

Dispersal and recruitment of juvenile Red-capped Robins, *Petroica goodenovii*

Damian K. Dowling^{A,D}, Mark Antos^B and Tobias Sahlman^C

^ADepartment of Zoology, University of Melbourne, Vic. 3010, Australia.

^BSchool of Ecology and Environment, Deakin University, Burwood, Vic. 3125, Australia.

^CEvolutionary Biology Centre, Department of Population Biology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden.

^DTo whom correspondence should be addressed. Email: d.dowling@pgrad.unimelb.edu.au

Abstract. Data on the dispersal and recruitment of juvenile birds following fledging are largely unreported for Australian birds. In this study, we investigated the short-distance dispersal of a sample of colour-banded, juvenile Red-capped Robins, *Petroica goodenovii*, in Terrick Terrick National Park, Victoria, Australia. Of 67 colour-banded juvenile birds that successfully reached independence during the 2000–01 breeding season, eight were recruited into the study area or adjacent areas for the following breeding season. A ninth bird was resighted in Gunbower State Forest, 36 km from where it was banded. This is the furthest recorded dispersal movement of a Red-capped Robin. Of 59 colour-banded juvenile birds that reached independence during the 2001–02 season, four remained within the study area for the remainder of the breeding season, but these birds were not present in the study area during the following breeding season. Juvenile birds that successfully reached independence and dispersed were heavier as nestlings, when controlled for age and date, than birds that disappeared (assumed dead) before reaching independence. Estimates of Red-capped Robin abundances within Terrick Terrick National Park were greater than those of nearby eucalypt woodlands, suggesting that the White Cypress-pine, *Callitris glaucophylla*, woodlands within the park offer good-quality habitat for Red-capped Robins and may be saturated with breeding territories. Thus, juveniles may be forced to establish breeding territories far from their natal territories. These results are discussed in relation to avenues for further research on juvenile dispersal in Australian birds and their conservation implications.

Introduction

Natal dispersal occurs in most bird species and influences both population dynamics and genetics. With the exception of group-living birds, in which some offspring may remain in their natal territories after fledging, juveniles are forced out of natal territories by their parents to establish territories elsewhere. Juvenile dispersal in birds is often female-biased, with males remaining closer to their natal territories (Greenwood 1980). This pattern is particularly pronounced in cooperatively-breeding birds, since fledglings of one sex (usually the male) are often more likely to remain as ‘helpers’ in their natal territories. In these species, natal dispersal is well studied (Stacey and Koenig 1990). Less is known about natal dispersal in non-group-living birds, particularly Australian species, although it can also be sex-biased, with one sex dispersing further than the other (Greenwood 1980).

The dispersal patterns of a species may be largely influenced by population density (Greenwood *et al.* 1979) and variation in habitat quality and suitability (Travis and Dytham 1999). For instance, in territorial species, the reproductive success of the individual depends on dominating a

suitable habitat patch in which to breed (Kokko and Lundberg 2001). If suitable habitats within a population are already occupied, juveniles may be forced to disperse further from their natal territories, or to less preferable habitat, to establish their own breeding territories.

In passerines, differential mortality according to nestling weight is common (Martin 1987). Individuals that are relatively heavier at fledging often have increased rates of survival to independence, and a greater probability of surviving to breeding age (reviewed in Magrath 1991). In fact, the probability of surviving to nutritional independence might be an adequate estimate of the relative probability of recruitment to the breeding population in many bird species (Magrath 1991). Individuals that were heavier as nestlings may be both better able to survive and also compete for limited breeding vacancies. Competition for limited suitable breeding habitat may potentially increase with increasing habitat loss, fragmentation and degradation.

The Red-capped Robin (mean weight = 8.92 g, s.e. = 0.04, $n = 169$) is an endemic passerine found in dry woodlands and scrub of mainland Australia (Blakers *et al.* 1984). Females

are predominantly buff-grey, whereas adult males (birds older than one year) possess a characteristic red cap and bib. Males in their first year (yearlings) resemble adult females, and moult into bright male plumage at the end of their first year, following the breeding season. Thereafter, they retain this bright plumage, moulting yearly at the conclusion of the breeding season (DKD, unpublished data). Red-capped Robins are socially monogamous and territorial, with a pair defending a defined area in which they feed and breed. Males in their first year also establish territories and yearlings of both sexes can breed successfully (DKD, unpublished data).

