

Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments

Liana Zanette

Zanette, L. 2001. Indicators of habitat quality and the reproductive output of a forest songbird in small and large fragments. – *J. Avian Biol.* 32: 38–46.

The distribution of individuals among habitats that vary in quality (i.e. resource availability) may affect reproductive output at a population level. I compared indicators of habitat quality including the breeding experience ratios (inexperienced:experienced birds), turnover rates, pairing success, and densities of a forest songbird, the Eastern Yellow Robin *Eopsaltria australis*, in two small, food-poor forest fragments, with those in two large, food-rich fragments. I then evaluated the likelihood that the breeding experience ratio affected the reproductive output of populations. Inexperienced males occurred in small fragments eight times as often as in large fragments. Male turnover rates were 1.5 times higher in the small than large fragments, and 20% (10/50) of the male population were unpaired in the small fragments compared to 0% (0/25) in the large. None of these measures differed significantly for females. Experienced birds of both sexes produced almost all of the offspring compared with inexperienced birds. Despite these findings, reproductive output did not vary with fragment size for robins. Thus, while breeding experience clearly influenced the reproductive success of individuals, there were no obvious population consequences of having disproportionately more inexperienced males in the small fragments. I conclude that while male traits may be good indicators of resource levels within fragments (specifically, food availability), they may not be adequate predictors of population performance. Thus, the reproductive output of populations must be measured directly before conclusions concerning population performance can be made. Interestingly, breeding densities were not accurate indicators of either resource levels or population performance. Densities were two times higher in the smaller fragments, and I suggest that this result reflects problems with male dispersal among fragments caused by isolation.

Liana Zanette, Departments of Ecosystem Management and Zoology, University of New England, Armidale, New South Wales, Australia 2351. Present address: Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada V6T 1Z4. E-mail: zanette@zoology.ubc.ca.

Small forest fragments are often deficient in resources necessary for successful songbird reproduction. In fragmented landscapes, food supply declines with decreasing fragment size (Burke and Nol 1998, Zanette et al. 2000), while other factors such as nest predation (Hoover et al. 1995) and brood parasitism may increase (Robinson et al. 2000). Consequently, small forest fragments may be of marginal quality for breeding songbirds, while large fragments may be of suitable quality. Some measures such as low male pairing success and low male densities may be reasonable predictors of such resource availability (e.g. Probst and Hayes 1987, Gibbs and Faaborg 1990). For instance, Burke and Nol

(1998) found that low food supply in small forest fragments was related to low male pairing success and low male densities for Ovenbirds *Seiurus aurocapillus* breeding in Ontario.

Another potential indicator of resource availability is the age distribution of birds. Young and inexperienced birds occur more frequently in unsuitable habitat than older individuals (Watson and Moss 1970, Krebs 1971). In a vast continuous forest in New Hampshire, older Black-throated Blue Warblers *Dendroica caerulescens* preempted yearlings and occurred more frequently in food-rich habitats, leaving the food-poor areas to younger birds (Holmes et al. 1996). By the same token,

within fragmented landscapes, more young and inexperienced birds could occur in small, resource-poor fragments. This possibility, however, has received little attention in the fragmentation literature.

In addition to being a possible predictor of habitat quality, the way in which birds of different ages distribute themselves among fragments could influence the reproductive output of populations. Young and inexperienced birds often produce fewer offspring than older, more experienced individuals (Nol and Smith 1987, Sæther 1990, Desrochers and Magrath 1993, Black 1996). Therefore, if a higher proportion of young birds occur in small fragments, then this could lead to low reproductive output there. In some cases, however, the age distribution of a population may have little influence on reproductive output. For instance, in birds the reproductive success of a pair is almost always related to the age or breeding experience of the female parent and rarely to that of the male (references in Black 1996). Thus, the presence of more yearling or inexperienced males in certain fragments or habitats may have little effect on reproductive output at a population level. To determine the likelihood that the age distribution of a population influences reproductive output, one must first show that young or inexperienced individuals of both sexes do in fact have lower reproductive success than older members of the population.

I studied a forest songbird, the Eastern Yellow Robin *Eopsaltria australis*, hereafter "robin", in two small and two large forest fragments. Male and female robins were classified by prior breeding experience, and I examined whether the breeding experience ratio (i.e. inexperienced:experienced birds) differed according to fragment size. Food availability was significantly lower in the two smaller fragments (Zanette et al. 2000) and I therefore expected to observe more inexperienced birds there. I also measured local turnover rates of breeding adults. Turnover rates are a measure of habitat suitability and fidelity to a particular site (Krebs 1971, Roth and Johnson 1993, Holmes et al. 1996). Thus, I expected higher turnover in the small fragments each year. I also measured other predictors of habitat suitability including pairing success, and breeding densities (Probst and Hayes 1987, Gibbs and Faaborg 1990, Burke and Nol 1998, Holmes et al. 1996), which were expected to be lower in the smaller fragments. Finally, I examined the relationship between breeding experience and the reproductive success of robins. Because the reproductive output of robin populations was known to be independent of fragment size (Zanette 2000), I expected that reproductive success would be similar for experienced as for inexperienced birds. Thus, while I expected to see more inexperienced individuals in small forest fragments, I did not expect the breeding experience ratio to affect the reproductive output of populations. The phrase "habitat quality" has been used to describe both resource availability and the

reproductive output of populations. In this paper, habitat quality refers only to the former. Reproductive output is the number of fledglings and independent young produced per pair per season.

