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Breeding and population parameters of robins in a woodland remnant in northern New South Wales, Australia

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Abstract. Breeding and population parameters of the Scarlet Robin (*Petroica multicolor*) and Eastern Yellow Robin (*Eopsaltria australis*) were studied by colour-banding and nest monitoring at Imbota Nature Reserve, a 270-ha woodland remnant, on the New England Tableland of New South Wales in 2000–02. Yellow Robin density was one pair or group to ~30 ha, or 0.1 bird ha^{-1}, with pairs or groups occupying home-ranges of ~5–6 ha. Scarlet Robin density was one pair to ~25 ha or 0.08 bird ha^{-1}, with pairs occupying home-ranges of ~10 ha. Yellow Robins laid in August–January, mainly August–November, and fledging reached a peak in September–October; Scarlet Robins laid in August–December, with a peak of laying and fledging in September–October. Nesting success was 33% for Yellow Robins ($n = 40$ nesting attempts), with overall production of 0.6 fledglings per attempt, and 9% for Scarlet Robins ($n = 45$), with production of 0.1 fledglings per attempt; Mayfield values for nest-survival were 24% and 8% respectively. Predation, frequently by medium-sized or large birds, was the main cause of nest-failure (71% for Yellow Robins, 86% for Scarlet Robins). Fledgling survival to independence was 73% for Yellow Robins and 64% for Scarlet Robins. Annual survival of adult Yellow Robins averaged 71%; that of Scarlet Robins was 58%. The Yellow Robin population in Imbota may be self-sustaining, whereas the Scarlet Robin population may depend on immigration.

Introduction

The Scarlet Robin (*Petroica multicolor*) and Eastern Yellow Robin (*Eopsaltria australis*, hereafter Yellow Robin) are small (~13 g and ~20 g respectively), socially monogamous passerines of forests and woodlands. The pair-breeding Scarlet Robin inhabits open forests and humid woodlands of temperate eastern and south-western Australia, and the facultatively co-operatively breeding Yellow Robin inhabits forests, dense woodlands or scrub in tropical to temperate, moist to semi-arid eastern Australia (Marchant 1985, 1987; Robinson 1990*a*; Higgins and Peter 2003). Some Yellow Robin pairs have one or two auxiliaries that help to feed the nesting female and young (Marchant 1985, 1987).

Both robin species are among the passerines thought to be declining in remnant woodland in south-eastern Australia (Reid 1999, 2000; Watson *et al*. 2003), although recent evidence on the Yellow Robin is contradictory (Barrett and Silcocks 2002; Barrett *et al*. 2003; Radford and Bennett 2005). The suite of declining passerines in the temperate woodlands includes ground-foraging insectivores of endemic or near-endemic families (robins and flycatchers: Petroicidae and Dicruridae) that build open, cup-shaped nests in the tree and shrub canopy (see Ford *et al*. 2001; Major *et al*. 2001; Mac Nally and Horrocks 2002; Cogger *et al*. 2003; Seddon *et al*. 2003; Watson *et al*. 2003; Antos and Bennett 2005). Robins have been identified as 'focal' species that appear most sensitive to loss, fragmentation and degradation of habitat in rural landscapes (Lambeck 2002; Watson *et al*. 2001, 2003).

Nest-success (the proportion of nests producing fledglings) for small, open-nesting woodland passerines in southern Australia, and specifically for robins and flycatchers in remnant woodland on the New England Tableland, northern New South Wales (NSW), is low, typically 10–40% (reviewed by Ford *et al*. 2001; Higgins *et al*. 2001; Higgins and Peter 2003; also Trémont and Ford 2000; Fitri and Ford 2003; Debus and Lollback 2005). The few available data indicate high adult survival for Yellow Robins (75%) and Scarlet Robins (67–88%) in mainland Australia, though lower for Scarlet Robins on Norfolk Island (40–70%) (Marchant 1985; Major 1989; Robinson 1990*a*). There are some site-specific estimates of density and territory or home-range for these two species, and most aspects of their breeding biology are well known (summarised in Higgins and Peter 2003). However, knowledge is deficient on the influence of breeding productivity and recruitment on population dynamics for these, and most other, Australian passerines, and especially how these may be influenced by habitat fragmentation.

The aim of this study was to collect data on the breeding success, productivity, recruitment and survival of Scarlet and Yellow Robin populations in a fairly large, though apparently isolated, woodland remnant. Some data were also collected on dispersal into and out of the remnant. The study site is large enough to have retained focal species in a cleared and fragmented landscape; there are potential source areas within 10 km, and smaller remnants in the surrounding matrix. Yellow

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Robins have disappeared from some of these remnants, but Scarlet Robins are still widespread among them. The main aim of the study was to determine whether the two species are self-sustaining in the study site, whether the site could act as a source of immigrants for smaller surrounding remnants, or whether robin populations are dependent on immigrants from more extensive areas of woodland and forest.