Since the species is both socially monogamous and territorial, offspring are forced off their natal territories by their parents and establish breeding territories of their own (DKD, unpublished data). The movements of these juvenile birds after independence are unknown. In this study, we investigate the short-distance movements, condition and sex ratio of a sample of colour-banded, juvenile Red-capped Robins following dispersal from their natal territories. We also estimate Red-capped Robin abundances across a variety of woodland types within northern Victoria, Australia. Using these abundance data, we suggest which woodland types offer the most suitable habitat for the species, and hence in which habitats it might be difficult for a dispersing bird to find a vacant territory.

Methods

This research is part of a three-year study by DKD on the breeding biology and evolutionary ecology of the Red-capped Robin. Most fieldwork for the project was conducted over two breeding seasons (2000–01, 2001–02). References to 'DKD, unpublished data' refer to results that will be published elsewhere.

Study site

The study was conducted within a roughly rectangular 80-ha area (Fig. 1), dominated by White Cypress-pine, *Callitris glaucophylla*, in the southern section of Terrick Terrick National Park (36°10'S, 144°13'E), located approximately 45 km west of Echuca, Victoria. The woodland section of the park is approximately 2493 ha and consists of dry open woodland, dominated by White Cypress-pine and Grey Box, *Eucalyptus microcarpa*. Annual rainfall in the area is approximately 400 mm (LCC 1983). Areas of the park that are dominated by White Cypress-pine woodlands appear to be saturated with Red-capped Robin breeding territories (DKD, unpublished data).

Capture, measurement and observations of birds

In this study, we monitored 50 breeding pairs of robins during the 2000–01 breeding season, and 60 pairs during the 2001–02 season. Birds ($n = 158$) were caught in mist-nets and banded with a numbered metal band provided by the Australian Bird and Bat Banding Scheme, and a unique combination of plastic colour-bands to permit individual identification.

Nests were located by following breeding females continuously for 20 min. This observation period was long enough to determine whether birds had begun nesting. Each territory was checked at least every three days to determine locations of colour-banded individuals, presence of nesting activity and stage of nesting. Every time a territory was visited, the presence and location of all individuals within the territory was recorded. Throughout the breeding season, the boundaries of each

territory were mapped. Territory boundaries were defined for each breeding pair over each breeding season, using movements of birds within territories, and locations of territorial disputes between neighbours. Once found, nests were checked every three days to determine their fate. A small number of nests ($n = 8$ in 2000–01, $n = 9$ in 2001–02) were inaccessible owing to their position in the tree. At all other nests, each nestling was weighed once, to 0.1 g. Age was recorded, or calculated if unknown by comparing body traits such as body size, size of tarsi, presence of wing feather shafts, degree of body down and whether the eyes had opened with the data for the same traits in nestlings of known hatching date. Nestlings ($n = 240$) were banded with a metal band and a unique combination of three colour-bands usually when they were ~6–8 days old. A small blood sample (50 µL) was taken by brachial venipuncture and stored in 100% ethanol for subsequent molecular determination of sex according to the method described in Griffiths *et al.* (1998).

Once fledged, colour-banded juvenile robins were monitored every 3–5 days in their natal territories until evicted by their parents. Parents stop feeding fledglings and begin to actively chase them when they beg for food usually 3–4 weeks after fledging (although if it is late in the breeding season and the breeding pair has stopped all nesting activity they are more tolerant towards their juveniles remaining in their territories) (DKD, unpublished data). If juveniles disappeared from their natal territories within two weeks of fledging, while still clearly dependent on their parents for food, we assumed that these juveniles had died. Once we had observed parents acting aggressively towards their offspring, three or four weeks after fledging, we assumed that any juveniles that subsequently disappeared had dispersed. We defined these juveniles dispersing from their natal territory as independent. Following this assumed dispersal, all territories within the 80-ha study area were scanned for the presence of these juvenile birds. During the 2001–02 breeding season we also searched areas adjacent to the study area (about 246 ha in total) for colour-banded individuals (Fig. 1).

Population abundance

Counts of Red-capped Robins were conducted along 5 ha (500 × 100 m) fixed belt transects by an experienced observer. Transects were located within the four main woodland types of the Victorian Riverina: (1) White Cypress-pine woodlands within Terrick Terrick National Park, (2) Black Box, *Eucalyptus largiflorens*, woodlands within Leaghur State Park, (3) Grey Box woodlands within Gunbower State Forest, and (4) River Red Gum, *E. camaldulensis*, woodlands also within Gunbower State Forest. Six transects were surveyed within each woodland type (except for the Grey Box woodland, which contained only five transects). Between 2000 and 2002, each transect was surveyed five times during the breeding season (September–January) and four times during the non-breeding season (March–July). All transects consisted of open woodlands with similar visibility. Each transect was surveyed over a 40-min period and birds were detected by visual scanning of the habitat and listening for their calls, providing approximate counts. Birds behind the observer or well above the canopy were excluded. Surveys were conducted between 0600 and 1100 hours during calm weather.