Methods

Study site and species

I worked in temperate north-eastern New South Wales, Australia (30°27' S, 151°13' E). The landscape was severely fragmented, with about 20% of the original forest remaining. Fragments of open eucalyptus forest were surrounded by pasture for sheep and cattle grazing. I marked one 55 ha study plot in 100 m intervals, in each of two small fragments (each 55 ha in size, termed S1, S2), and two large fragments (> 400 ha, termed L1, L2). The size of fragments in each size category were chosen *a priori*, as robins rarely occur in fragments under 50 ha in size but commonly occur in fragments over 400 ha (Barrett 1995). In the small fragments, the study plots covered the entire site. In the large fragments, the plots were near the centre of the fragment and > 150 m from the boundary between forest and pasture. The plots were separated from each other by an average minimum distance of 6.1 km (range 1.8 to 11.8 km), and each was similar in terms of vegetation and general geographic features. All plots were dominated by rough-barked eucalypts, mainly *Eucalyptus caliginosa*, *E. macrorhynca*, and *E. andrewsii*, with a shrub layer consisting primarily of *Cassinia* spp., *Bursaria* spp., and *Acacia* spp.

Robins are endemic Australian flycatchers (Family Eopsaltriidae) that hold all purpose territories year-round. They can start breeding at 1 year of age, and they are socially monogamous and multi-brooded. Breeding generally begins in August and ends in December. Open cup nests are built by females usually < 3 m above ground (Marchant 1984), and most clutches consist of two eggs. The female alone incubates the eggs and broods the nestlings. The male brings food to the female as she tends the nest, but the female will leave the nest occasionally to forage on her own. The male brings food to young nestlings, though the female also feeds the nestlings late in the nestling period.

Indicators of habitat quality

In 1994, 79% (19/24) of breeding adults in S1 were captured using mist-nets and colour banded for individual recognition. In addition, all fledglings in S1 were banded, mainly as nestlings, with unique combinations of colours. In 1995 and 1996, 94% (68/72) of breeding females and 74% (53/72) of males in all four plots, were colour banded as were all of the fledglings. Robins were

categorized as experienced or inexperienced from these banding records. Experienced breeders were banded individuals that had bred in at least one previous year. Inexperienced breeders were fresh recruits to the plots. These birds included banded young born locally who later became breeders, and unbanded immigrants that took the place of a previously banded bird. Misclassification of experienced, unbanded breeders for inexperienced, unbanded breeders was possible, but was probably only an issue for females because only females have been observed successfully re-settling on new territories in different parts of the study plots (pers. obs., also see Nol and Smith 1987). As most females were colour banded, the possibility for misclassification was minimal. Also, whenever an unbanded female recruited, I made sure that the other unbanded females known to be breeding nearby were accounted for. I classified pairs as experienced, inexperienced and mixed, the latter being pairs with one experienced and one inexperienced parent.

I surveyed the study plots and determined the birds' breeding experience at the beginning of each breeding season (August and September) in 1995, 1996, and 1997. I could not age robins based on morphology, so age effects are not considered directly. However, breeding experience typically contributes more to reproductive performance than does age in birds (Sæther 1990).

Annual survival rates of banded adults were calculated for 1995 and 1996 by multiplying survival during the breeding season (29 July to 31 December) by survival in the non-breeding season (1 January to 28 July) (following Zanette 2000). I used the staggered entry Kaplan-Meier procedure (Krebs 1999) to estimate survival rates in the breeding season based on weekly censuses, and calculated the sampling variance following Pollock et al. (1989, equation 3). I used the minimum number alive to calculate survival rates in the non-breeding season and the binomial distribution to estimate the variance. The sampling variance for annual survival probabilities was calculated by summing the variance of each of the two survival estimates (following Zanette 2000). Survival estimates in the breeding season were analysed using the Log-rank Test (Krebs 1999), while the remaining estimates were analysed using contingency tables (number lost vs number remaining). My survival values represent local survival rates. They are not estimates of true survival because I was unable to distinguish death from emigration.

Pairing success of robins was estimated in the 1995 and 1996 breeding seasons. Males without a known mate were followed within their territories at least once per week for 40 min. Males were considered unpaired if no female was observed. I also noted other signs likely to indicate paired status, including persistent singing by the male.

Territories of breeding pairs were mapped in 1995 and 1996 by using playbacks of robin calls and songs,

and by observing the locations of border disputes which occurred frequently (Zanette et al. 2000). Densities of breeding pairs were calculated as the number of territories fully within the plots, and were adjusted for territories that fell partly outside the plots. For instance, if 25% of a territory was estimated as being within the plot, then an additional score of 0.25 would be added to the total. I estimated proportions in intervals of 0.25 (i.e. 0.25, 0.50, 0.75). The sizes of territories falling fully within the plots were estimated using minimum convex polygons and were log-transformed for analysis. Territory sizes were analysed with a 2-factor nested ANOVA (McKone 1993) with fragment size and year as the main effects, and the replicate plots as the nested subgroup (i.e. S1 and S2 were nested in the Small Fragment treatment, and L1 and L2 in the Large Fragment treatment).