Materials and methods

Study area

Armidale (30°30′S, 151°40′E), at 1000 m elevation on the New England Tableland, NSW, has a moderately humid climate with ~800 mm annual rainfall and cold winters (average July minimum 0°C). The study region is described in more detail in Debus *et al*. (2006). The site for the present study was Imbota Nature Reserve (NR) (formerly Eastwood State Forest), 10 km south-east of Armidale. This gently undulating patch of woodland of ~270 ha, including contiguous woodland on private land, has been described by Ford *et al*. (1985, 1986), NPWS (2002) and Hunter (2003); in size it falls between the 'small' (55 ha) and 'large' (>500 ha) remnants in which Zanette (2000) studied the demography of Yellow Robins on the western New England Tableland. The habitat is grassy open forest or woodland dominated by Broad-leaved Stringybark (*Eucalyptus caliginosa*) with Apple Box (*E. bridgesiana*) on ridges, Yellow Box (*E. melliodora*) and Blakely's Red Gum (*E. blakelyi*) on slopes, Manna Gum (*E. viminalis*) in drainage lines and on lower flats, and a patchy mid-storey, mainly of Fern-leaved Wattle (*Acacia filicifolia*) with occasional thickets of *Cassinia* and *Olearia* spp. A dry ridge, stony on the highest points, runs approximately north–south. Imbota NR is 7–10 km from other patches known to support Yellow Robins. Landscape details and the context of Imbota are described in Debus *et al*. (2006).

The study was conducted across three breeding seasons from July 2000 to February 2003. The study years 2000–02 had below-average rainfall (83–86%) and winter minimum temperatures (by 0.5–2°C). Of the three years, 2002 was the driest with a particularly dry and cold autumn–winter and record frosts (83% average annual rainfall, almost nil in April and July; winter minimum 2°C below average (P. Burr, unpublished University of New England (UNE) weather data).

Methods

I searched Imbota intensively for Yellow Robin and Scarlet Robin territories, on a grid-pattern over 8 days in late July and early August 2000. North–south traverses at 50-m intervals covered the entire reserve. I searched for nests intensively (daily to weekly, around efforts to band adult robins) throughout the entire reserve, over three breeding seasons from September 2000 to January 2003, mostly by following nest-building females, although some nests (those that failed early) may have been missed. I made the greatest effort to find nests in the third spring (2002), by searching daily from August and only banding nestlings or fledglings.

Robins were mist-netted and individually colour-banded, including nestlings or new fledglings, from early July 2000 on. Several adult male Scarlet Robins were also captured by luring them into nets with call-playback and a museum specimen mounted on the cassette player (a method attempted unsuccessfully for Yellow Robins).

Approximate boundaries of home-ranges were inferred from sightings of colour-banded, breeding adults during the breeding season, the location of boundary disputes between neighbouring pairs, and the mid-point between nearest nests of neighbours. The defended area enclosing a pair's cumulative nest-sites was assumed to be the breeding territory. Unpaired males, because they sang and defended the territory, were used in calculations of pair density. The only unpaired female detected, a Yellow Robin, was a 'floater' not included in pair density until she acquired a mate and territory. Total population and mean pair densities were calculated by averaging the number of pairs or groups in the 270 ha over the 3 years; population density included unpaired adults and auxiliaries. The woodland extended just beyond the north-western corner of Imbota (Figs 1, 2), but grazed private land was not occupied by the robins, except marginally as shown. For the purpose of this paper, Yellow Robin pairs include groups (i.e. pair plus helper(s)).

Robin nests were monitored daily, or almost daily, until success or failure was confirmed by the presence of fledglings, by the behaviour

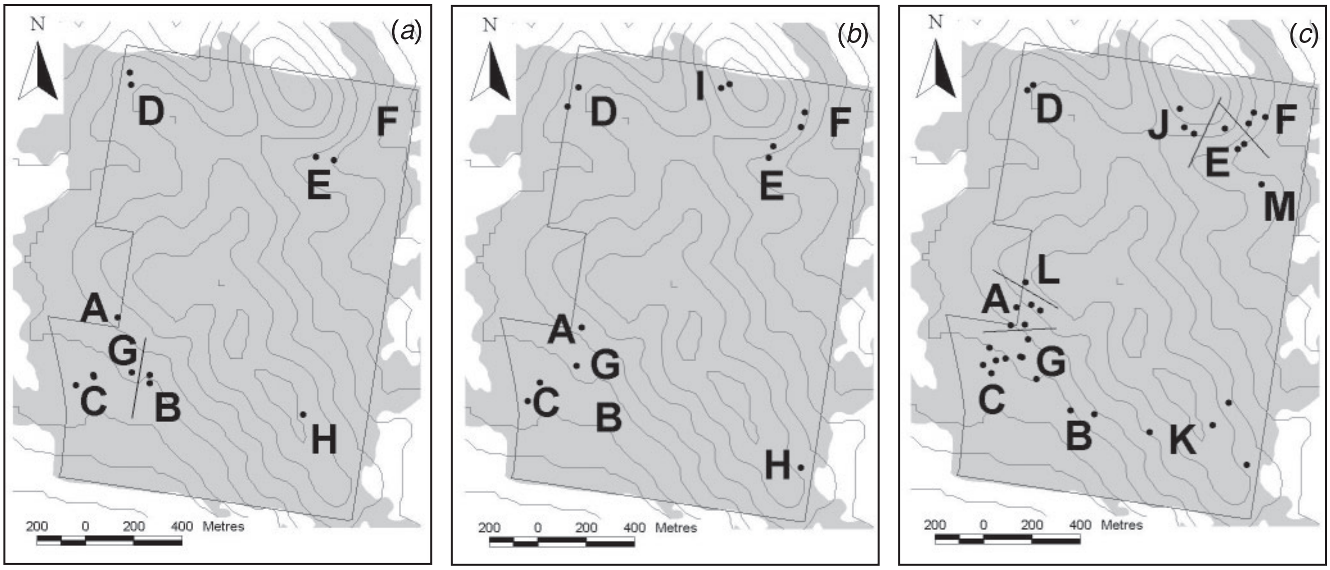

Fig. 1. Distribution of Eastern Yellow Robin nests (●) in Imbota Nature Reserve, Armidale: (*a*) 2000, (*b*) 2001, and (*c*) 2002. Territories coded A–M according to colour-banded adult male; shading = open forest and woodland. Some pairs were not found in 2000; and active nests of some pairs were not found in some years. In 2002, in early spring, new pair K expanded into vacated territory H, and in late spring pair G expanded into vacated territory C; by summer pairs A and M had disappeared.