Statistical analysis

A combined application of ANCOVA, paired *t*-tests and the binomial probability distribution was used to analyse these data. All tests are two-tailed with a significance criterion of 0.05.

We tested whether birds that fledged and successfully reached independence (and those that were resighted later) were heavier when weighed as nestlings than were those birds that did not reach independence. Nestling weight was controlled for age at weighing by taking the residuals from the logarithmic regression of weight on age. Since brood size has a marked effect on nestling weight (DKD,

unpublished data), only birds that hatched from clutches of two eggs were used in this analysis (two eggs is the modal clutch size). Date of hatching is related to nestling weight (DKD, unpublished data), and was included as a covariate in the analysis. The residuals for individual nestlings were chosen as the units for statistical analysis rather than the average for a brood because we were interested in the effects of nestling weight on dispersal success and sex, and these factors are specific to individuals rather than broods. To confirm that the results were not influenced by possible ‘within-brood’ effects, we repeated the ANCOVA without sex as a factor, after averaging within-brood residuals. Although the results were unaffected when ‘within brood’ residuals were averaged, some statistical power is lost since broods in which one nestling became independent while the other did not were omitted from the analysis.

Results

Resightings of 2000–01 juveniles

During the 2000–01 breeding season, 84 juveniles were raised to independence within the study population; 67 (70.8%) of these were colour-banded. Of the colour-banded juveniles reaching independence, nine (13.4%) were resighted during the subsequent (2001–02) breeding season. Eight of these had established their own breeding territories

within the White Cypress-pine woodland of Terrick Terrick National Park (Table 1). Half of these successfully dispersing birds (4 of 8) established territories within the study area itself. One female paired with her putative father in her natal territory (his mate disappeared between seasons). However, paternity analysis, using polymorphic DNA microsatellite markers (Dowling *et al.* 2003), revealed that this female was not sired by her putative father, but probably by an adult male in the neighbouring territory. In her first breeding season, she produced two fledglings that reached independence. Another female paired with a yearling male in a territory adjacent to her natal territory and successfully raised two offspring to independence in her first breeding season. The other two birds to acquire territories within the study area were males. One of these males fledged two offspring that reached independence, although it is not known whether he was the genetic sire. The other male did not fledge offspring. The other four birds established territories in areas adjacent to the study population in which they fledged. Data regarding their breeding success were not collected.

We were unable to account for the number of birds that successfully dispersed outside of the study area and adjacent areas that we searched. However, on 14 November 2001, a yearling male was resighted in Gunbower State Forest (35°51’54”S, 144°21’34”E), a distance of 36 km from where it was colour-banded as a nestling (36°10’22”S, 144°13’49”E) on 2 January 2001.

Resightings of 2001–02 juveniles

During the 2001–02 breeding season, 76 juveniles were raised to independence within the study population; of these, 59 (77.6%) were colour-banded (Table 1). Of the colour-banded juveniles, four (6.8%) remained within the study area following independence, occupying abandoned territories. Two female siblings were able to remain in and adjacent to their natal territory after their parents disappeared. A juvenile male also moved into this newly vacated territory from

