID) were recorded for each sighting. The data on colour-banded birds were used to define Minimum Convex Polygons (MCP) to determine territorial limits. Juvenile movements consisted of exploratory forays not far from the natal territory and back again, and permanent movements to other territories or habitat. Permanent movements were measured from last sighting to the following sighting, and these made up the trips/stages of the journey.

Chasing and dispersal behaviour

Juveniles were aged approximately based on date of first sighting minus 12 days of nesting (consistently around late September/early October) (Higgins and Peter 2002). If juveniles were observed being chased, their approximate age (in days) and location (natal territory/other territory) were recorded. The mean lengths (± 1m) of juvenile exploratory forays were compared between male and female birds. To determine if juveniles left natal territories at different ages in each of the habitat patches studied, their ages when they were first sighted outside the natal territory were documented and compared among the four patches. Similarly, to determine if juveniles left natal territories at different ages in the various years of the investigation, the mean age of male and female juveniles at their first movement were compared over the three years of the field study. All measurements were calculated using the measure tool in ArcGIS (ESRI 2010).

Vegetation surveys

Within each territory, high use ('hotspot') and low use ('coldspot') areas were determined based on the locations of the accumulated observations of the territory's occupants. For each colour-banded individual, the accumulated waypoint fixes were imported into ArcGIS (ESRI 2010) and the spatial density of these fixes was analysed using the Point Density (Spatial Analyst) tool. This analysis defined a 20 m space around the centre of each raster cell (matrix pixel), and the quantity of waypoints inside this space (representing the amount of use by the scrub-robins) was divided by the area of the defined space to give each defined area a value of magnitude and a colour (ESRI 2010). A 30 m^2 quadrat (marked every 5 m) was studied within each of these areas, recording the plant species present, and visually estimated per cent cover of understorey and tree canopy.

Other dispersal metrics

The total combined understorey percentage cover of hotspot areas in the territory just left and of the destination at the end of a movement were graphed to determine if birds of either sex visited territories with understorey vegetation cover other than the territory they had just vacated. Returns to the natal territory after an external foray were excluded from these analyses.

The average number of territories visited by all travelling scrub-robin juveniles and the average number visited by males and by females were calculated. These calculations included brief forays and permanent movements (i.e., bird settled on the territory). The means of the distances (trips or stages of the journey) travelled by all male and female juveniles that made extra-natal territory movements were compared. Characteristics of the occupants of the territories visited by juveniles (i.e., their likely relationship to the dispersing bird and their gender) were examined to help determine why juveniles visited particular areas.

Non-dispersers

The characteristics of juvenile birds that remained on the natal territory beyond one year of age were examined to determine the reasons why these birds were philopatric. Factors such as natal patch identity, percentage understorey cover per natal territory hotspot, sex, and the occupants of the natal territory were considered.

Data analysis

Descriptive statistics rather than significance testing were used in the analysis of dispersal events owing to the small sample sizes available, and a conservative approach was accordingly taken in interpreting the data. Throughout the text, mean values are presented together with the standard error.

RESULTS

Chasing behaviour

Four birds (three males and one female) were observed being chased on their natal territory by both their putative parents and these juveniles permanently left the natal territory. Another female juvenile was chased on the territory on which she settled after moving. The minimum age of a chased bird was 59 days, and the maximum was 479 days (mean 191 days). In seven of the twenty-seven inter-territorial movements recorded, the juvenile was chased on the territory on which it was last observed, and chasing was observed on nine of the thirty territories to which travelling birds moved or returned. Adult birds were observed to rebreed on 8 of the thirteen territories that produced dispersing juveniles.

Proportion of juveniles that dispersed

Thirteen of the 33 juveniles that were colour-banded were re-sighted on territories other than their natal territory, seven being males and five females, plus one that could not be sexed (Table 1). Ten of these birds survived for more than one year. Twelve juvenile birds remained on their natal territory for more than one year. Successful juvenile inter-territorial movements were observed on all habitat patches except the Northwest Patch (Figs. 3 – 5 and Table 1). Eight juveniles that were not observed to disperse were not detected again before reaching one year of age.

Age at first extra-territorial movement

There was no substantial difference between the age of male and female juveniles on their first recorded extra-natal territory forays (means: males = 299 ± 162 days; females = 310 days ± 300 days. Juveniles of both sexes that moved off their natal territories tended to do so earlier in 2010 than in 2008 (Table 2).

Mean number of territories visited

The juvenile scrub-robins that were observed to leave their natal territory visited an average of 2.8 territories (including all forays and permanent departures from the natal territory), with males visiting a mean of 2.7 and females 3.3 territories.