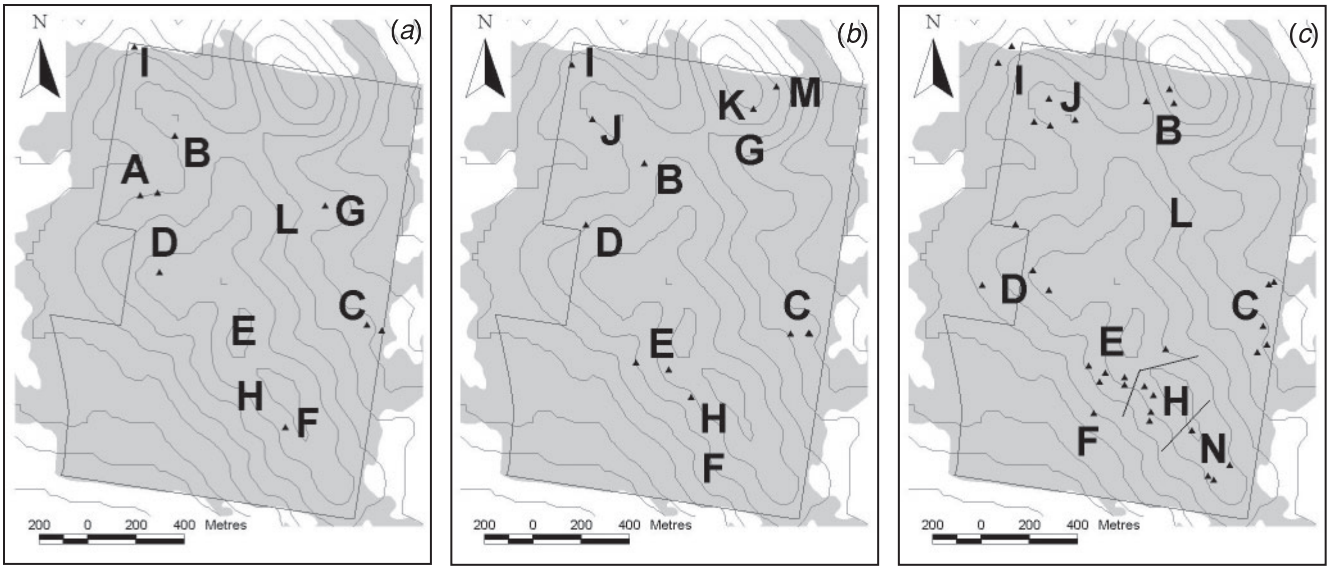

Fig. 2. Distribution of Scarlet Robin nests (▲) in Imbota Nature Reserve, Armidale: (*a*) 2000, (*b*) 2001, and (*c*) 2002. Codes as in Fig. 1. Some pairs, or their active nests, were not found in 2000; some males had no mate or nest in 2001 or 2002.

of the adults (e.g. rebuilding), or by evidence such as destroyed or deserted nests or eggs, or chicks missing before fledging age was reached. For failed nests checked at intervals >1 day, the date of failure was taken as the midpoint between penultimate and final checks (from Mayfield 1975). Causes of failure were ascertained where possible. Care was taken to avoid revealing nests to predators, because Pied Currawongs (*Strepera graculina*) followed and watched humans and investigated activities such as mist-netting. Nests were marked by surveyor's tape ~20 m from the nest, observed from a distance through binoculars, and visited or checked as briefly as possible in the apparent absence of Currawongs (e.g. when Currawongs left the reserve to forage outside it). Nests above eye-level up to 6–7 m were checked with a mirror, 3-m telescopic pole and 2-m step-ladder sparingly, as necessary, only in the absence of parental cues; eggs or nestlings at higher, inaccessible nests were inferred from parental behaviour and known incubation and nestling periods.

Laying dates of robins, if not determined directly from observation of nests found at building, laying or start of incubation, were estimated from the fledging date, from known nestling and incubation periods (Higgins and Peter 2003; this study). Only those nests in which laying occurred (or was inferred from parental behaviour) were included in calculations of nest-success, i.e. nests abandoned before completion were excluded, and all nests active from laying on were included. Most nests in 2002 were found before or during laying. The Mayfield method (Mayfield 1975; Johnson 1979) was used to calculate nest-survival from daily survival probabilities, but apparent nest-success (the proportion of nests receiving eggs that fledged young, regardless of the stage when found) was also used for comparison with previous studies. The Mayfield method overcomes biases associated with missing nests that fail early, and with finding nests at various stages of progress.

Predation of eggs was attributed to small birds if damaged egg(s) remained *in situ* with a characteristic rectangular hole pecked in the shell (Zanette 1997). Nestling predation was attributed to a Currawong (*Strepera*) or butcherbird (*Cracticus*) if the carcass was wedged in the crotch of a tree and stripped of flesh in the manner characteristic of these large artamids (Strahan 1996).