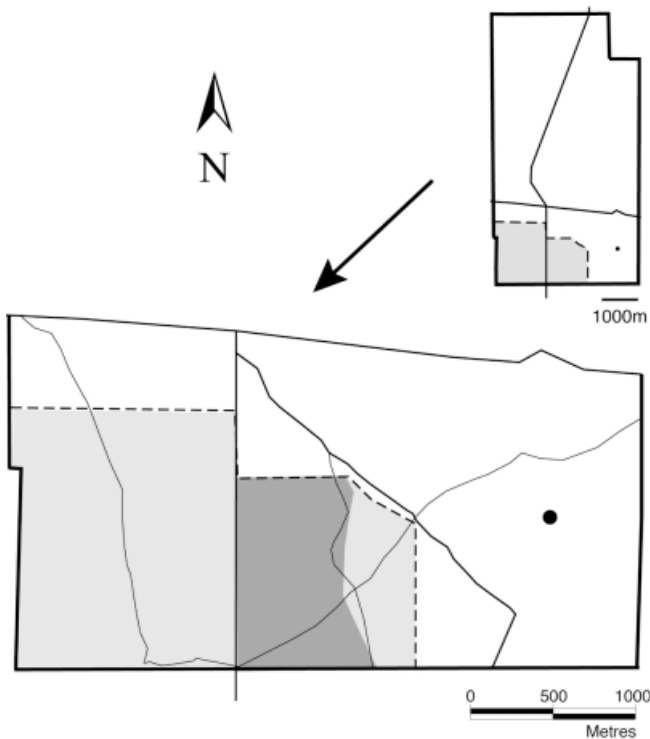


Fig. 1. Map of the study area and its position within the woodland section of Terrick Terrick National Park. Top right-hand map shows the location (grey shading) where this study was carried out within the park. The bottom diagram, an enlargement of the grey-shaded area of the top map, shows the location of the study area where breeding pairs were colour-banded and their breeding success monitored (dark grey shading), and also the location of the areas adjacent to the study area that were scanned for the presence of birds that had dispersed from the study area (light grey shading). Tracks running through the area are marked, and ● indicates Mount Terrick Terrick.

Table 1. Breeding success of study population

	2000–01	2001–02
No. of breeding pairs	50	60
No. of nesting attempts	138	142
No. of eggs	250	230
No. of nestlings	159	141
No. of fledglings	96	79
No. of juveniles reaching independence	84	76
No. of short-distance recruits ^A	8 ^B	0 ^C

^AIncludes colour-banded birds resighted only within or adjacent to the study area.

^BA ninth bird was resighted in Gunbower State Forest.

^CFour juveniles remained in the study area following dispersal, but did not hold territories here as yearlings during the following breeding season. For the 2001–02 season, only the study area (not the adjacent areas) was searched for yearlings recruited into the population.

an adjacent territory. The other bird to remain within the study area was a female that moved into an abandoned area beside her natal territory. However, these territory acquisitions were temporary since none of these juvenile birds were present in the study area during the next breeding season (2002–03). However, only five days were spent in the 80-ha study area during this season, and we spent no time in the adjacent areas. Thus, birds that had dispersed to areas adjacent to the study area went undetected and therefore estimates of recruitment following the 2001–02 breeding season are conservative.

Dispersal and nestling weight

The residuals of a logarithmic regression of weight by age, described by the function $y = 2.331x^{0.572}$ ($r^2 = 0.731$, $n = 193$), indicate relative nestling weight, controlled for age. Nestlings that are heavier than expected for their age have positive residuals while those that are lighter than expected have negative residuals. Juveniles that successfully reached independence, and were assumed to have dispersed, were heavier as nestlings, when controlled for age and date, than were birds that disappeared before reaching independence (Table 2). Additionally, there is some suggestion that juvenile birds that established their own territories after dispersal within the 246 ha area we searched were heavier as nestlings than those individuals that dispersed but were not resighted (Fig. 2). However, this statistical analysis lacks power since only 12 birds were resighted.

An analysis using averages of residuals for nestlings from the same brood gave similar results (ANCOVA: Dispersal status: $F_{2,95} = 4.557$, $P = 0.013$; Date: $F_{1,95} = 12.46$, $P = 0.001$, season and sex omitted from ANCOVA due to loss of degrees of freedom).

Paired *t*-tests (within brood tests) were conducted comparing relative weight of female and male siblings ($n = 40$),

Table 2. Effects of nestling weight on dispersal status, sex and season

Results of 3-factor ANCOVA testing the effects of nestling weight on dispersal status of juvenile birds, sex and season. Nestling weight is standardised by age when weighed (residuals of regression), with date of weighing as a covariate. Dispersal status describes at what stage an individual was last sighted and is classified into 3 categories: disappeared (assumed dead) before reaching independence, reached independence and assumingly dispersed from natal territory, or resighted following dispersal from natal territory

Factor / Interaction	<i>F</i>	<i>P</i>
Dispersal status	$F_{2,162} = 7.770$	0.001
Sex	$F_{1,162} = 0.608$	0.437
Season	$F_{1,162} = 1.076$	0.301
Dispersal status × Sex	$F_{2,162} = 0.872$	0.420
Dispersal status × Season	$F_{2,162} = 0.294$	0.746
Sex × Season	$F_{1,162} = 0.183$	0.669
Dispersal status × Sex × Season	$F_{2,162} = 0.734$	0.481
Date	$F_{1,162} = 18.832$	0.000

the relative weight of individuals that reached independence with their siblings that did not reach independence ($n = 15$ cases), and also the relative weight of individuals that were resighted within the study area and adjacent areas following dispersal with their siblings that were not resighted ($n = 10$ cases). These tests were not statistically significant, but lacked statistical power due to low sample sizes.

