Fragment size and the demography of an area-sensitive songbird

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Summary

1. Many songbird species are absent from small forest fragments. One possible explanation for this finding is that populations in small fragments decline to extinction because reproductive success is too low to compensate for adult mortality ($\lambda < 1$). I tested this hypothesis from 1995 to 1997 by measuring reproductive success, adult survival, and population viability for four banded populations of the Eastern yellow robin (*Eopsaltria australis*, White), an area-sensitive songbird. The populations inhabited two small (55 ha, termed S1, S2) and two large (500–1000 ha, termed L1, L2) forest fragments set within an agricultural landscape.

2. Females produced more fledglings but a similar number of independent young per capita in the small compared to the large fragments. Local female survival did not vary with fragment size.

3. Population models were used to calculate the finite rate of increase (λ) from the number of young produced (female yearlings per female per year) and adult female survival rates. Combining data from all four populations, $\lambda = 0.96$, indicating that robins produced 4% fewer female young per year than were needed to compensate for adult losses. Combining data from the two small fragments, $\lambda = 1.02$, suggesting that populations in small fragments were viable on average. In contrast, $\lambda = 0.85$ for the two large fragments combined, indicating that, on average, 15% fewer young were produced than were needed to replace missing adults each year. Averaging across fragments within the same size class masked the variability in population dynamics that existed between the replicates. Considering each of the four fragments separately, there was one potential demographic source (S2, $\lambda = 1.12$; L2, $\lambda = 1.23$) and one demographic sink (S1, $\lambda = 0.90$; L1, $\lambda = 0.46$) within each of the fragment size categories.

4. Observed changes in population sizes were similar to those predicted by the population models. Combining all populations, recruitment replaced most but not all missing females, and the observed population size declined by 8% per year. In both the small and large fragments, observed recruitment was insufficient to replace missing females and population sizes declined 5% and 8% per year, respectively. Within each of the fragment size categories, there was one stable population (S2 and L2) and one population that declined in size (S1 and L1, respectively, declined by 14% and 20% per year).

5. Reproductive success, adult survival, and population viability did not vary with fragment size. To explain area-sensitivity, I suggest that a threshold in fragment size exists below which populations are never viable, but above which populations may or may not be viable depending on factors unrelated to fragment size, such as nest predation rates.

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Introduction

Many forest-dwelling songbird species are considered to be area-sensitive because they are found less often in small than large forest fragments (e.g. Ambuel & Temple 1983; Blake & Karr 1984; Barrett 1995; Bellamy, Hinsley & Newton 1996). Researchers have documented the decline or disappearance of some of these songbirds from small fragments (Ambuel & Temple 1983; Blake & Karr 1984). Reductions in population viability with decreasing fragment size are one hypothesis proposed to explain these declines in numbers and extirpations (see Temple & Cary 1988 and Roth & Johnson 1993). The predictions of this hypothesis are that reproductive success declines with decreasing fragment size, such that the production of offspring becomes so low in small fragments that it is unable to compensate for adult mortality. Accordingly, small fragments are expected to contain populations that are demographic sinks (birth rate < death rate), while large fragments contain potential source populations (birth rate > death rate) (*sensu* Pulliam 1988; Donovan *et al*. 1995a).

Area-dependent changes in reproduction are often proposed to explain area-sensitivity in songbirds (e.g. Wilcove 1985; Porneluzi *et al*. 1993; Wenney *et al*. 1993; Hoover, Brittingham & Goodrich 1995), but this hypothesis has not been tested directly. Increased nest predation rates (e.g. Hoover *et al*. 1995) and lower food abundance in small fragments (Zanette, Doyle & Trémont 2000) offer some indirect evidence that reproductive success may be lower in small fragments. However, these factors may not be accurate estimates of the yearly, per capita production of young (see Donovan *et al*. 1995b; Pease & Grzybowski 1995). Male pairing success in small and large fragments is another index of reproductive success that has been used (e.g. Porneluzi *et al*. 1993). Demographic performance depends on females, so indices using males may be unreliable (Beissinger & Westphal 1998).

Adult survival is generally not measured in fragmentation studies and it is assumed to be independent of fragmentation effects (e.g. Roth & Johnson 1993; Donovan *et al*. 1995b). However, area-dependent changes in adult survival could result in poor demographic performance in small fragments even if no differences in reproductive success were evident. Analyses of life-history parameters have revealed that population growth rates can be far more sensitive to changes in adult female survival than to

changes in reproductive success (e.g. Lande 1988 for birds, Gaillard, Festa-Bianchet & Yoccoz 1998 for mammals). Therefore, direct measures of both adult survival and reproductive success in fragments of varying size would help to pin-point the demographic problems faced by songbirds in small fragments. Reproductive success and adult survival have been directly measured in a single small fragment (Roth & Johnson 1993), but studies comparing these two demographic parameters in small vs. large fragments currently are lacking.