Comparison of habitat at territory of origin and destination

Initial observations of scrub-robins at Bakara revealed that 85% of the areas that they occupied contained Hard-leaf Wattle *Acacia sclerophylla* (naturally regrown farmland habitat) and Green or Mallee Tea-tree *Leptospermum coriaceum* (old-

Table 1

Movements of juvenile scrub-robins at Bakara, 2008–2011. Age 1st = the age in days at which bird seen outside of the natal territory. Dist 1st (m) = the distance in metres of the first observed movement. #stages = the number of recorded movements by the individual bird. Mean dist (m) = mean distance of all recorded movements, in metres. Total dist. (m) = total observed distance of travel (the accumulated distances of the stages). Total dist. SL = total straight-line distance from first sighting to last, in metres. No birds were observed to disperse on the Northwest patch.

BirdID	Sex	Patch	Age 1st	Dist. 1st (m)	#stages	Mean dist. (m)	Total dist. (m)	Total dist. SL (m)
BMOR	F	South	758	646	2	646	1,292	0
GMRY	F	South	186	848	2	678	1,343	369
GMRG	F	South	181	462	3	483	1,456	434
BMGN	?	South	101	1,789	1	1,789	1,789	1,789
BMYB	M	South	525	440	3	319	957	108
BMWY	M	South	113	64	2	58	115	117
YMGY	F	North	115	2,162	5	985	4,925	2,234
YMRY	F	North	?	?	>1	137	>137	137
YMGB	M	North	495	119	2	46	332	183
YMGR	M	North	357	362	4	428	1,746	1,028
YMGG	M	North	210	20	3	158	700	256
NMBO	M	HA	196	115	3	212	734	445
NMGR	M	HA	196	124	1	124	124	124

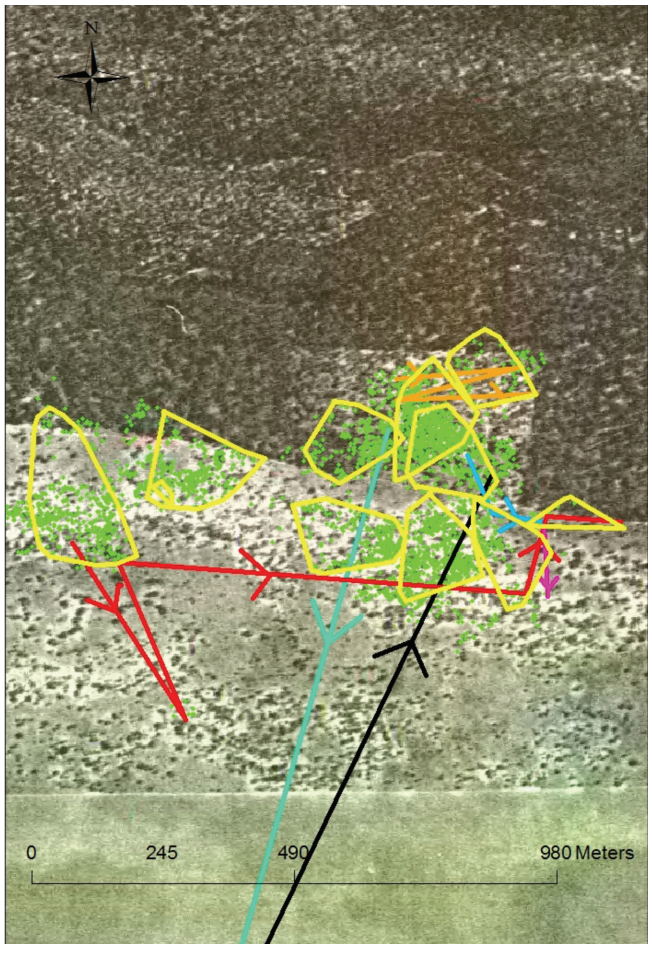

Figure 3. *Juvenile dispersal on the North Patch 2008–2011. Green dots indicate where adult and juvenile scrub-robins were detected, and yellow lines show territory boundaries. Red line = movement of ♂YMGR, blue line = ♂YMGB, orange line = ♂YMGG, pink line = ♀YMRY. Black line = BMGN (inter-patch movement from South Patch) and aqua line = ♀YMGY (inter-patch movement to South Patch). Arrows indicate direction of movement. Lines do not necessarily reflect actual dispersal paths, but are shortest routes between consecutive sightings. Scale = 1:8,000.*