Sex ratio of resighted birds within the study area and adjacent areas.

In all, 52% of nestlings ($n = 239$) were female, and 53% of colour-banded offspring that reached independence and dispersed ($n = 123$) were female. Of the colour-banded juvenile birds resighted within the study area and adjacent areas, following short-distance dispersal from their natal territories, 67% were female (binomial probability distribution, $n = 12$, $P = 0.12$; Table 3).

Population abundances

Red-capped Robins were more abundant in White Cypress-pine woodlands than in Black Box, Grey Box or Red Gum woodlands ($F_{3,38} = 11.185$, $P < 0.001$). There was no difference in abundance of robins between breeding and non-breeding seasons for any woodland type ($F_{1,38} = 0.049$, $P = 0.827$) and no interaction between season and woodland type ($F_{3,38} = 0.061$, $P = 0.980$, Fig. 3). According to transect counts, the mean abundance of Red-capped Robins in White Cypress-pine woodland throughout the year was 0.64 birds per hectare.

Discussion

Population abundance, habitat quality and dispersal

Many colour-banded juveniles appeared to successfully reach independence ($n = 126$), but few were subsequently located once they dispersed from their natal territories.

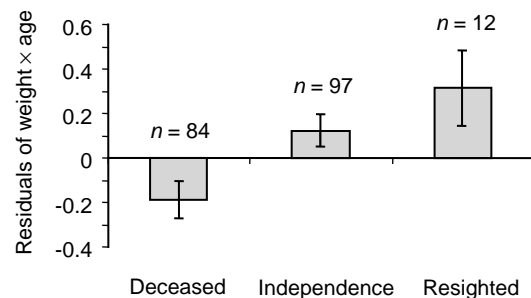


Fig. 2. Residuals of the logarithmic regression of weight (g) × age (days) of nestlings for three categories of birds: deceased – birds that disappeared (assumed dead) before they reached independence and dispersed; independence – birds that successfully fledged and became independent of their parents, dispersing from their natal territories; resighted – birds that were resighted within the study area or adjacent areas following dispersal from their natal territories. Bars indicate standard error (± 1 s.e.).

Table 3. Sex ratios of juveniles that were resighted following independence (females : males)
Percentage of females for each category is indicated in parentheses

Locality	Between seasons 2000–01 to 2001–02			Within seasons	Total
	In study area	Adjacent area	Combined	In study area	
Terrick Terrick	2:2 (50%)	3:1 (75%)	5:3 (62.5%)	3:1 (75%)	8:4 (66.7%)
Gunbower	0:1 (0%)				0:1 (0%)

Recruitment of colour-banded juveniles that reached independence during the 2000–01 breeding season into the study area and adjacent areas in the following season was 11.9%. It is unknown how far the remaining juveniles disperse, or how many survive.

We suggest that the White Cypress-pine woodland of Terrick Terrick National Park offers good-quality habitat for Red-capped Robins, based on the high abundance of birds detected there in comparison to eucalypt-dominated woodlands of northern Victoria. It has been previously noted that Red-capped Robins have a preference for native pine woodlands (Blakers *et al.* 1984; Major *et al.* 2001). Additionally, we observed that the woodland section of Terrick Terrick National Park appears to be saturated with contiguous Red-capped Robin breeding territories (authors' unpublished data), unlike the eucalypt-dominated woodlands of northern Victoria where breeding territories appear to be non-contiguous (DKD, MA, unpublished data). The study population within Terrick Terrick National Park is resident and sedentary (DKD, MA, unpublished data) and the birds do not migrate outside of the breeding season, unlike their congener the Flame Robin, *Petroica phoenicea* (Robinson 1990). Consequently, there may be few opportunities within Terrick Terrick National Park for an incoming bird to establish a territory without usurping another individual, and thus dispersing juveniles may need to establish breeding territories far from their natal territories. So, juveniles may be over-represented in relatively poor-quality habitat. Major *et al.* (1999) found that the age structure of Red-capped Robin populations in linear strips of forests, such as roadside corridors, is juvenile-biased in comparison to that of large forest blocks. Juveniles may use these linear strips as dispersal corridors, or may establish breeding territories within them.