Although reduced birth rates or survival rates are reasonable suggestions to explain area-sensitivity, other hypotheses exist. For instance, songbirds may be absent from small fragments because of problems with dispersal. Andrén (1994) proposed that suitable habitat may not be occupied in fragmented landscapes due to isolation among fragments, which reduces colonization rates. Because populations in small fragments are prone to extinction from stochastic events, then low colonization rates may result in decreased occupancy there. Alternatively, Burke & Nol (1998) found that female ovenbirds (*Seirus aurocapillus,* Linnaeus) avoided settling in smaller fragments and preferred to establish territories in larger fragments probably because they held relatively more food.

In this paper, I test the hypothesis that demographic performance declines with decreasing fragment size by monitoring four banded populations of Eastern yellow robins (hereafter 'robins'), breeding in two small (about 55 ha) and two large (about 500 and 1000 ha) forest fragments set within an agricultural landscape. I had four objectives.

1. To compare annual reproductive success in small and large fragments by counting the number of fledglings and independent young produced per female.

2. To estimate local survival rates of adult females.

3. To compare population growth rates in fragments of varying size using population viability models.

4. To measure recruitment into the four fragments and monitor actual changes in population sizes to compare with the results of the population viability models.

I chose the robin as a model study species for the following reasons: (i) in Australia, resident species that forage on the ground, like the robin, are particularly sensitive to anthropogenic disturbances (Garnett 1992); (ii) it is a forest-interior songbird because it is primarily found > 25 m from the forest edge (Howe 1984); and (iii) it is area-sensitive (Bar-

rett 1995). In my study area (see below), robins regularly occur in large fragments (> 400 ha) but do not occur in fragments of ≤ 20 ha. Also, this species is more likely to occupy fragments of 20–50 ha only if larger forest tracts are nearby (< 100 m; data from Barrett 1995).

Methods

STUDY AREA

This study was conducted in north-eastern NSW, Australia (30°27′ S, 151°13′ E). The study area sits atop the Great Dividing Range at 730–1300 m a.s.l. The climate is temperate and the forest cover is severely fragmented, with about 20% of the original forest remaining (Barrett 1995). Forest remnants are surrounded by pasture used by sheep and cattle. Most of the clearing occurred between the 1830s and 1930s.

Robins were studied in four forest fragments: two small fragments of 55 ha (plots S1, S2) and two large fragments of 500 ha and 1000 ha (plots L1 and L2, respectively). Both large fragments abutted other tracts of forest. The size of fragments in each size category were chosen *a priori*, based on the known distribution of robins in the study area (Barrett 1995; see the Introduction). Each fragment contained a 55-ha study plot marked in 100-m intervals. In the small fragments, the 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 1·8–11·8 km), and each was similar in terms of vegetation and general geographical 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. No permanent creeks, streams or rivers ran through any plot.

STUDY SPECIES

Robins are small (16–24 g) endemic Australian flycatchers from the family Eopsaltriidae (Simpson & Day 1996). They hold all-purpose territories year-round and are socially monogamous and multi-brooded. Breeding generally begins in August and ends in December. Open cup-shaped nests are built at a median height of 1·8 m (Marchant 1984), and the majority of clutches consist of two eggs. Despite the potential to rear up to three broods every season, successful pairs typically produce only one (61%, $n = 44$) or two (32%) broods (data from 1995 and 1996; also see Marchant 1986). When young robins leave the nest they are incapable of extended flight until 5 days post-fledging (also see Sullivan

1989). Both parents feed their young until the beginning of the next nesting attempt, which occurs at a median of 21 days post-fledging (L. Zanette, unpublished data).

REPRODUCTION

Total fledgling production by all resident females was enumerated on each plot between August 1995 and January 1997, over two breeding seasons. Fledglings were banded with unique combinations of three plastic colour bands and one numbered aluminium band for individual recognition. One colour band identified the site and year in which fledglings were born. Most birds were banded as nestlings between 6 and 10 days post-hatch. Where nests were too high to reach (> 3 m), young were captured by hand and banded a few hours after they left the nest. Surgical gloves were worn while handling all birds to reduce the amount of human scent left behind. Birds were banded at least 5 m from their original location, but they were always returned to where they were found. Two of 128 fledglings (1·6%) escaped banding using these methods but were subsequently captured within a few weeks using mist nets. No unbanded young were seen with breeding adults on any study plot.

In a study that I conducted in the S1 fragment in 1994, 16 of 17 fledglings produced in that year were monitored every 1–2 days for the entire breeding season. Ten fledglings died before reaching independence (defined as 22 days post-fledge), and of these, 100% died between 0 and 10 days post-fledge. Thus, the fate of young 11 days post-fledge was an accurate predictor of survival to independence. For the current study, I began searching for young in their natal territories 11 days post-fledge, and all young observed at this time were considered independent. A fledgling was considered dead if it was not seen after spending a minimum of 4 hours in active search over 4 search days. Observations collected while looking for or monitoring nests and adults during the course of the project also were used. In no case did a fledgling categorized as dead reappear later in the season.