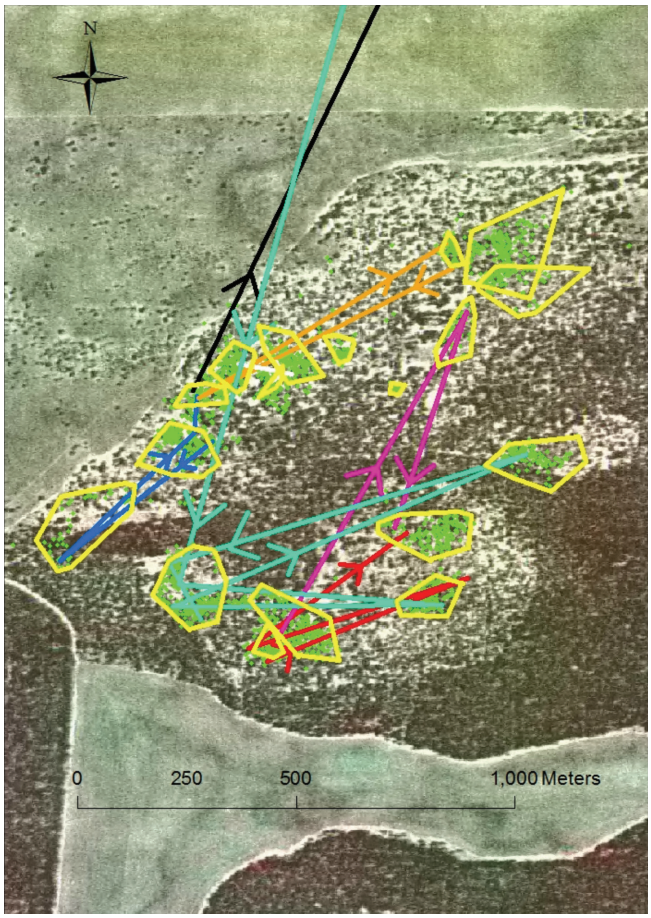

Figure 4. *Juvenile dispersal on the South Patch 2008–2011. Green dots indicate where adult and juvenile scrub-robins were detected, and yellow lines show territory boundaries. Red line = movement of ♀GMRG, blue line = ♂BMYB, orange line = ♀BMOR, pink line = ♀GMRY, black line = BMGN (inter-patch movement to North Patch), white line = ♂BMWY and aqua line = ♀YMGY (inter-patch movement from North Patch). Arrows indicate direction of movement. Lines do not necessarily reflect actual dispersal paths, but are shortest routes between sightings. The two overlapping territories are a result of numerous incursions by the northernmost group. Scale = 1:8,000.*

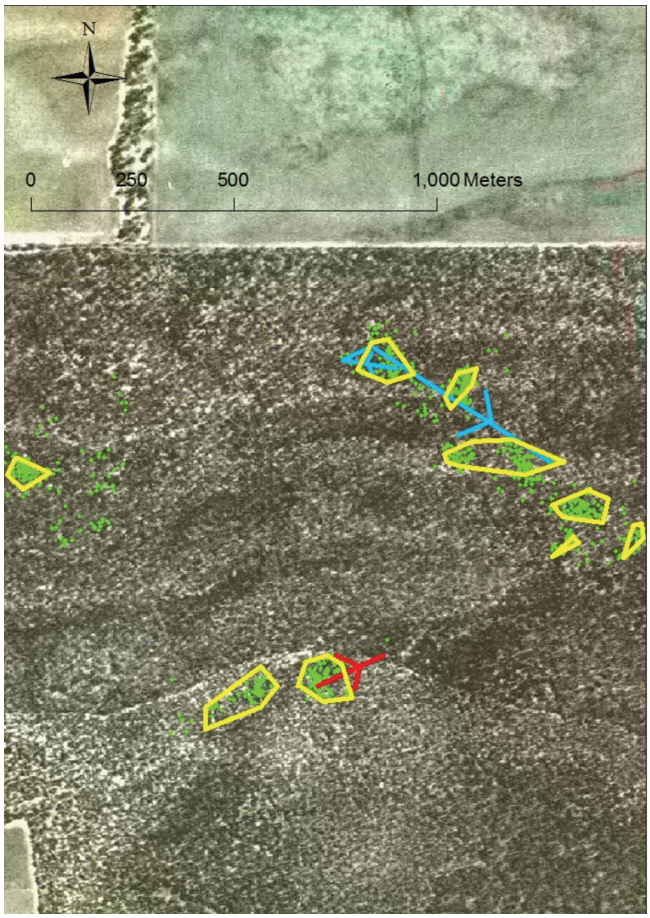

Figure 5. *Juvenile dispersal on the Heritage Agreement Patch 2008–2011. Green dots indicate where adult and juvenile scrub-robins were detected, and yellow lines show territory boundaries. Blue line = movement of ♂NMBO, red line = ♂NMGR. Arrows indicate direction of movement. Lines do not necessarily reflect actual dispersal paths but are shortest routes between sightings. Scale = 1:8,000.*

Table 2

Mean first dispersal age (in days) of male and female scrub-robins at Bakara.