We may not have detected yearlings that found territories further from their natal territories within the Terrick Terrick woodlands, or in other forest patches, given the observation of a colour-banded yearling within Gunbower State Forest. This is the longest recorded movement (36 km) by a Red-capped Robin, and is more than twice as far as the previous recorded longest movement (14 km) (Coventry 1988). Cale (1990) determined that Red-capped Robins (particularly adult females and/or juveniles) show a yearly cyclical change in the number of individuals in roadside reserves, with the lowest numbers recorded during the breeding season. He proposed that this cyclical pattern arises from juveniles from the previous breeding season using roadside reserves as

corridors for dispersal before the commencement of the following breeding season. Our observation of a movement to Gunbower State Forest is of interest because the area between the two forests is mainly agricultural land with limited vegetation cover, and no contiguous roadside corridors of habitat. The vegetation that exists between the forests is limited to incomplete and degraded links mainly along creeks (CFA 2000; DKD, MA, unpublished data).

Some Australian birds are able to disperse over very fragmented landscapes. For instance, the Blue-breasted Fairywren, *Malurus pulcherrimus*, is capable of dispersing at least 9 km through agricultural land that does not provide breeding habitat (Brooker and Brooker 1997, 2002). However, habitat corridors may be important in this dispersal. Brooker *et al.* (1999) created a dispersal simulation model to generate movement frequencies and distances for comparison with real dispersal frequencies collected in the field for two habitat-specific, sedentary species, the Blue-breasted Fairywren and the White-browed Babbler, *Pomatostomus superciliosus*. They found evidence that both species use habitat corridors during dispersal, and that Blue-breasted Fairywrens were inhibited by gaps in the corridors greater than about 60 m whereas White-browed Babbler would cross gaps at least 270 m wide.

Dispersal and nestling weight

Nestlings that subsequently reached independence were heavier than those that did not. Two explanations may be proposed for this pattern. First, heavier nestlings may be better

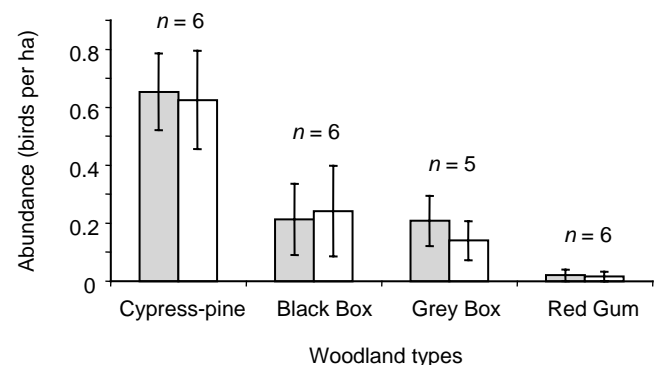


Fig. 3. Mean abundance (birds per hectare) of Red-capped Robins across four woodland types in the Victorian Riverina. Shaded columns denote abundances during breeding seasons and non-shaded columns denote non-breeding seasons. Bars indicate standard error (± 1 s.e.).

able to survive and eventually acquire their own territories. Heavier Blackbird, *Turdus merula*, nestlings have an increased probability of survival to independence (Magrath 1991). However, in this Red-capped Robin population, starvation of nestlings was very rare ($n = 2$ broods), and it appeared that most nest failure was caused by predation (DKD, unpublished data). It was rare for one nestling within a brood to survive to fledging while the other did not. Generally entire broods survived or died in the nest. Furthermore, mortality between fledging and independence was rare ($n = 15$). Thus, nestling weight did not appear to be related to starvation within the nest, with predation instead the major determinant of nesting success. Alternatively, parental quality may explain the observed correlation. Good-quality parents may be potentially better able to conceal their nest from potential predators, defend the nest, and feed their nestlings. If good-quality parents produce both more fledglings (lower nest predation) and heavier fledglings (increased food provisioning), this could explain the relationship between offspring survival to independence and their weight as nestlings.

Sex ratios and local recruitment

Two-thirds of birds resighted within the study area and adjacent areas following their independence were female. Although not significant, this test lacked statistical power due to the low number of resighted birds. Sex-specific dispersal has been noted in other bird species and is usually female-biased, with males recruited closer to their natal territories (Greenwood 1980). It occurs in cooperatively breeding species since, in these species, offspring delay dispersal from their natal territories to help their parents raise subsequent offspring, and these helpers are predominantly the one sex (Russell and Rowley 1993; Mulder 1995; Komdeur 1996; Brooker and Brooker 1997). However, sex-biased natal dispersal also occurs in non-group-living birds. In these cases, the sex-bias in dispersal is related to distance dispersed rather than the likelihood of dispersal (Greenwood 1980).