Effects of breeding experience on reproductive success

I considered how reproductive success (fledglings and independent young produced per pair per season) was related to male and female breeding experience while controlling for habitat quality. Data from 1996 were used with an additional year (1995) from the S1 fragment. Reproductive success did not vary between years in S1 (Zanette 2000). I adjusted data on seasonal fecundity for differences in habitat quality by subtracting annual population means for each plot from the raw data. Population means were calculated using experienced birds only, to avoid variation due to differences in population structure (following Desrochers and Magrath 1993). A residual of -1.5 would mean that inexperienced robins produced 1.5 fewer offspring than experienced birds.

Results

Breeding experience ratio

Inexperienced breeders comprised 27.6% (16/58) of the male, and 23.6% (17/72) of the female breeding population. However, inexperienced males were almost eight times more common in the plots in the small than large fragments ($\chi^2 = 6.2$, $df = 1$, $P = 0.013$, Table 1). Inexperienced females, by contrast, occurred in similar proportions on average in fragments of different sizes ($\chi^2 = 0.03$, $df = 1$, $P = 0.85$, Table 1). The proportions of birds with and without breeding experience were similar between years (1996 vs 1997, % inexperienced birds: males, 32% of 25 vs 20% of 25; females, 16% of 31 vs 26% of 31, Fisher's Exact Tests, $P > 0.28$) and between the plots in the two small fragments for both males and females (Fisher's Exact Test, $P > 0.35$, Table

1). When I compared the plots in the two large fragments, no significant differences in breeding experience were found for males (L1 vs L2: Fisher's Exact Test, $P = 1.00$); however, 5/5 inexperienced females were in one of the large fragments (L1) (Fisher's Exact Test, $P = 0.01$, Table 1). Inexperienced pairs were significantly more common in the two small than in the two large fragments ($\chi^2 = 6.6$, $df = 2$, $P = 0.037$, Table 1), with no significant differences between replicates ($P > 0.14$, Table 1), or years ($\chi^2 = 3.0$, $df = 2$, $P = 0.22$).

Local survival rates

More inexperienced males recruited into the small fragments every year. Correspondingly, survival rates of breeding adult males were significantly lower in the small than large fragments (Fisher's Exact Test, $P = 0.026$, Table 2). These differences were due mainly to losses in the non-breeding season (small vs large fragments: Fisher's Exact Test, $P = 0.030$) rather than in the breeding season (Log-rank Test, $z = 0.3$, $P = 0.77$, Table 2). I detected no significant differences in survival rates between replicates (Fisher's Exact Tests, S1 vs S2: $P = 0.48$; L1 vs L2: $P = 1.00$) or years (Fisher's Exact Test, $P = 0.13$; 1995: 0.641 ± 0.091 (se) $n = 29$; 1996: 0.830 ± 0.074 , $n = 25$).

Female survival rates were similar in the small and large fragments (Fisher's Exact Test, $P = 0.78$, Table 2), with no differences between years (Fisher's Exact Test, $P = 0.59$; 1995: 0.71 ± 0.074 , $n = 38$; 1996: 0.739 ± 0.080 , $n = 25$), or between the two plots in the small fragments (Fisher's Exact Test, $P = 1.00$, Table 2). Local survival rates, however, were significantly higher in L2 than in L1 (Fisher's Exact Test, $P = 0.03$, Table 2; also see Zanette 2000).

The loss of birds from the fragments was not related to breeding experience (males: $\chi^2 = 0$, $df = 1$, $P = 1.0$; females: $\chi^2 = 0.2$, $df = 1$, $P = 0.65$). Overall, 77% of 22

experienced males and 70% of 10 inexperienced males bred again in the following year. For females, 78% of 32 experienced and 67% of 8 inexperienced birds bred again in the subsequent year. Adults that fledged young successfully were as likely to breed again in the following season as were unsuccessful adults (males: $\chi^2 = 1.2$, $df = 1$, $P = 0.28$; females: $\chi^2 = 0.5$, $df = 1$, $P = 0.47$). Similar results were obtained for all of these measures when the small and large fragments were considered separately ($P > 0.10$).

Pairing success

Males had more difficulty finding a mate in the small than large fragments. Eight per cent of males (4/50) in the two small fragments held territories but were unable to secure a mate at any time in the breeding season. An additional six males lost their mates in the first half of the breeding season (before October 15), and only one of these was able to attract a new mate and resume breeding. By contrast, all territorial males in the large fragments paired successfully and both males whose initial mate disappeared during the breeding season found a new mate. Thus, in total, 20% (10/50) of males went unpaired for all or most of the breeding season in the small fragments compared to 0% (0/25) in the large fragments (Fisher's Exact Test, $P = 0.025$). I knew the histories of five of the 10 unpaired males; all were new breeders that had recruited locally. All but one female paired successfully, the exception being a female in S1.

Breeding densities

Nearly twice as many territories were in the study plots in the small as in the large fragments (11.5/year vs 7/year, respectively, Table 3). Comparing average territory sizes using a 2-way nested ANOVA, I found significant variation with fragment size ($F = 45.5$, $df =$

Table 1. Percentage of inexperienced to experienced male and female Eastern Yellow Robins in two small forest fragments (S1 and S2) and two large fragments (L1 and L2). Pairs were experienced (male and female parent both have breeding experience), mixed (one parent has breeding experience, the other is inexperienced), or inexperienced (male and female both inexperienced breeders). Sample sizes are denoted by n.