Year fledged	Male mean age in days (± SE)	Female mean age in days (± SE)
2008	368 (157.5) *n* = 2	758 *n* = 1
2009	322 (136.8) *n* = 3	115 *n* = 1
2010	196 (0) *n* = 2	183.5 *n* = 3
All years	299 (61)	310 (300)

growth habitat). Most territories had one or both of these "key" understorey species. The majority of juvenile male movements were to territories with less understorey vegetation in habitat hotspots than the previously visited territory (Fig. 6); however, less disparity was observed in juvenile female movements. Juvenile birds were not observed to travel from areas dominated by *Acacia sclerophylla* to areas dominated by *Leptospermum coriaceum* or vice versa. There were no differences between eucalyptus canopy cover in origin or destination habitat for either sex.

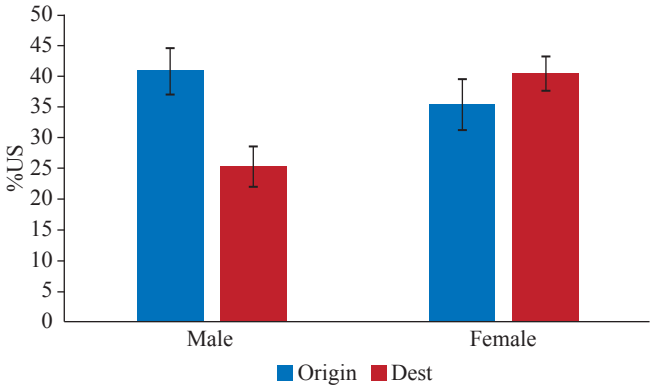

Figure 6. *Percent total in habitat hotspots of understorey cover (%US) of the origin (blue) and destination (red) territories where juvenile male and female scrub-robins were observed. Error bars= standard error of the mean. Bakara 2008–2011.*

Distances travelled

On average, female juvenile scrub-robins moved a greater accumulated distance (i.e., in all their recorded movements combined) than males (means: females 1,832 ± 724 m; males 604 ± 202 m). The mean total distance travelled by all juveniles of both sexes combined was 1,116 m. The total distances travelled by the birds that left their natal territories are shown in Table 1.

The mean distance of individually recorded movements (i.e., a trip or stage of a journey as opposed to the accumulated distance of all movements made) was 432 m. The mean distance travelled in males' trips was 234 ± 48 m, and the mean female individual trip distance was 704 ± 128 m. The accumulated and individual trip distances for each travelling bird are shown in Figures 7 and 8.

Most of the 33 movements recorded were within the natal habitat patch, with only two (6%) being between two patches (North and South; the shortest straight line between these patches was 809 m) (Figs. 2 – 4). One juvenile (♀YMGY) eventually travelled at least 4,925 m between two patches and across six territories before settling on a 'new' territory, a linear distance of 2,234 m from the natal territory to where the bird eventually settled (Figs. 2 – 4). The shortest distances between the MCPs of the four patches were 548 m (Northwest and Heritage Agreement patches), 876 m (Heritage Agreement and North patches) and 811 m (North and South Patches). The mean length of individual trips made by female juvenile scrub-robins appeared to be greater than that of trips made by males (Fig. 9).

Non-dispersers

Eleven juveniles were observed to survive for more than one year and remain on the natal territory, with 73% of these birds having fledged on the South Patch, the majority of these non-dispersers (73%) were fledged on the territories with the highest understorey cover on habitat hotspots. Sixty per cent (*n* = 9) of males that survived more than a year were never observed to disperse, whereas only two females (29%) that survived more than a year stayed on the natal territory without ever leaving. These females appear to have remained on the natal territory in the absence of their probable mothers.