Owing to the low number of resighted birds, we are unable to determine whether sex-biases in dispersal and recruitment occur in this population. However, 8 of the 12 juveniles that were later resighted within Terrick Terrick National Park were females and this potential bias may be related to the higher turnover of breeding females within the study population. At the beginning of the 2001–02 breeding season 30 of 48 (62.5%) banded males that had held territories during the previous season remained within the study area compared with 13 of 42 (31%) females (although retention rates within the study area between the sexes at the start of the 2002–03 season were similar – males, 27 of 60 [45%]; females, 18 of 43 [41.9%]: DKD, unpublished data). Although we have no data on turnover rates of breeding birds for areas adjacent to the study area, where three dispersing juvenile females established territories compared with one

male, the above data suggest that breeding females may have higher dispersal or mortality rates between seasons, and thus there may be more opportunities for juvenile females to find vacant territories close to their natal territories.

Conclusions

This study suggests interesting avenues for further research into the dispersal and recruitment of juvenile Red-capped Robins, and other bird species from source populations. One useful approach may be to attach radio-transmitters to dispersing juveniles to enable collection of comprehensive data on dispersal distance and survival for both sexes. This would provide valuable information on movements over relatively short distances, whether different habitat types are used by different age-classes or sexes, and also whether habitat corridors are important in promoting dispersal of juvenile birds. Radio-tracking, used to collect data on natal dispersal in the Acorn Woodpecker, *Melanerpes formicivorus*, showed that long-distance dispersal is much more frequent than previously suspected in this species (Koenig *et al.* 1996, 2000).

Modern genetic techniques are useful in determining gene flow at larger scales, thereby indicating whether movement of individuals between populations occurs. Such analyses suggest detectable levels of gene flow over 1599 km in Australian Magpie, *Gymnorhina tibicen*, populations (Baker *et al.* 2001) and between populations separated by over 1000 km in Grey-crowned Babblers, *Pomatostomus temporalis* (Edwards 1993).

The dispersal of a juvenile Red-capped Robin from Terrick Terrick National Park to Gunbower State Forest is an encouraging sign for this species, which is in decline in eastern Australia (Robinson 1994). It confirms that juvenile Red-capped Robins can move between forest patches, and conserving the few corridors and remnant patches of vegetation still remaining will conceivably facilitate this dispersal. Apart from providing corridors and stepping stones for dispersal, such patches may serve as sinks for juvenile birds. Further knowledge regarding the biology of dispersal and habitat requirements of dispersing birds will have implications for future conservation management.

Acknowledgments

We are grateful to Raoul Mulder for advice and assistance throughout this project. We thank Sophie Allebone-Webb, Michelle Simeoni, Jessica Feder, Wouter van Dongen, and Thijs van Overveld for field assistance. We are grateful to David Morgan, Michael Magrath, Greg Adcock and Iain Woxfold for helpful discussions and statistical advice. We thank Raoul Mulder and David Morgan for commenting on an earlier draft of the manuscript. Comments by two referees during the review process greatly improved the manuscript. We thank David Paul for his help in drawing Fig. 1. We thank Barry and Lois Schramm for their kind hospitality during our stay in Mitiamo. This research was supported by the

Department of Zoology, University of Melbourne, and grants from the Holsworth Wildlife Research Fund and Birds Australia, through the Stuart Leslie Bird Research Fund and the VicGroup Research Fund. It was carried out under relevant permits from the Department of Sustainability and Environment, Victoria.