	Study plots				Fragment size		Total
	S1	S2	L1	L2	Small	Large	
Males							
% inexperienced	30	50	0	10	39	5	28
n	20	18	10	10	38	20	58
Females							
% inexperienced	23	25	50	0	24	23	24
n	26	24	10	12	50	22	72
Pairs							
% experienced	64	47	50	90	56	70	63
% mixed	12	24	50	10	18	30	24
% inexperienced	24	29	0	0	26	0	13
n	17	17	10	10	34	20	54

Table 2. Mean local survival rates (\pm se) of male and female Eastern Yellow Robins breeding in two small fragments (S1 and S2) and two large forest fragments (L1 and L2). Survival rates for the breeding season (21 week period) and non-breeding season are shown separately. Annual survival rates were calculated by multiplying the breeding and non-breeding season values. Data are averaged over a two-year period, 1995 and 1996.

	Study plots				Fragment size	
	S1	S2	L1	L2	Small	Large
Males						
Breeding	0.917 \pm 0.076	0.867 \pm 0.082	0.909 \pm 0.083	1.000 \pm 0	0.894 \pm 0.056	0.950 \pm 0.046
Non-breeding	0.750 \pm 0.131	0.625 \pm 0.125	1.000 \pm 0	0.900 \pm 0.100	0.679 \pm 0.085	0.952 \pm 0.048
Annual rates	0.688 \pm 0.133	0.542 \pm 0.120	0.909 \pm 0.083	0.900 \pm 0.100	0.607 \pm 0.085	0.905 \pm 0.063
n	13	19	12	10	32	22
Females						
Breeding	0.944 \pm 0.052	0.826 \pm 0.077	0.566 \pm 0.132	0.909 \pm 0.079	0.881 \pm 0.050	0.741 \pm 0.091
Non-breeding	0.778 \pm 0.100	0.900 \pm 0.071	0.714 \pm 0.161	1.000 \pm 0	0.842 \pm 0.063	0.900 \pm 0.069
Annual rates	0.735 \pm 0.101	0.744 \pm 0.089	0.404 \pm 0.132	0.909 \pm 0.079	0.742 \pm 0.067	0.667 \pm 0.105
n	19	24	13	12	43	25

1, 68, $P = 0.0001$), no effect of year ($F = 0.3$, $df = 1$, 68, $P = 0.61$), and no interaction ($F = 1.2$, $df = 1$, 68, $P = 0.27$), but the nested term was significant ($F = 6.3$, $df = 2$, 68, $P = 0.003$). Average territory sizes were half as large in the plots in the small as in the large fragments, but territories in L1 were smaller than those in L2 (Table 3).

Effects of breeding experience on reproductive success

The pattern of reproductive success across the fragments varied by breeding experience for both males and females (Table 4). Controlling for habitat quality, I found that experienced males reared 1.4 more fledglings and 1.2 more independent young per capita per year than inexperienced males (fledglings: Mann-Whitney U-test, $z = 3.2$, $P = 0.001$, $n = 31$; independent young: $z = 2.9$, $P = 0.003$, $n = 31$, Table 5). Similarly, experienced females produced 1.5 more fledglings ($z = 2.8$, $P = 0.005$, $n = 39$), and 1.1 more independent offspring per capita than inexperienced females ($z = 2.2$, $P = 0.03$, $n = 39$, Table 5). Experienced pairs produced more young than either mixed or inexperienced pairs (Kruskall-Wallis, fledglings: $H = 11.3$, $df = 2$, $P = 0.004$; independent young: $H = 8.4$, $df = 2$, $P = 0.02$, Table 5).

Overall, birds in S2 and L2 produced more offspring (S2, fledglings: 2.45 ± 0.46 ; independent young: 1.89 ± 0.33 , $n = 11$; L2, fledglings: 2.83 ± 0.98 ; independent young: 2.14 ± 0.88 , $n = 6$) than those in S1 and L1 (S1, fledglings: 1.48 ± 0.32 ; independent young: 0.93 ± 0.25 , $n = 21$; L1, fledglings: 0.14 ± 0.14 independent young: 0.14 ± 0.14 , $n = 7$). Therefore, I used t-tests to compare the reproductive success of experienced pairs in S2 and L2 (combined) with S1 and L1 (combined) to determine the extent to which experienced birds benefitted from living in fragments that were relatively productive. The data were square-root transformed. A similar analysis

was conducted for inexperienced pairs. In this case, mixed pairs and inexperienced pairs were combined to increase sample sizes. Experienced pairs produced a similar number of offspring in both types of habitat (fledglings: $t = 0.8$, $df = 14$, $P = 0.43$; independent young: $t = 1.1$, $df = 14$, $P = 0.28$, Table 6). By contrast, inexperienced pairs had significantly higher reproductive success in S2 and L2 than S1 and L1 (fledglings: $t = 5.1$, $df = 10$, $P < 0.001$; independent young: $t = 4.2$, $df = 10$, $P = 0.002$, Table 6).