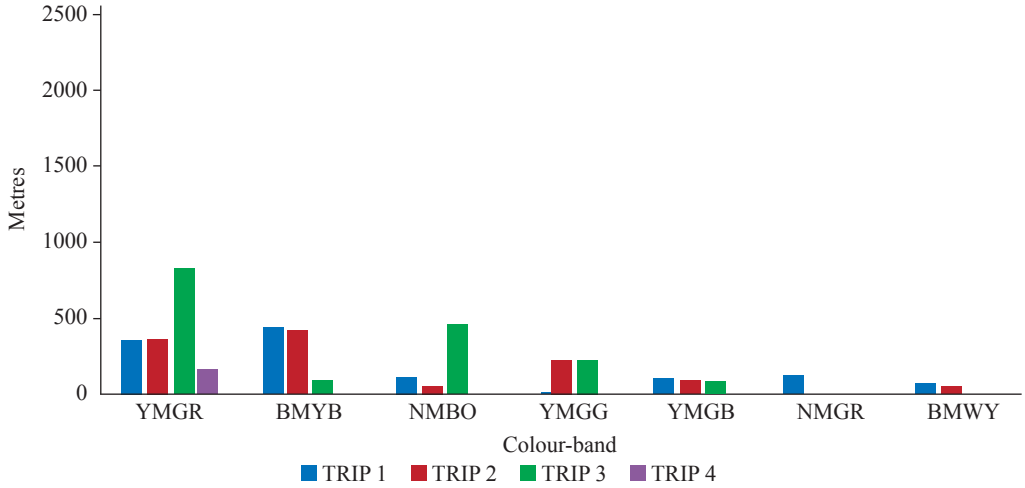

Figure 7. *Distances of the individual trips or stages of male juvenile Scrub-robins, Bakara 2008–2011. The different colours represent the ordinal number of each trip/stage. Colour-band refers to the identity of the bird.*

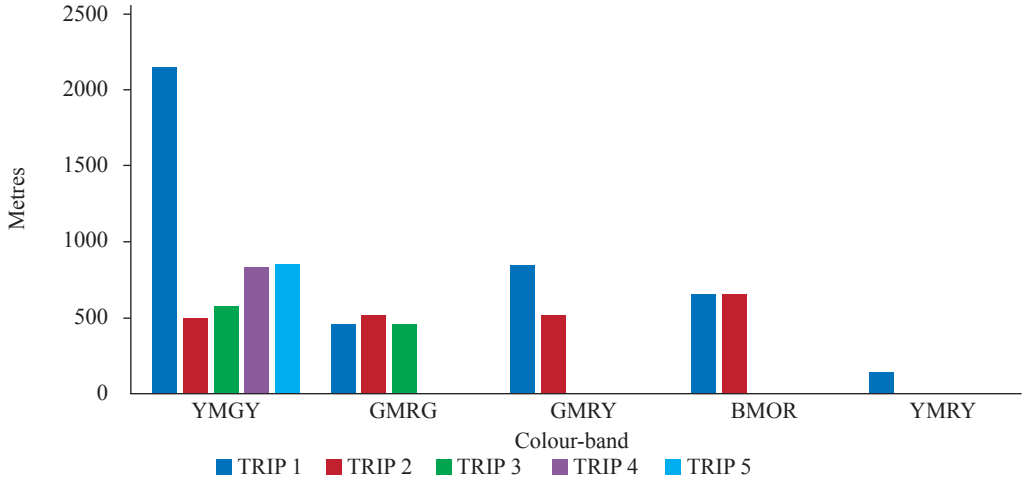

Figure 8. *Distances of the individual trips of female juvenile scrub-robins, Bakara 2008–2011. The different colours represent the ordinal number of each trip/stage. Colour-band refers to the identity of the bird.*

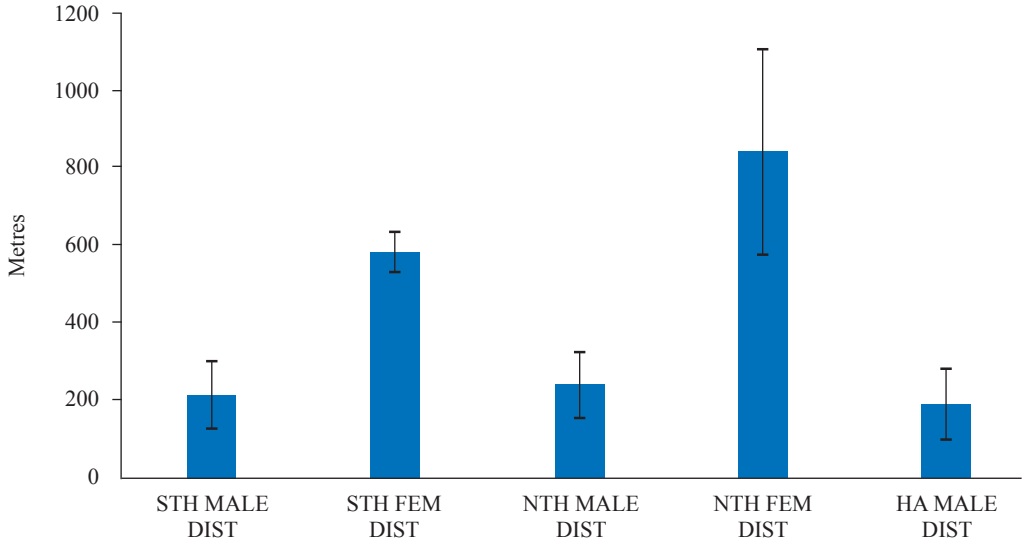

Figure 9. *Mean distances (DIST) of individual trips or stages of the journey of male and female (FEM) juvenile scrub-robins at Bakara 2008–2011. No dispersal was observed by juveniles from the Northwest Patch. Error bars = Standard Error of the Mean.*

Return to natal territory

Seven of the thirteen juveniles (54%) that dispersed were observed to return to their natal territory at least once (mean time away from the natal territory was 88 ± 33 days)), and five of the birds that returned to the natal territory eventually settled on another territory altogether. The mean distance of these forays was 329 ± 209 m. Seventy-one percent (*n*=5) of male juveniles that left their natal territory were observed to return to it, compared to 40% (*n*=2) of the 5 female juveniles that departed their natal territories.