Fledgling Yellow Robins and Scarlet Robins, colour-banded as nestlings or new fledglings, were observed approximately weekly until independence (17 Yellow Robin broods; four Scarlet Robin broods). On each occasion, the territory was searched and observed sufficiently long (usually ~20 min) to confirm provision of food by parents and the presence of dependent or foraging juveniles. Juveniles were assumed to be no longer in the natal territory if two or more repeat searches failed to detect them; there were no subsequent resightings that refuted this assumption. Juveniles of each species (four Yellow, four Scarlet) were also retrapped in their natal territory one or more times between fledging and independence.

Annual adult survival (spring to spring) was calculated as the proportion of banded birds still alive on their banding anniversary (or from their first to second anniversary if banded as juveniles) in each of the two periods 2000–01 and 2001–02. All adult Yellow Robins, all breeding male Scarlet Robins and most female Scarlet Robins in the patch were banded during this period. Years were treated as independent, as most birds were observed over a single 1-year interval. It was assumed that no live birds were missed in this small, isolated, intensively monitored population, because movements between territories were easily detected and no birds presumed dead were later detected alive. However, it is possible that adults left Imbota, although Imbota is surrounded by mostly cleared country. Male Yellow Robins are philopatric (Marchant 1985, 1987; this study).

Chi-square tests were used to compare survival between years and sexes, and fledging rate by stage of season.

The finite rate of increase (λ) of robins was calculated by the method and assumptions of Zanette (2000), i.e.

$$\lambda = (\text{female survival} + n \text{ independent female young per female per year}) \times \text{subadult survival},$$

except that in this study there were insufficient data on subadult survival, so the latter figure was assumed to be the same as adult survival.

Means are presented ± one standard error.

Results

Home-ranges and occupancy

For the Yellow Robin at Imbota (Fig. 1), there were eight known pairs throughout spring 2000, nine pairs plus an apparently unpaired adult female (with brood-patch) throughout spring 2001, and 12 pairs plus an unpaired adult female in early spring 2002, though numbers declined to eight pairs by late spring in 2002. Another two pairs disappeared in early summer 2002–03, leaving six pairs. There were on average nine pairs or groups in ~270 ha of woodland, giving one pair or group per ~30 ha (18–26 adults in any one year, or 0.07–0.1 birds ha^{-1}). They occurred only at the periphery of Imbota (Fig. 1); their absence from the middle of the reserve was genuine, related to habitat (S. J. S. Debus, unpublished data) and not attributable to lack of searching. Pairs appeared to occupy home-ranges of 5–6 ha where they had neighbours, or double this area where they lacked neighbours or they were able to occupy the former range of their absent neighbours. Pairs extended their foraging range in winter, overlapping with their occupied neighbours' home-ranges. Auxiliaries usually stayed within the home-range of their parents.

In 2000, two Yellow Robin pairs at Imbota (B and C; 25% of pairs) had an auxiliary; in 2001 four pairs (44%) had either one (F, H) or two (B, C) auxiliaries; and in 2002 two of 12 pairs (D and H; 17%) and later two of eight pairs (D and E, 25%) had an auxiliary. Seven of 11 auxiliaries were known to be previous young of the pair; one breeding male was also a helper in the previous year; and five helper males became breeders in their natal territory or a neighbouring territory.

Scarlet Robins at Imbota occurred in pairs, with all breeding males in full adult plumage. There were nine known pairs plus one apparently unpaired male in spring 2000; 10 pairs plus two unpaired males in spring 2001 (male D was also unpaired in early spring); and nine known pairs plus one unpaired male in 2002. There were on average 11 occupied territories in 270 ha (Fig. 2), giving one territory per ~25 ha (0.07–0.08 birds ha^{-1}). Their distribution was fairly even, though with gaps in the middle and south-west of the reserve; pairs appeared to occupy home-ranges of ~10 ha. Pairs extended their foraging ranges in winter: either into adjacent paddocks or, for more centrally located pairs, into parts of the reserve otherwise unoccupied by conspecifics. Nearly half (42%) of known females, in a population of 9–10 pairs, disappeared and were replaced between spring 2000 and spring 2002, and between one and three adult males (of a population of 10–12 territorial males) were unpaired for all or part of a given spring in that time. There were minor influxes of unbanded Scarlet Robins, including 1–2 adult males per year, to Imbota in autumn, but most of these evaded banding.

Nesting seasonality

Yellow Robins laid eggs from mid-August to early January, mainly in August–November (*n* = 52 clutches; Fig. 3). Scarlet Robins laid eggs from mid-August to early December, with a peak in September–October (*n* = 46 clutches; Fig. 3).

Half the Yellow Robin broods fledged in September, from early clutches, with fewer fledging in later months (Fig. 3). However, the difference between early fledged broods (September–October, *n* = 9) and late-fledged broods (late November–January, *n* = 2, 2, 1 broods in November, December and January respectively) was not significant, perhaps owing to small sample size ($\chi^2_1 = 1.14$, $P > 0.25$). Fledged Scarlet Robin broods were also mainly from early clutches: one in September and three in early to mid-October (all of which survived to independence), versus one in November (which died within a week of fledging).

Productivity and survival

Nest-success of Yellow Robins in Imbota was 33% over three breeding seasons 2000–02 (*n* = 40 nests that received eggs); the Mayfield-adjusted probability of nest-survival from laying to fledging was 0.24 ± 0.011. Mean clutch-size was 2.2 ± 0.11 (range 2–3, *n* = 15); mean brood-size at hatching was 1.9 ± 0.15 (range 1–3, *n* = 16); and mean brood-size at fledging was 1.8 ± 0.18 (range 1–3, *n* = 12). Where clutch-size and outcome were known, of 33 eggs, 21 hatched (64% hatching success) and six (18%) produced fledglings (29% of eggs that hatched). Brood-sizes in nests (B/1 = brood of one, etc.) were B/1 × 4, B/2 × 10, B/3 × 2, with two cases of B/1 plus an unhatched egg near the fledging stage. Brood-sizes at fledging were B/1 × 4, B/2 × 7, B/3 × 1. Overall (data for pairs and groups pooled), Yellow Robins raised 0.6 fledglings per attempt, and 1.0 young per pair per year; these outcomes were the same for pairs and groups (30 attempts/19 pair-years *v.* 13 attempts/8 pair-years respectively).