Discussion

Inexperienced robins produced fewer young per season than experienced birds. In fact, inexperienced robins had very poor reproductive success, producing less than one offspring a year on average. Many other researchers have found that younger, inexperienced birds have lower reproductive success than older, more experienced individuals. Unlike my study, however, this relationship between age or breeding experience on reproduction is usually only found for females (references in Black 1996). Sparrowhawks *Accipiter nisus* are one exception (Newton and Wyllie 1996). In that case, male age was correlated with seasonal fecundity presumably because males provide females and nestlings with the majority of their food during the breeding season. In general, higher reproductive success in older birds has been attributed to increased foraging efficiency (Wunderle 1991, Desrochers 1992), so it is not surprising that male age and reproductive success are related in Sparrowhawks. This explanation may apply to robins because during breeding male robins also bring females and nestlings most of their food.

While breeding experience clearly influenced the reproductive success of individuals of both sexes (i.e., inexperienced birds produced few offspring), there were no obvious population consequences of having disproportionately more inexperienced males in the small

fragments. These findings suggest that some other factor had a stronger influence on the reproductive output of robin populations than did the breeding experience ratio. One possibility is pair type. Pairs consisting of two experienced robins produced more offspring than other pairs. If I compare the percentages of experienced pairs versus other pairs (% mixed pairs and % inexperienced pairs pooled from Table 1) in small versus large fragments, the differences in pair type are not significant (Fisher's Exact Test, $P = 0.39$). In this case, one may also expect to see similar levels of reproductive output in small and large fragments. Closer inspection of Table 1, however, shows that this explanation is unsatisfactory. For instance, 47% of pairs in S2 were experienced compared to 50% in L1. While the differences in these percentages are small, the differences in the reproductive output of these two populations are large (Table 5). Birds in S2 produced 18 times more fledglings and 14 times more independent offspring than did birds in L1. Similarly, S1 had a higher percentage of experienced pairs than S2 (64% vs 47% respectively) though, again, reproductive output was higher in S2.

A more likely possibility involves nest predation. In a previous paper (Zanette 2000), I showed that the plots with relatively low reproductive output, S1 and L1, also had low nesting success (average nest success \pm se: S1, 0.11 ± 0.03 ; L1, 0.08 ± 0.02 ; results from Zanette and Jenkins 2000). By contrast, S2 and L2 had high reproductive output coupled with high nesting success (S2, 0.36 ± 0.01 ; L2, 0.22 ± 0.07). No such correspondence between reproductive output and food availability occurred among the plots. Food availability was low in S1 and S2 relative to L1 and L2 while reproductive output followed the pattern described above. Based on this evidence, I concluded that nest predation rates may be more important than food availability in determining the reproductive output of robin populations in the fragmented landscape in which I worked. Similarly, the results of the current study suggest that nest predation rates had a stronger effect on robin reproduction than did the breeding experience ratio.

Most studies of passerines have considered the effects of age or breeding experience on reproduction at a single site only (e.g. Perrins and McCleery 1985, Desrochers and Magrath 1993). These studies, therefore, cannot draw conclusions about the relative influence that age or the breeding experience ratio has on the reproductive output of populations. One exception is a study on Black-throated Blue Warblers conducted in New Hampshire (Holmes et al. 1996). Holmes et al. found that yearling Black-throated Blue Warblers occurred more often in sparsely vegetated, food-poor habitats, where reproductive output was also low. They concluded that resource availability within habitats had a stronger influence on reproductive output than did the age structure of warblers. While yearlings produced fewer offspring than older birds within each type of habitat, all warblers produced fewer offspring in food-poor habitats, regardless of age. These conclusions are similar to mine except that nest predation, rather than food availability, appeared to be the principal factor influencing the reproductive output of robin populations.

For robins, low nest predation appeared to benefit inexperienced birds most. Inexperienced birds in the plots with low nest predation (S2 and L2) reared more offspring per pair than did those in the other plots. No differences in offspring production per pair were observed for experienced birds in S2 and L2 compared with S1 and L1. Young birds are usually the ones that benefit most when resource limitation is relieved. For instance, experimental work has shown that foraging efficiency for yearlings improves far beyond that of older birds when they receive supplemental food (e.g. Desrochers 1992). In the cooperatively breeding White-browed Scrubwren *Sericornis frontalis*, the reproductive success of yearling females is much higher with than without group help, but group help makes little difference to the reproductive success of older females (R. M. Magrath unpubl. data).

Although the reproductive output of robin populations did not vary with fragment size, males were

Table 3. Breeding densities of Eastern Yellow Robins, in two small forest fragments (S1 and S2) and two large forest fragments (L1 and L2) in 1995 and 1996. Territories are the total number of territories with breeding birds observed on each study plot. Mean territory sizes ($ha \pm se$, n in parentheses) were calculated using minimum convex polygons.

	Study plots				Fragment size	
	S1	S2	L1	L2	Small	Large
Breeding territories						
1995	12.00	13.00	7.00	6.75	12.50	6.90
1996	9.00	12.00	7.50	6.75	10.50	7.10
	10.50	12.50	7.25	6.75	11.50	7.00
Mean territory size						
1995	1.6 ± 0.2 (12)	2.1 ± 0.2 (13)	3.1 ± 0.4 (6)	5.6 ± 0.5 (6)	1.9 ± 0.2 (25)	4.4 ± 0.5 (12)
1996	2.3 ± 0.2 (9)	2.5 ± 0.3 (12)	2.9 ± 0.4 (6)	5.3 ± 0.5 (6)	2.4 ± 0.2 (21)	4.1 ± 0.5 (12)
Mean	1.9 ± 0.2 (10.5)	2.3 ± 0.2 (12.5)	3.0 ± 0.3 (6)	5.5 ± 0.3 (6)	2.1 ± 0.1 (23)	4.2 ± 0.3 (12)

Table 4. Mean number (\pm se) of fledglings and independent offspring produced per season, by male and female Eastern Yellow Robins with and without breeding experience, in each of four forest fragments (S1 to L2). n is the number of individuals sampled.