Demographics of destination territories

Most (59 %) of the recorded juvenile movements were to territories with an apparently non-parent bird of the opposite sex. On external trips (i.e. not including returns to the natal territory), female juveniles always visited territories which had a probable non-parent male present, whereas ten of eighteen juvenile male movements were to a territory lacking a resident female. On four of seven occasions, male juveniles visited unoccupied areas on their first recorded visit outside the natal territory.

DISCUSSION

This study was conducted to document and try to understand the extra-territorial movements of juvenile Southern Scrub-robins in the Murray Mallee of South Australia. It shows that many juvenile scrub-robins leave the natal territory, with males (mean departure age 299 days) possibly being expelled by their parents after the departure of female juveniles (mean departure age 310 days). Females were observed to move further away from the natal territory than males. Birds on the North Patch appeared to disperse further than those on the Northwest and Heritage Agreement patches, but no birds were observed to leave the natal territory on the Northwest patch. Juvenile females always visited occupied territories, whereas males frequently visited unoccupied areas. Females visited territories with similar shrub cover to that of the previous territory visited, whereas males often visited territories with less shrub cover than that on the previous territory visited.

Non-dispersers

Less than half of all banded juveniles that survived more than one year were not observed to leave the natal territory and at one year of age most surviving birds had not left the natal territory. Most of these birds were on the South patch, which unlike the Heritage Agreement patch, had very little vacant key understorey habitat. Additionally, 73% of all juvenile birds that survived more than a year and remained on the natal territory were fledged on territories with the shrubbiest territory hotspots. The generally favourable shrubby habitat found on areas like the South Patch may have permitted the retention of the previous season's juveniles without seriously compromising the ability of parents to raise another juvenile, as has been observed in some other bird species (Koenig *et al.* 1992). In one such area of the South Patch, the likely father of one juvenile abandoned his territory (although his 10-month-old probable son remained there) and invaded a nearby territory where he went on to fledge two juveniles consecutively, one of which had not dispersed after attaining one year of age. On the North patch, ♂YMBB dislodged ♂YMRO from his territory, but this territory was reduced in size as a neighbouring male (♂YMBO) then acquired some of it, possibly because YMRO's ex-territory had the most *Acacia sclerophylla* of any territory in the entire North patch. Subsequently, the putative male offspring of YMBO (juvenile YMGB, Fig. 3) remained on the area once occupied by his likely father. In another patch (Northwest), a male juvenile appeared to have inherited the natal territory, with only his likely mother later being observed on a neighbouring territory. No juvenile dispersal was observed on the Northwest Patch, where habitat was of low quality and juveniles had higher mortality rates. The survival rate over one year of juveniles in this patch was the lowest of all the patches studied at 0.14 (Barker, in press).

No observations were made of scrub-robins being fed by their probable parents into adulthood, but in other bird species philopatry and delayed dispersal are known to have advantages such as reduced predation, less stress and access to better quality habitat (Ekman *et al.* 1999; Yoder *et al*. 2004). Male Collared flycatchers *Ficedula albicollis* that disperse further may be reproductively disadvantaged (Pärt 1990). At Bakara, juvenile scrub-robins often remained on the natal territory in the absence of a parent, a phenomenon also observed amongst males of the Great Tit *Parus major*, another non-cooperatively breeding species (Greenwood *et al*. 1979). Ceding of entire territories and the partitioning of part of the territory to young males was also observed in this study. More territories were abandoned than were newly established, suggesting a limited amount of suitable, available habitat, which could explain the benefit of remaining on the natal territory for as long as possible. Brooker (1998) recorded that two juvenile scrub-robins banded in 1996 at Point Peron in Western Australia were resighted in 1997 at one year of age close to their natal territory, with one of the birds appearing to have occupied its probable parents' territory. Greenwood and Harvey (1982) state that the tendency is for immature birds to establish themselves as close as possible to their natal territory, but that their inexperience frequently prevents them doing so.

In the present study, more male than female scrub-robins that survived over a year remained on the natal territory during that time and the two females that did may have remained under exceptional circumstances (i.e. they were occupying vacancies left by their absent mothers but were still on the territory with their likely fathers, although they were not observed to breed with them).