Scarlet Robin nest-success was 9% over three breeding seasons 2000–02 (*n* = 45 nests that received eggs); the Mayfield-adjusted probability of nest survival was 0.08 ± 0.016. Insufficient data were obtained on clutch-size. Brood-sizes in nests were B/1 × 2, B/2 × 2, B/3 × 1 (mean 1.8), with

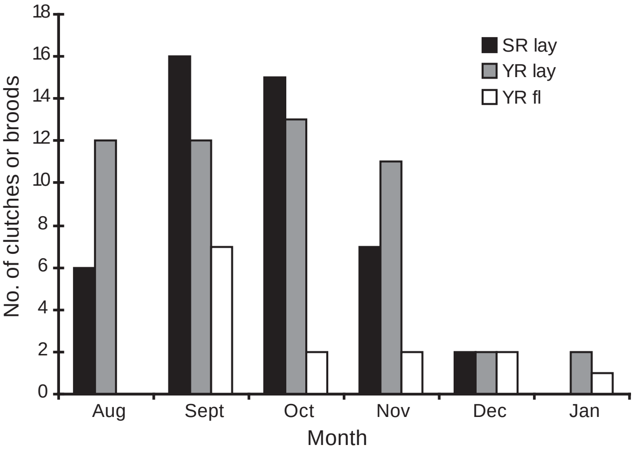

Fig. 3. Number of clutches initiated by Scarlet Robins and Yellow Robins, and number of successful broods fledged by Yellow Robins, per month in Imbota Nature Reserve, Armidale, 2000–02.

one case of B/1 plus an unhatched egg and one of B/1 plus two unhatched eggs near the fledging stage. Brood-sizes at fledging were B/1 × 2, B/2 × 3 (mean 1.6). Scarlet Robins raised 0.1 fledglings per attempt, and 0.3 young per pair per year.

Predation on eggs or nestlings was the primary cause of nest-failure, accounting for 71% of failed Yellow Robin nests, 86% of failed Scarlet Robin nests, and 80% for both species combined (Table 1). One incubating Yellow Robin was killed and plucked on the nest, as well as her eggs eaten. Unknown causes included three Yellow Robin nests that were empty and dislodged around the time of laying, and seven Scarlet Robin nests that were missing, damaged or empty and dislodged around the time of laying, possibly the result of predation, although weather or poor attachment of the nest could not be discounted.

Nests not included in Table 1 include one Yellow Robin nest that was dislodged by gale-force winds before the laying stage, and six Yellow Robin nests that were abandoned halfway through construction. Of the latter, the male Robin disappeared in one case (the female subsequently moved to another territory), the female disappeared in two cases, and there was no apparent cause in the other three cases, as the pairs proceeded with a new nest and clutch.

The identity of nest predators was seldom confirmed. Small birds damaged the egg(s) of four Yellow Robin clutches, and probably of four Scarlet Robin clutches (holed or broken eggshells found below nests). A honeyeater breast-feather (from Fuscous (*Lichenostomus fuscus*) or Brown-headed (*Melithreptus brevirostris*) Honeyeater) was stuck with egg yolk to the nest substrate. A Brown-headed Honeyeater was observed investigating a Yellow Robin nest with eggs, but the returning female Robin successfully defended the nest and resumed incubating.

Pied Currawongs were twice observed robbing Scarlet Robin nests containing eggs. A currawong or butcherbird robbed one Scarlet Robin nest: the single large feathered nestling was found wedged and stripped of flesh, artamid-style, in a crotch in the nest-shrub, 0.8 m above the nest. At a Yellow Robin nest with young at the fledging stage, a Pied Currawong was disturbed by the observer and retreated; the parent Yellow Robin approached the nest and called softly (piping call), whereupon the fledglings jumped from the nest and fluttered down to hide on the ground. The Currawong later returned, and searched and destroyed the nest.

One of a brood of three Yellow Robin hatchlings taken from their low (0.8 m) nest was left on the ground; the situation and head-wound (triangular peck-mark) suggested that a large ground-foraging bird (probably Australian Magpie (*Gymnorhina tibicen*)) had pulled the nest down. Other records of predation during the study period on open, cup-shaped nests in the tree canopy at Imbota included Grey Shrike-thrushes (*Colluricincla harmonica*), Black-faced Cuckoo-shrikes (*Coracina novaehollandiae*), Grey Butcherbirds (*Cracticus torquatus*) and Currawongs robbing the eggs or nestlings of the Leaden Flycatcher (*Myiagra rubecula*), Restless Flycatcher (*M. inquieta*), Red Wattlebird (*Anthochaera carunculata*) and other passerines (B. Chaffey, S. Trémont, C. Turbill, and K. Tokue, personal communications).

Of 45 fledglings from 26 successful Yellow Robin broods, 12 (27%) disappeared, presumed dead, within 1–2 weeks of fledging while still fully dependent. A Pied Currawong was observed with prey that resembled a newly fledged robin, near the latter's hiding place; the fledgling in that robin territory had been out of the nest for 2 h, and was not seen again. Another fledgling robin was found dead (it had been injured) less than 1 week after fledging.