		Fledglings		Independent offspring	
		Experienced	Inexperienced	Experienced	Inexperienced
Males					
S1	Mean \pm se	1.89 \pm 0.51	0.25 \pm 0.25	1.28 \pm 0.43	0.00 \pm 0.00
	n	9	4	9	4
S2	Mean \pm se	2.33 \pm 0.33	1.00 \pm 0.32	1.67 \pm 0.33	0.80 \pm 0.37
	n	3	5	3	5
L1	Mean \pm se	0.20 \pm 0.20		0.20 \pm 0.20	
	n	1		5	
L2	Mean \pm se	3.50 \pm 1.26	3.00 \pm 0.00	3.00 \pm 1.08	0.00 \pm 0.00
	n	4	1	4	1
Females					
S1	Mean \pm se	2.33 \pm 0.38	0.20 \pm 0.20	1.54 \pm 0.33	0.00 \pm 0.00
	n	12	5	12	5
S2	Mean \pm se	2.60 \pm 0.48	1.00 \pm 0.00	1.90 \pm 0.35	1.00 \pm 0.00
	n	10	1	10	1
L1	Mean \pm se	0.50 \pm 0.50	0.00 \pm 0.00	0.50 \pm 0.50	0.00 \pm 0.00
	n	2	3	2	3
L2	Mean \pm se	2.80 \pm 0.48		2.08 \pm 0.90	
	n	6		6	

having obvious difficulties in the two small fragments. Inexperienced male robins were more common in the small fragments, where males also disappeared at a faster rate, and where males were less successful at securing a mate. Other researchers have obtained similar results for male songbirds breeding in suboptimal habitats (e.g. Krebs 1971, Probst and Hayes 1987, Gibbs and Faaborg 1990). Thus, the age/breeding experience ratio, turnover rates, and pairing success of male songbirds may be adequate predictors of resource availability among habitats. In my case, food was the resource most closely associated with these variables (also see Holmes et al. 1996, Burke and Nol 1998).

Male traits such as breeding experience, pairing success, and survival rate all affect the fitness of individuals. However, the latter two factors also have been used as indicators of how well populations perform in terms of reproductive output (e.g., Gibbs and Faaborg 1990, Perneluzi et al. 1993, Roth and Johnson 1993, Donovan et al. 1995a, b, Burke and Nol 1998). Given my results, I suggest that caution be exercised when drawing conclusions about population performance based on fitness measures related to individual characteristics.

The discrepancy in my results between what was happening to individuals versus populations probably came about because different limiting factors were influencing different fitness variables. On the one hand, food supply was affecting the breeding experience ratio, survival, pairing success, and hence the reproductive success of individual robins. On the other hand, nest predation had a stronger influence on the reproductive output of populations than did any of the other variables. I suggest, therefore, that fitness measures related to individuals should be adequate predictors of population performance in cases where the same factor (e.g.

food supply) strongly influences animals at both spatial scales (e.g. Sherry and Holmes 1992, Holmes et al. 1996). For example, in heavily forested landscapes, food availability for animals will vary among patches while, overall, nest predation rates remain relatively low (Robinson et al. 1995, Zanette 2000). Thus, food availability will likely be the main influence on reproduction for both individuals and populations. In fragmented landscapes, food supply will vary spatially, but overall, nest predation rates tend to be much higher. In this case, food supply should still have an effect on individuals but nest predation will be the main influence on populations.

Interestingly, breeding densities were not adequate predictors of habitat quality, nor were they any indication as to how well populations performed in terms of

Table 5. Mean residuals of fledglings and independent offspring produced per season, by male and female Eastern Yellow Robins with and without breeding experience. Pair type includes experienced (both parents with breeding experience), mixed (one parent with, the other without breeding experience), and inexperienced pairs (both parents without breeding experience).

	Fledglings	Independent offspring	n
Males			
Experienced	0.00 \pm 0.31	0.00 \pm 0.26	21
Inexperienced	-1.37 \pm 0.26	-1.20 \pm 0.24	10
Females			
Experienced	0.00 \pm 0.28	0.00 \pm 0.17	30
Inexperienced	-1.53 \pm 0.28	-1.12 \pm 0.24	9
Pair type			
Experienced	0.00 \pm 0.33	0.00 \pm 0.32	16
Mixed	-0.83 \pm 0.18	-0.92 \pm 0.31	8
Inexperienced	-1.67 \pm 0.14	-1.30 \pm 0.25	4

Table 6. Mean number of fledglings and independent offspring produced per season by Eastern Yellow Robins breeding in fragments where reproductive output was high (High output, S2 and L2 fragments combined) and low (Low output, S1 and L1 fragments combined). Experienced pairs and inexperienced pairs (pairs with at least one inexperienced parent) were analysed separately.