Chasing of juveniles on the natal territory

Over a third of all dispersing juveniles were observed to be chased on the natal territory and the majority of these birds were males. The fewer records of female juveniles being chased could be due to them having moved from the natal territory relatively early. In some other bird species, the forced dispersal of juveniles from the natal territory could be a mechanism that increases resources for the breeding pair and reduces the possibility of inbreeding (Greenwood and Harvey 1982; Green and Cockburn 2001; Matthysen 2012). At Bakara, adult scrub-robins on eight of the thirteen territories that produced dispersing juveniles were observed to re-nest the following season. On one very large and densely shrubbed territory at Bakara (BMGR, South Patch), the breeding pair nested twice in the same season (2010) and so had two juveniles living simultaneously on the same territory. Brooker (1998) also observed one instance of scrub-robins breeding again immediately after successfully rearing a brood. In other avian species, this cohabitation of successive broods may be possible if resources are abundant because of the size and quality of the territory and/or because of an extremely wet spring and summer

resulting in a greater invertebrate abundance (Bolger *et al*. 2005). Interestingly, in the present study at nearby Mantung the annual rainfall in 2010 was over double the annual rainfall recorded in the other years of this investigation (BOM 2013).

At Bakara, juvenile scrub-robins were also observed to apparently be absent from their natal territories (i.e., could not be located) soon after their putative male parent was displaced by an invading male. Given the intensity of searching that I conducted in the study area, it is likely that these juvenile birds died after leaving the natal territory.

Returning to the natal territory

Although sample sizes were small, seven of 13 dispersing juveniles (five males and two females) were observed to return to their natal territory after having left it, essentially inflating male philopatry. Male-biased philopatry is common in other avian species (e.g., Huntington 1951; Greenwood 1980; Runciman *et al*. 1995). Initial scrub-robin extra-territorial forays were typically for only a few hundred meters away from the natal territory. In the Ruffed Grouse *Bonasa umbellus*, such explorations serve to familiarise birds with the occupied and unoccupied areas around the natal territory and provide experience which may reduce the risk of predation (Yoder *et al.* 2004).

Distances travelled

Most of the detected movements by juveniles were within the natal habitat patch, and the mean linear distance of these movements was approximately 370 m; Males visited a mean of 2.7 and females 3.3 territories, however, this could be an underestimate, as data were only recorded every two weeks. Female scrub-robins were also observed to visit more territories than did males, as was also noted in juvenile Great Tits (Greenwood *et al.* 1979). The only other record of juvenile scrub-robin dispersal was published by Brooker (1998) who recorded two one-year old birds between 100–200 m from their natal territories.

As expected, female birds dispersed much further and generally earlier than males (e.g., Dhondt 1979; Greenwood *et al*. 1979; Greenwood 1980; Mulder 1995; Clarke *et al.* 1997), probably because it reduced inbreeding (e.g., Nilsson 1989; Daniels and Walters 2000). Additionally, it is quite possible that crossings between habitat patches were only made by females. This suggests that some females in the study area would have traversed a potentially hostile matrix of agricultural land, sparse shrubland and/or a 100 m wide eucalypt woodland corridor, whereas the other dispersal movements would have involved moving through relatively benign eucalypt woodland to arrive at their destinations (Figs. 2–5). In other bird species, inexperienced younger individuals have difficulty competing with older, established territorial individuals and therefore must often search over a considerable distance for a suitable territorial vacancy (Greenwood and Harvey 1982). A study of Marsh Tits *Parus palustris* found that natal dispersal distance increased with population density (Nilsson 1989), cf. the relatively short distances travelled by scrub-robins within the large Heritage Agreement Patch at Bakara. Longer dispersal distances have been positively correlated with poor natal area habitat in the Great Reed Warbler *Acrocephalus arundinaceus* (Bosschieter *et al.* 2010) and in female Sparrowhawks *Accipiter nissus*, and poorer outcomes in adulthood (Newton and Marquiss 1983).

Habitat comparisons between dispersal movements

Dispersing juvenile females moved to territories with a similar percentage cover of key shrubs and overall understorey in their hotspots to that of the territories they had left, whereas male juveniles moved to territories with substantially less cover than the area they had vacated. Additionally, juvenile females also visited more territories than males. Females preferentially only visited occupied, established, presumably high-quality territories. Young males of other bird species have been observed to settle on inferior habitat compared to that chosen by females (e.g., Sherry and Holmes 1989; Zanette 2001). At Bakara, lone male scrub-robin territories had less *Acacia* and *Leptospermum* cover than territories occupied by breeding pairs, and these territories may be actively rejected by dispersing females. Females may be able to select territories with a large amount of understory more readily than males, as between 20–30% of all territories contained single birds (always male) that would presumably tolerate or even attempt to attract arriving females (Barker, in press). Whereas an arriving male juvenile will inevitably encounter conflict with a more experienced male on any occupied territory. Neither juvenile females nor males visited territories with significant differences in overstorey canopy cover, suggesting a uniform cover of this habitat feature across patches or that it has less influence on where birds settle.