SURVIVAL

Offspring

Yearlings were those fledglings born in year t that survived to the following breeding season, year $t + 1$. Yearling survival was broken down into two components. First, survival to independence was estimated by dividing the number of young known to reach independence by the number of fledglings produced. Second, subadult survival was estimated by calculating the percentage of independent young

born in 1995 that were seen alive on the natal grid any time during the 1996 breeding season.

I considered that data from the two small fragments provided a better estimate of local subadult survival because, if subadults in the large fragments settled to breed in a territory adjoining but outside the study plots, they would not be observed or counted. Such short-distance movements would be observed in the small fragments because the study plots there completely covered the sites (see Tanaka 1972). As a result, I calculated an estimate of subadult survival based on data from the small fragments and applied it to all fragments.

Because the survival probabilities of independent young and subadults had a binomial sampling distribution, the sampling variance was estimated so that $s_p^2 = p(1-p)/N_p-1$, where p represents the estimate of each parameter. Survival estimates were analysed using contingency tables that compared the numbers of dead and living young across the fragments.

ADULT FEMALES

Breeding adults were captured using mist nets and colour banded as for fledglings. Various morphological measures were also taken including body mass and tarsus length. Annual survival of adult females consisted of two components: (i) survival during the breeding season, and (ii) survival over winter. All survival estimates were based only on banded females. Females were monitored weekly during the breeding season, beginning on 29 July and ending on 31 December. Survival estimates for this 21-week period were calculated using the staggered entry Kaplan–Meier estimate (Pollock *et al.* 1989; Krebs 1999). The sampling variance was estimated following Pollock *et al.* (1989; equation 3). Local overwinter survival (1 January–28 July) was estimated by dividing the number of banded females seen at the beginning of breeding in season $t+1$ by the number of banded females known to be alive at the end of breeding in season t. Annual survival was then calculated by multiplying these two estimates. This estimate of local survival reflected the rate at which breeding vacancies became locally available, and hence, the rate at which young needed to be produced to sustain populations.

Overwinter survival probabilities had a binomial distribution so the sampling variance was calculated as for offspring survival. The sampling variance was estimated for annual survival probabilities (s_{BW}^2) by summing the variance of each random variable, including breeding season survival probabilities (B) and overwinter survival probabilities (W),

$$s_{BW}^2 = s_B^2 \times s_W^2 + s_B^2 \times \overline{W}^2 + s_W^2 \times \overline{B}^2$$

The standard error was calculated by taking the square-root of the variance. Survival estimates in

the breeding season were analysed using the Log-rank Test (Krebs 1999), while survival overwinter and annual survival were analysed using contingency tables (number dead vs. number alive).

POPULATION VIABILITY

Models

My goal here was to determine whether the local production of female young was sufficient to balance adult female losses. Several demographic variables were calculated: (i) number of breeding females; (ii) adult female survival; (iii) number of independent female young; and (iv) survival of subadults. I assumed that breeding robins produce a 1 : 1 ratio of females to males on average. With these variables I assessed population viability using two techniques. First, I calculated the finite rate of increase for the populations using the equation,

$$\lambda = S_f + N_i \times S_i$$

where S_f = annual survival of breeding females, N_i = number of independent female young per female per year, S_i = survival of subadults. When populations are exactly replacing themselves, $\lambda = 1\cdot0$; when they are increasing, $\lambda > 1\cdot0$; when they are decreasing, $\lambda < 1\cdot0$. Therefore, demographic sinks have negative population growth rates while potential sources have positive ones. I first considered the population performance of birds in the small vs. large fragments and then I considered each of the four fragments separately. Finally, I compiled the data for all fragments to determine whether the combined population was viable. The sampling variance was calculated for each estimated value of λ by summing the variance of each random variable as previously described. I considered the estimated value of λ to be different from a stable population when λ was more than twice its standard error from $1\cdot00$ (following Lande 1988).

For the second technique, I modified the equation for λ to construct a stage-based population projection model that showed changes in population size through time,

$$N_{t+1} = N_{ft} \times (S_{ft} + N_{it} \times S_{it})$$

where t is time of the simulation, N_{ft} is total number of breeding females at time t, S_{ft} is local survival probability of breeding females from the beginning of the breeding season in year t to $t+1$, N_{it} is number of independent female young produced per female at time t, S_{it} is local survival probability of subadults from the end of the breeding season in year t to the beginning of the breeding season in year $t+1$. All values were calculated from the observed data. In these models, I made three simplifying assumptions about the population dynamics of the birds: (i) reproductive success and adult survival

were equal for each age class; (ii) yearling survival rates were the same for both sexes; and (iii) all yearlings recruited into the breeding population. This last assumption means that all population viability results were best case scenarios.