References

- Baker, A. M., Mather, P. B., and Hughes, J. M. (2001). Evidence for long-distance dispersal in a sedentary passerine, *Gymnorhina tibicen* (Artamidae). *Biological Journal of the Linnean Society* **72**, 333–343.
- Blakers, M., Davies, S. J. J. F., and Reilly, P. N. (1984). 'The Atlas of Australian Birds.' (Royal Australasian Ornithologists Union/Melbourne University Press: Melbourne.)
- Brooker, L., and Brooker, M. (2002). Dispersal and population dynamics of the Blue-breasted Fairy-wren, *Malurus pulcherrimus*, in fragmented habitat in the Western Australian wheatbelt. *Wildlife Research* **29**, 225–233.
- Brooker, L., Brooker, M., and Cale, P. (1999). Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal mortality. *Conservation Ecology* [online] **3**: 4. Available from the Internet. URL: <http://www.consecol.org/vol3/iss1/art4>.
- Brooker, M., and Brooker, L. (1997). Dispersal of the Blue-breasted Fairy-wren in fragmented habitat in the wheatbelt of Western Australia. *Pacific Conservation Biology* **3**, 295–300.
- Cale, P. (1990). The value of road reserves to the avifauna of the central wheatbelt of Western Australia. *Proceedings of the Ecological Society of Australia* **16**, 359–367.
- CFA (2000). 'CFA Region 20 – Rural Directory.' 2nd Edn. (Country Fire Authority: Kerang, Victoria.)
- Coventry, P. (1988). Notes on the breeding behaviour of the Red-capped Robin *Petroica goodenovii*. *Australian Bird Watcher* **12**, 209–216.
- Dowling, D. K., Adcock, G. A., and Mulder, R. A. (2003). Novel polymorphic microsatellite markers for paternity analysis in the Red-capped Robin (*Petroica goodenovii*: Aves). *Molecular Ecology Notes*. DOI: 10.1046/j.1471-8286.2003.00497
- Edwards, S. V. (1993). Long-distance gene flow in a cooperative breeder detected in genealogies of mitochondrial DNA sequences. *Proceedings of the Royal Society of London – Series B* **252**, 177–185.
- Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* **28**, 1140–1162.
- Greenwood, P. J., Harvey, P. H., and Perrins, C. M. (1979). The role of dispersal in the great tit (*Parus major*): the causes, consequences and heritability of natal dispersal. *Journal of Animal Ecology* **48**, 123–142.
- Griffiths, R., Double, M. C., Orr, K., and Dawson, R. J. G. (1998). A DNA test to sex most birds. *Molecular Ecology* **7**, 1071–1075.
- Koenig, W. D., Van Vuren, D., and Hooge, P. N. (1996). Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology and Evolution* **11**, 514–517.
- Koenig, W. D., Hooge, P. N., Stanback, M. T., and Haydock, J. (2000). Natal dispersal in the cooperatively breeding Acorn Woodpecker. *Condor* **102**, 492–502.
- Kokko, H., and Lundberg, P. (2001). Dispersal, migration, and offspring retention in saturated habitats. *The American Naturalist* **157**, 188–202.
- Komdeur, J. (1996). Facultative sex ratio bias in the offspring of Seychelles warblers. *Proceedings of the Royal Society of London – Series B* **263**, 661–666.
- LCC (1983). Report on the Murray Valley Area. Land Conservation Council, Victoria.
- Magrath, R. D. (1991). Nestling weight and juvenile survival in the Blackbird *Turdus merula*. *Journal of Animal Ecology* **60**, 335–352.
- Major, R. E., Christie, F. J., Gowing, G., and Ivison, T. J. (1999). Age structure and density of Red-capped Robin populations vary with habitat size and shape. *Journal of Applied Ecology* **36**, 1–8.
- Major, R. E., Christie, F. J., and Gowing, G. (2001). Influence of remnant and landscape attributes on Australian woodland bird communities. *Biological Conservation* **102**, 47–66.
- Martin, T. E. (1987). Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* **18**, 452–487.
- Mulder, R. A. (1995). Natal and breeding dispersal in a co-operative, extra-group-mating bird. *Journal of Avian Biology* **26**, 234–240.
- Robinson, D. (1990). The nesting ecology of the sympatric Scarlet Robin *Petroica multicolor* and Flame Robin *P. phoenicea* populations in open eucalypt forest. *Emu* **90**, 40–52.
- Robinson, D. (1994). Research plan for threatened woodland birds of southeastern Australia. Arthur Rylah Institute for Environmental Research, Technical Report Series No. 133. (DCNR: Melbourne.)
- Russell, E. M., and Rowley, I. (1993). Philopatry or dispersal: competition for territory vacancies in the Splendid Fairy-wren, *Malurus splendens*. *Animal Behaviour* **45**, 519–539.
- Stacey, P. B., and Koenig, W. D. (Eds) (1990). 'Cooperative Breeding in Birds: Long Term Studies of Ecology and Behavior.' (Cambridge University Press: Cambridge.)
- Travis, J. M. J., and Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London – Series B* **266**, 723–728.

Manuscript received 2 January 2003; accepted 3 September 2003