A juvenile female (YMGY) left the North Patch which had a low juvenile survival rate to eventually settle in the South Patch where juveniles survived longer (Barker, in press). For approximately one year, it was observed to intermittently occupy the periphery of a territory in this patch occupied by a breeding pair and their juvenile, before eventually appearing to become the breeding female on that territory. This example may illustrate how some dispersing birds secure a breeding opportunity in superior habitat to that in which they were raised (Matthysen 2012).

No birds were recorded moving between the two different habitat types (i.e., *Acacia sclerophylla* to *Leptospermum coriaceum* or vice versa), despite there being recorded juvenile movements between the North and South habitat patches. A hypothetical journey of a North patch bird to the Heritage Agreement patch would have been through continuous open woodland, and to an area with abundant vacant *L. coriaceum* shrubland. A preference of dispersing birds for habitats similar to their natal environment has been noted in other bird species (e.g., Davis and Stamps 2004; Fletcher *et al.* 2015).

Demographics of destination territory

Over half of all recorded visits (and all female visits) were to territories occupied by a member of the opposite sex that was probably not the visiting bird's parent. Females always visited occupied territories, whereas over a third of all male juvenile visits were to unoccupied areas. Male scrub-robins are generally longer lived and overall, more philopatric than females (Barker, in press), although some appear to be forced off the natal territory at about one year of age. Males that cannot inherit or bud off a portion of the natal territory (i.e., partially inherit as defined by Komdeur and Edelaar (2001)) are possibly forced to establish new territories and compete for the attentions of dispersing females (e.g., Burke and Nol 1998) or become floaters

(without territory). This could partly explain the existence of non-permanent, lone male territories which may attract a comparatively rare dispersing female, as was observed in Superb Fairy-wrens *Malurus cyaneus* (Pruett-Jones and Lewis 1990). This type of dispersal may reflect the fact that scrub-robins are not co-operative breeders in which typically some juveniles are tolerated on the natal territory (Russell 2000).

Timing of dispersal

Males dispersed at a mean age of 299 days versus a mean female dispersal age of 310 days (mean for all birds = 286). Green and Cockburn (2001) noted that female Brown Thornbills *Acanthiza pusilla* dispersed before males, and this is generally considered to be the norm amongst other avian species (Greenwood 1980). The greater female age seen at Bakara is likely due to one juvenile briefly spotted off the natal territory who then returned to occupy the vacancy left by her probable mother. Nonetheless, delayed dispersal amongst birds tends to improve survival. Juvenile scrub-robins that fledged in 2010 left earlier than those that fledged in previous years, possibly because 2010 was a particularly wet year. A very early female departure in 2009 may have been due to her natal territory being successfully invaded. The average rainfall at nearby Mantung in the 2008–2009 years was 264 mm compared to 476 mm in the 2010–2011 years (BOM 2013); Barker (in press) noted that juvenile scrub-robin survival was higher in these latter years.

Habitat patch crossing

Scrub-robins generally avoid open areas, so it is unlikely that the crossings between the North and South habitat patches 824 m apart at the nearest point were via the direct route through a 350 m wide continuously cultivated oat field. Such movements may have been through very open woodland and/or along a 100 m wide roadside verge of *Eucalyptus* spp. trees. Although no birds were observed in the roadside corridor, two observations were made of unidentified scrub-robins very close to it, although still quite far from the nearest patch (i.e., South patch).

Based on the observations of juvenile scrub-robin dispersal routes in this study, all dispersing juveniles would have moved across some areas of open woodland with extremely sparse or no understorey cover. Scoble (2012) concluded that shrub types with less structure would impede scrub-robin movements. However, although generally considered to be an understorey-dependent bird species, the Southern Scrub-robin frequently occupies areas of eucalypt woodland (e.g., Schodde 1990; Higgins and Peter 2002), so it is quite plausible that it can disperse across open woodland and Mallee habitat. Scrub-robins in isolated patches of habitat have declined to a greater degree than birds in connected and extensive habitat at Bakara in the South Australian Murray Mallee (Barker, in press). It may be that a lack of opportunities to move to and from these areas is key to explaining the demise of scrub-robins in this area.

Caveat

It is acknowledged that the sample sizes in this investigation were relatively small and did not permit meaningful statistical analysis, but the research will hopefully provide a foundation for further studies of scrub-robin dispersal which is currently not well documented.

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