Of 14 fledglings from eight successful Scarlet Robin broods, five (36%) disappeared, presumed dead, within 1–2 weeks of fledging. Predation on Scarlet Robin nests and young in Imbota was high, with no fledglings reaching independence in 2001 from a breeding population of 10 pairs.

Forty-five Yellow Robins fledged, 33 (73%) survived to independence, and 14 (42%) subsequently disappeared from Imbota, presumably having died or dispersed, within their first year. Fifteen (45%) remained in Imbota a year later; and the fate of four unbanded birds was undetermined, although up to three of these could have joined the breeding population, in other territories in Imbota, a year later. Two dis-

Table 1. Causes of nest-failure for Eastern Yellow Robins and Scarlet Robins, 2000–02
Predation assumed if eggs disappeared or nestlings disappeared before fledging age

Species	Predation[A]	Weather	Desertion	Unknown	Total
Eastern Yellow Robin	27 (14, 10, 3)	2[B]	4[C]	5	38
Scarlet Robin	44 (24, 14, 6)	0	0	7	51
Both species	71 (38, 24, 9)	2	4	12	89

[A] Figures in parentheses are, respectively: predation on eggs, predation on nestlings, and predation on either.

[B] One early clutch (mid-Aug.) was abandoned at time of snowfall; one high nest with eggs was dislodged by strong wind.

[C] All at egg stage: two of these possibly research-induced, and two possibly predator-induced (apparent predation attempt on incubating female, which lost feathers; and Pied Currawongs foraging within 10 m of nest, which was not robbed).

persed 7 km to Yina Nature Reserve, but one later returned to Imbota (S. J. S. Debus, unpublished data).

Those Yellow Robins that remained in Imbota became helpers in their natal territory (*n* = 7), the breeding male in the neighbouring territory (*n* = 2), or the breeding male in their natal territory (*n* = 2). Of the yearling helpers, two disappeared in their second year and two subsequently became breeding males in other territories in Imbota. Five of the fifteen banded subadults that stayed in Imbota for 1+ years were known males and seven were helpers (i.e. suspected males) whereas, at most, two became breeding females within Imbota; one other bird disappeared. Conversely, both the birds that dispersed to Yina were females that paired with banded males. Subadult survival could have been at least 52–61%, with some dispersing birds unaccounted for.

Nine (64%) of 14 young Scarlet Robins were known to survive the fledgling phase, but only four of these were banded; the others comprised three females and two sibling males. One banded male was still in his natal territory at 7 weeks after fledging, when independent and acquiring adult plumage, but by 7 months he had dispersed 1 km away within Imbota; he then disappeared. Two banded females became the breeding female in the neighbouring or nearby territory a year later, and one banded female disappeared. Thus, two of four birds remained in Imbota for at least 1 year. At least three unbanded females joined the breeding population in Imbota (replacing banded adult females, which had disappeared). One of the unbanded males left his natal territory 8 weeks after fledging, when independent and in adult-like plumage. The other (his sib) apparently inherited the natal territory: he was acquiring adult plumage and started singing and defending the area after their father died, and he apparently remained there (as an adult-plumaged, unbanded male) after their banded mother disappeared.

Probability of survival (spring to spring) for adult Yellow Robins at Imbota averaged 0.71 ± 0.07 over 2 years: 0.83 ± 0.09 in 2000–01 (*n* = 18) and 0.58 ± 0.1 in 2001–02 (*n* = 24; $\chi^2_1 = 3.1$, $P = 0.08$). Probability of survival of adult males was 0.78 ± 0.15, and of breeding females 0.89 ± 0.11 in 2000–01 (*n* = 9 males, 9 females), and 0.46 ± 0.14 and 0.73 ± 0.14, respectively, in 2001–02 (*n* = 13 males, 11 females), or 0.59 ± 0.04 for adult males versus 0.80 ± 0.09 for females overall (not significantly different: $\chi^2_1 = 2.14$, $P = 0.14$). From their remains, two adult females had been killed by predators (probably birds).

Probability of survival for adult Scarlet Robins at Imbota averaged 0.58 ± 0.08 over 2 years: not significantly higher in 2000–01 (0.67 ± 0.12, *n* = 18) than in 2001–02 (0.50 ± 0.14, *n* = 20) ($\chi^2_1 = 1.08$, $P = 0.30$). Survival of males was not significantly higher than for females: 0.65 ± 0.1 versus 0.42 ± 0.15 over 2 years 2000–02 (*n* = 26 males, 12 females) ($\chi^2_1 = 1.9$, $P = 0.17$). Male survival was higher in 2000–01 (0.92 ± 0.08, *n* = 13) than in 2001–02 (0.38 ± 0.14, *n* = 13). However, all of the males that disappeared in the hard winter of 2002 were compromised in some way: three had a crippled foot (apparently caused by colour-bands; see later), and one had a split lower mandible. Other potential mortality factors included attempted predation by an Australian Magpie on an adult male, and a foot lesion (causing a crippled foot) on an unbanded breeding female.

Population dynamics

With 29% annual mortality on a mean population of 23 adults in Imbota, or a loss of seven birds per year, and a mean of nine recruits per year, the Yellow Robin population is apparently self-sustaining, and a few recruits emigrate. However, λ was 0.83, below replacement level of λ (1.0). There was limited evidence of a low level of immigration: in each spring one or two unbanded females (i.e. apparently not locally produced young) joined the population as breeding females.