	Fledglings	Independent offspring	n
Experienced			
High output	1.57 ± 0.30	1.40 ± 0.28	7
Low output	1.29 ± 0.20	1.01 ± 0.22	9
Inexperienced			
High output	1.23 ± 0.15	0.82 ± 0.24	5
Low output	0.14 ± 0.14	0.00 ± 0.00	7

reproductive output (also see Van Horne 1983). Animals with abundant food may have small territories and high densities (e.g. Mares et al. 1982). In my study, however, small territories and high densities occurred in the habitats with less food. Thus, a mechanism other than food availability must be determining robin densities, and I suggest that isolation may be important. Small forest fragments surrounded by pasture may discourage local emigration (Stamps et al. 1987), resulting in increases in numbers of potential breeders within these fragments. Increases in breeding numbers, and decreases in territory sizes, may then ensue as a result of increased competition for territories. Several studies have reported decreases in territory sizes with increased contender pressure (e.g. Knapton and Krebs 1974), while at the same time, finding no significant relationship between food availability and territory sizes (Myers et al. 1979, Smith et al. 1980, Norton et al. 1982, Stamps 1990). I am presently unable to test the idea that contender pressure in the small fragments increased due to isolation for robins.

In fragmented systems, higher densities of songbirds may be indicative of problems with male dispersal due to isolation as suggested. However, these isolation effects may be most relevant to resident species, and of less importance to migratory species. For instance, some neotropical migrants in North America occur at lower densities in small, food-poor fragments (e.g. Burke and Nol 1998). My results could differ from those for neotropical migrants because of the different procedures used in estimating densities (Zanette et al. 2000). However, they could also reflect true differences between migrants and residents. Migrants should be better able to sample a variety of fragments and make settlement decisions based mainly on the resources available (Holmes et al. 1996), while being less influenced by isolation. In this case, skew in the age distribution of migrants among habitats with different resource levels could occur if older individuals pre-empt younger birds from occupying high quality sites (e.g. Holmes et al. 1996). However, I know of no studies on the age distribution of neotropical migrants in small and large fragments to test this idea.

My measures for females did not vary with fragment size as consistently as they did for males. Although the ratio of inexperienced to experienced females and turnover rates were consistently higher in S1 and S2 compared with L2, females were having extreme difficulties in the L1 fragment. Turnover rates were highest in L1, and this plot contained the highest proportion of inexperienced females. Robins had very low levels of nest success due to high nest predation in the L1 fragment (see above). As most female losses from L1 occurred during the breeding season, it is possible that females were directly affected by nest predation. Following the failure of a nest, females will sometimes leave (i.e. divorce) their mates (references in Black 1996). Alternatively, the females in L1 could have died during nest attacks. In either case, in addition to being affected by low food supply (Zanette et al. 2000), females may also respond negatively in situations where nest predation is intense.

Songbirds breeding in fragmented landscapes are confronted with a variety of problems. First, food availability declines with decreasing fragment size. Low food availability, in turn, correlates with low breeding experience, poor survival, poor pairing success, and other factors related to individual fitness (e.g. nestling weights etc., see Zanette et al. 2000). Second, nest predation levels can be high in fragmented landscapes (Robinson et al. 1995, Zanette and Jenkins 2000), which may affect local survival of females in particular, but which also seems to have a strong influence on the reproductive output of populations. Thus, a songbird settling in a small fragment may compromise its individual fitness due to low food supply. However, at the same time, settling in a large fragment could have negative consequences on reproductive output as a result of relatively high nest predation rates. Based on this scenario, I would conclude that there are few good habitats for songbirds to inhabit when breeding in fragmented landscapes.

Acknowledgements – Thanks to the landholders and managers at “Tullimba”, “Lansdale”, “Glenby”, and “Matoni”, who graciously allowed me access onto their properties. Thanks to Steve Trémont, Stephen Debus, and Kate MacGregor who helped band the adults. This work benefitted from discussions with Jamie Smith, Tony Sinclair, Robert Magrath, Michael Clinchy, and Daniel Haydon. Jamie Smith, Robert Magrath, Anna Lindholm, and two anonymous reviewers kindly provided feedback on previous versions of the manuscript. This research was funded by the University of New England and by an award from the Australian Department of Education and Employment Training to the author.

References

- Barrett, G. W. 1995. Woodland bird assemblages on the New England Tablelands, Northeastern New South Wales. – Ph.D. Diss., University of New England, Australia.
- Black, J. M. 1996. Partnerships in birds: the study of monogamy. – Oxford University Press, New York.

- Burke, D. M. and Nol, E. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. – *Auk* 115: 96–104.
- Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. – *Anim. Behav.* 43: 885–894.
- Desrochers, A. and Magrath, R. D. 1993. Age-specific fecundity in European blackbirds (*Turdus merula*): individual and population trends. – *Auk* 110: 255–263.
- Donovan, T. M., Lamberson, R. H., Kimber, A., Thompson, F. R. III and Faaborg, J. 1995a. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. – *Cons. Biol.* 9: 1396–1407.
- Donovan, T. M., Thompson, F. R. III, Faaborg, J. and Probst, J. R. 1995b. Reproductive success of migratory birds in habitat sources and sinks. – *Cons. Biol.* 9: 1380–1395.
- Gibbs, J. P. and Faaborg, J. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. – *Cons. Biol.* 4: 193–196.
- Holmes, R. T., Marra, P. P. and Sherry, T. W. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. – *J. Anim. Ecol.* 65: 183–195.
- Hoover, J. P., Brittingham, M. C. and Goodrich, L. J. 1995. Effects of forest patch size on nesting success of wood thrushes. – *Auk* 112: 146–155.
- Knapton, R. W. and Krebs, J. R. 1974. Settlement patterns, territory size, and breeding density in the song sparrow (*Melospiza melodia*). – *Can. J. Zool.* 52: 1413–1420.
- Krebs, C. J. 1999. *Ecological methodology*. 2nd edn. – Benjamin/Cummings, Menlo Park, CA.
- Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. – *Ecology* 52: 2–22.
- Marchant, S. 1984. Nest-records of the Eastern Yellow Robin *Eopsaltria australis*. – *Emu* 84: 167–174.
- Mares, M. A., Lacher, T. E. Jr., Willig, M. R., Bitar, N. A., Adams, R., Klinger, A. and Tazik, D. 1982. An experimental analysis of social spacing in *Tamias striatus*. – *Ecology* 63: 267–273.
- McKone, M. J. 1993. Statistical analysis of experiments conducted at multiple sites. – *Oikos* 67: 184–186.
- Myers, J. P., Conners, P. G. and Pitelka, F. A. 1979. Territory size in wintering sanderlings: the effects of prey abundance and intruder density. – *Auk* 96: 551–561.
- Newton, I. and Wyllie, I. 1996. Monogamy in the sparrowhawk. – In: Black, J. M. (ed.). *Partnerships in birds: the study of monogamy*. Oxford University Press, New York, pp. 249–267.
- Nol, E. and Smith, J. N. M. 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. – *J. Anim. Ecol.* 56: 301–313.
- Norton, M. E., Arcese, P. and Ewald, P. W. 1982. Effect of intrusion pressure on territory size in Black-chinned Hummingbirds (*Archilochus alexandri*). – *Auk* 99: 761–764.
- Perrins, C. M. and McCleery, R. H. 1985. The effect of age and pair bond on the breeding success of Great Tits *Parus major*. – *Ibis* 127: 306–315.
- Pollock, K. H., Winterstein, S. R., Bunck, C. M. and Curtis, P. D. 1989. Survival analysis in telemetry studies: the staggered entry design. – *J. Wildl. Manage.* 53: 7–15.
- Porneluzi, P., Bednarz, J. C., Goodrich, L. J., Zawada, N. and Hoover, J. 1993. Reproductive performance of territorial ovenbirds occupying forest fragments and a continuous forest in Pennsylvania. – *Cons. Biol.* 7: 618–622.
- Probst, J. R. and Hayes, J. P. 1987. Pairing success of Kirtland's warblers in marginal vs suitable habitat. – *Auk* 104: 234–241.
- Robinson, S. K., Thompson, F. R. III, Donovan, T. M., Whitehead, D. R. and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. – *Science* 267: 1987–1990.
- Robinson, S. K., Hoover, J. P. and Herkert, J. R. 2000. Cowbird parasitism in a fragmented landscape: effects of tract size, habitat, and abundance of cowbirds and hosts. – In: Smith, J. N. M., Cook, T. L., Rothstein, S. I., Robinson, S. K. and Sealy, S. G. (eds). *The ecology and management of cowbirds: studies in the conservation of North American passerine birds*. Univ. of Texas Press, Texas.
- Roth, R. R. and Johnson, R. K. 1993. Long-term dynamics of a wood thrush population breeding in a forest fragment. – *Auk* 110: 37–48.
- Sæther, B.-E. 1990. Age-specific variation in reproductive performance of birds. – In: Power, D. M. (ed.). *Current Ornithology*. Vol. 7. Plenum Press, New York, pp. 251–283.
- Sherry, T. W. and Holmes, R. T. 1992. Population fluctuations in a long-distance neotropical migrant: demographic evidence for the importance of breeding season events in the American Redstart. – In: Hagan, J. M. III and Johnston, D. W. (eds). *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington, D.C., pp. 431–442.
- Smith, J. N. M., Montgomerie, R. D., Taitt, M. J. and Yom-Tov, Y. 1980. A winter feeding experiment on an island song sparrow population. – *Oecologia* 47: 164–170.
- Stamps, J. A. 1990. The effect of contender pressure on territory size and overlap in seasonally territorial species. – *Am. Nat.* 135: 614–632.
- Stamps, J. A., Buechner, M. and Krishnan, V. V. 1987. The effect of edge permeability and habitat geometry on emigration from patches of habitat. – *Am. Nat.* 129: 533–552.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. – *J. Wildl. Manage.* 47: 893–901.
- Watson, A. and Moss, R. 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. – In: Watson, A. (ed.). *Animal populations in relation to their food resources*. Blackwell Scientific Publications, Oxford, pp. 167–218.
- Wunderle, J. M. Jr. 1991. Age-specific foraging proficiency. – In: Power, D. M. (ed.). *Current Ornithology*. Vol. 8. Plenum Press, New York, pp. 273–325.
- Zanette, L. 2000. Fragment size and the demography of an area-sensitive songbird. – *J. Anim. Ecol.* 69: 458–470.
- Zanette, L. and Jenkins, B. 2000. Nesting success and nest predators in forest fragments: a study using real and artificial nests. – *Auk* 117: 445–456.
- Zanette, L., Doyle, P. and Trémont, S. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. – *Ecology* 81: 1654–1666.

(Received 8 January 2000, revised 10 April 2000, accepted 4 May 2000.)