With 42% annual mortality on a mean population of 20 adults, or a loss of eight birds per year, and a mean of only three recruits per year, the Scarlet Robin population was not self-sustaining over the 3 years of the study. The λ of 0.30 was well below replacement level. Immigration of adults of both sexes was detected, although not enough females arrived to ensure that all males were paired.

Discussion

Population and breeding parameters

Estimated density of the Yellow Robin at Imbota was lower than values previously reported for this site, and that of the Scarlet Robin was higher than values previously reported (0.3 and 0.03 birds ha^{-1} respectively; Ford *et al.* 1985). Estimated home-range size of the Yellow Robin was larger than previously reported for Imbota (1–3 ha; Ford *et al.* 1985). These differences may reflect changes in robin populations, or differences in survey methods; one area occupied by Yellow Robins in the 1980s (Ford *et al.* 1985) was vacant in 2000–03. The proportion of Yellow Robin pairs with helpers at Imbota (mean 28%) was similar to that reported elsewhere (25%; Marchant 1985).

Population and breeding parameters of robins at Imbota were generally within the range of values previously reported elsewhere, or otherwise similar to previous accounts of relevant aspects, for the two robin species (Yellow Robin: Marchant 1984, 1985, 1987; Zanette 2000; Zanette and Jenkins 2000; Zanette *et al.* 2000; Scarlet Robin: Robinson 1990*a*, 1990*b*; both species: Higgins and Peter 2003; see Table 2). Density of Yellow Robins at Imbota was lower, and home-ranges larger, than in denser, richer or moister habitats elsewhere in eastern Australia (cf. Marchant 1985, 1987; Higgins and Peter 2003). Scarlet Robin density was within values previously reported for mainland Australia, and home-range size was similar to that elsewhere in NSW (cf. Robinson 1990*b*; Higgins and Peter 2003).

Survival of adult Yellow Robins at Imbota was similar to previously reported values for the western New England Tableland (females 72%; Zanette 2000) or southern coastal NSW (66–82%; Marchant 1985). Survival of Scarlet Robins at Imbota was lower than for southern NSW (males 88%, females 67%; Robinson 1990*a*). Survival for males was somewhat lower than reported for richer, predator-poor forest on Norfolk Island (70%), and similar for females (40%), although some missing females on Norfolk Island may have changed territories (Major 1989). Scarlet Robin survival at Imbota may also have been affected by colour-banding, which caused lameness in four of 13 banded adult males; the problem occurred on the leg carrying two of the new Darvic bands (S. J. S. Debus, unpublished observations).

Laying dates for both robins were within laying seasons previously reported, though the season was somewhat shortened, especially for Scarlet Robins, at the high elevations on the New England Tableland compared with elsewhere (cf. Marchant 1984, 1985; Robinson 1990*b*; Zanette *et al*. 2000; Higgins and Peter 2003). Nest-success (33%) and other measures of breeding success for Yellow Robins at Imbota were similar to those reported elsewhere (e.g. nest-success 23–39%; reviewed by Higgins and Peter 2003). Nest-success for Scarlet Robins was as poor as that reported elsewhere in NSW (10%; Robinson 1990*b*). Nest-success for other open-nesting small passerines at or near Imbota is also low, variously 13–30% for Fuscous Honeyeater, Hooded Robin (*Melanodryas cucullata*), Rufous Whistler (*Pachycephala rufiventris*), Leaden Flycatcher, Restless Flycatcher and Dusky Woodswallow (*Artamus cyanopterus*) (Trémont and Ford 2000; Higgins *et al*. 2001; Higgins and Peter 2003; Fitri and Ford 2003; Debus and Lollback 2005; S. J. S. Debus, unpublished data). Productivity was somewhat lower than that reported elsewhere for the Yellow Robin (1.8 young per pair per year; Zanette 2000) and the Scarlet Robin (0.4 young per pair per year; Robinson 1990*b*). Productivity of Yellow Robin pairs versus groups was identical at Imbota; in south-eastern NSW, Marchant (1985) found that nest-success was slightly greater for pairs than for groups, but fledgling productivity per attempt was significantly greater for groups than for pairs.

Continued predation on young Yellow Robins after fledging, through the dependence phase, was as found by Zanette (2000), who similarly reported 76% survival to independence and a young female dispersing 2.5 km to breed in another patch. As elsewhere (Marchant 1985, 1987), male Yellow Robins were philopatric and auxiliaries tended to be yearling males in their natal territory, whereas young females appeared to disperse. Yearling Scarlet Robins either found vacant territories in Imbota or disappeared. Unbanded Scarlet Robins arrived in Imbota in 2002 despite the lack of local recruits in 2001, indicating some inter-patch dispersal consistent with the mobility of the species (Higgins and Peter 2003) and the presence of a source population.

Comparing the breeding biology of Yellow Robins at Imbota with that of the White-breasted Robin (*Eopsaltria georgiana*) in south-western Australia, the latter had a higher incidence of pairs with helpers, density was higher and territory size smaller, nest success and productivity were much higher, and the incidence of nest predation was much lower (cf. Russell *et al*. 2004). Comparing the results for Scarlet Robins at Imbota with those for the Red-capped Robin (*Petroica goodenovii*) elsewhere in south-eastern Australia, and allowing for differences in territory size related to differences in habitat and climate, the latter species had higher nest success and productivity (cf. Dowling 2003; Dowling *et al*. 2003; Powys 2004).

Nest predation

The results of the present study are consistent with other studies of nest-success, fledging success and the causes of nest-failure in robins (Yellow, Scarlet and Hooded) of temperate woodlands in eastern Australia (Marchant 1984, 1985; Robinson 1990*b*; Zanette and Jenkins 2000; Berry 2001; Zanette 2002; Fitri and Ford 2003; Higgins and Peter 2003).

Table 2. Breeding and population parameters of Eastern Yellow Robins and Scarlet Robins in eastern Australia

Home-range = mean home-range size of breeding adults; productivity = fledglings per pair per year[A]; mean annual adult survival is for both sexes combined. Sources for other studies: Marchant (1984, 1985, 1987), Robinson (1990*a*, 1990*b*), Zanette (2000), Zanette and Jenkins (2000), Zanette *et al*. (2000), Berry (2001), and Higgins and Peter (2003)

Species	Density (birds ha^{-1})	Home-range (ha)	Nest-success (%)	Productivity (young $pair^{-1}$ $year^{-1}$)	Survival (%)
This study					
Yellow Robin	0.1	5–6	33 (24)[B]	1.0[A]	71
Scarlet Robin	0.08	10	9 (8)[B]	0.3	58
Other studies					
Yellow Robin	0.3–1.7	1–5	23–39	1.8[A]	75
Scarlet Robin	0.04–2.9	3–7	10	0.4	78

[A] Data for Yellow Robin pairs and groups (i.e. pair plus helper(s)) combined.

[B] Mayfield-adjusted value in parentheses.

These studies have all reported low breeding success, with predation the main cause of nesting failure. As elsewhere on the New England Tableland (Zanette and Jenkins 2000), early robin nests tended to be more successful than later nests, when nest predators are also breeding (S. J. S. Debus, personal observation), but there was no resurgence of robin nest-success near the end of the season at Imbota.

The identity of nest predators at Imbota is consistent with, and provides empirical support for, previous studies in southern Australia, many of which relied on artificial nests (Major *et al*. 1996; Zanette and Jenkins 2000; Berry 2002; Piper *et al*. 2002; Zanette 2002; Boulton and Clarke 2003). These studies highlight the role of kookaburras (*Dacelo*), small and larger honeyeaters (including the Noisy Miner (*Manorina melanocephala*)), shrike-thrushes, cuckoo-shrikes, butcherbirds, currawongs and corvids. However, studies using artificial nests may overestimate the role of large birds, by over-attributing unidentified beak imprints to currawongs, or fail to distinguish predation from scavenging of unattended eggs by small birds (Bayly and Blumstein 2001; Zanette 1997, 2002). Artificial nests may also overestimate the rate of predation on real nests (Berry and Lill 2003).

Population dynamics

For the Yellow Robin in a medium-sized remnant, there were enough locally produced recruits to replace birds that died or left the study site. However, for the Scarlet Robin, there were insufficient locally produced recruits to replace birds that died or left. The Scarlet Robin apparently depends on immigration from other sources, perhaps far from Imbota, such as the extensive woodlands and open forest to the east. For either species, given their small populations in Imbota, immigration may also be necessary to prevent inbreeding. Research is required on the population dynamics of Scarlet Robins in large areas of continuous habitat, to determine whether sufficient recruits are produced to maintain populations in small remnants. Imbota may act as a source of immigrant Yellow Robins for surrounding remnants, but it may not provide sufficient Scarlet Robin recruits to maintain populations in surrounding remnants.

The Yellow Robin may be declining at Imbota, consistent with its $\lambda < 1.0$: in this study it was absent from the location where Ford *et al*. (1985) studied colour-banded birds. This apparent trend matches its loss from the nearby Yina Nature Reserve (~150 ha) since 2000, and from other smaller remnants in the local area (Debus *et al*. 2006; S. J. S. Debus and H. A. Ford, unpublished data). Conversely, the Scarlet Robin's populations in the same fragments may be stable. Such a situation seems paradoxical in light of the data on population dynamics. Perhaps many female Yellow Robins emigrate from their natal patches, but suffer high mortality while dispersing, whereas many Scarlet Robins disperse successfully to these small fragments from distant source-patches where nest predation is lower.

Imbota falls within the range of patch sizes and λ values found by Zanette (2000) for Yellow Robins on the western New England Tableland (~1.0 for two small patches, >1.0 and <1.0 for two large patches). Sustainability of this species' population may not depend on patch-size; poor years and random events may have a greater impact on small populations.

Conclusions

Yellow Robins at Imbota appear to have fairly high breeding success, high female survival and no shortage of adult females, whereas Scarlet Robins appear to have low breeding success, low female survival, high female turnover and perhaps a shortage of breeding females. Yellow Robins produced sufficient young to maintain a breeding population in Imbota in 2000–02, perhaps supplemented by a low level of immigration, and produced a few emigrants to other patches. Conversely, Scarlet Robins may be unable, owing to high rates of nest predation, to maintain their population by local breeding and recruitment, and may be dependent on regular immigration from more productive patches or more extensive habitat. Incubating or brooding female Scarlet Robins may also be vulnerable to predation.

It appears, therefore, that the two robin species differ in their susceptibility to nest predation and low dispersal rates. The somewhat better ability of the Yellow Robin to cope with nest predation, and to provide some recruitment for inter-patch dispersal, is consistent with its lack of decline on the New England Tableland or NSW generally, whereas the Scarlet Robin is declining seriously on the New England Tableland and in NSW generally and its major nest predators are increasing (Barrett and Silcocks 2002; Barrett *et al*. 2003). Scarlet Robins appear not to be suffering low dispersal rates, so presumably their nesting success is greater in unstudied patches within dispersal distance of Imbota.

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