Observed recruitment and population size

Actual recruitment into the populations was monitored by counting (i) banded female young born in a plot who later joined the breeding population there, and (ii) unbanded females that took the place of a previously banded female. Over the course of the study, 94% (68 of 72) of breeding females were banded, so I was unlikely to mistake any new, unbanded recruit for a previously breeding unbanded female. However, I minimized the possibility for error by checking that when a new unbanded bird recruited, the other unbanded females were still on their territories.

I determined whether population sizes actually changed from one year to the next by counting breeding pairs on each plot beginning in late August in 1995, 1996 and 1997. At least 40 person-hours were spent in these censuses on each study plot in each year. The censuses involved actively searching for breeding pairs in known territories and broadcasting the calls and songs of robins every 200 m on each study plot to search for newly formed territories.

Results

REPRODUCTIVE SUCCESS

On average, I monitored 22·5 females year^{-1} in the small fragments and 13·5 females year^{-1} in the large ones. These females produced a total of 282 active nests over both seasons, of which 64 nests (23%) fledged at least one young. Significantly more females successfully bred (i.e. produced at least one fledgling) in the smaller fragments (small fragments, 73% of 45 females; large fragments, 41% of 27 females; Fisher's exact test, $P = 0.01$).

A total of 128 fledglings were produced by 72 females over the 2 years, so per capita reproduction averaged 1·78 fledglings per female year^{-1} (Table 1). In the small fragments, 45 females produced 94 fledglings (2·09 fledglings per female year^{-1}) com-

Table 1. Reproductive success for female Eastern yellow robins breeding in two small (S1 and S2) and two large (L1 and L2) forest fragments over two breeding seasons. Values calculated from all offspring produced (female and male) per adult female

	Year	No. females	Fledglings per female ± SE	Independent young per female ± SE	Survival to independence ± SE
Study site					
S1	95	12	1.08 ± 0.38	0.75 ± 0.30	0.69 ± 0.13
	96	9	2.00 ± 0.53	1.18 ± 0.46	0.59 ± 0.12
	95/96	21	1.48 ± 0.32	0.93 ± 0.25	0.63 ± 0.09
S2	95	13	2.77 ± 0.61	2.34 ± 0.58	0.82 ± 0.06
	96	11	2.45 ± 0.46	1.89 ± 0.33	0.76 ± 0.08
	95/96	24	2.63 ± 0.39	2.14 ± 0.35	0.79 ± 0.05
L1	95	7	0.71 ± 0.47	0.43 ± 0.30	0.60 ± 0.22
	96	7	0.14 ± 0.14	0.14 ± 0.14	1.00 ± 0
	95/96	14	0.43 ± 0.25	0.29 ± 0.16	0.67 ± 0.19
L2	95	7	1.57 ± 0.69	1.55 ± 0.68	0.96 ± 0.06
	96	6	2.83 ± 0.98	2.14 ± 0.88	0.74 ± 0.11
	95/96	13	2.15 ± 0.59	1.82 ± 0.53	0.82 ± 0.07
Fragment size					
Small	95	25	1.96 ± 0.40	1.58 ± 0.36	0.79 ± 0.06
	96	20	2.25 ± 0.34	1.57 ± 0.28	0.69 ± 0.07
	95/96	45	2.09 ± 0.27	1.58 ± 0.23	0.74 ± 0.05
Large	95	14	1.14 ± 0.42	0.99 ± 0.39	0.84 ± 0.09
	96	13	1.38 ± 0.58	1.07 ± 0.49	0.75 ± 0.10
	95/96	27	1.26 ± 0.35	1.03 ± 0.30	0.79 ± 0.07
Total	95	39	1.67 ± 0.30	1.37 ± 0.25	0.80 ± 0.05
	96	33	1.91 ± 0.31	1.37 ± 0.27	0.71 ± 0.06
	95/96	72	1.78 ± 0.22	1.37 ± 0.19	0.75 ± 0.04

pared to 27 females who produced 34 fledglings in the large fragments (1·26 fledglings per female year^{-1}, Table 1). Significantly more fledglings were produced per capita in the small than the large fragments (Mann–Whitney U-test, $z = 2·09$, $P = 0·037$), but the replicates did not vary in a consistent manner. Significantly more fledglings were produced in S2 than S1 (M-W U, $z = 2·01$, $P = 0·044$), and in L2 than L1 (M-W U, $z = 2·11$, $P = 0·035$) (Table 1). A similar number of fledglings were produced per capita in 1995 as in 1996 (M-W U, $z = 0·74$, $P = 0·46$).

Fledglings in the different-sized fragments survived to independence equally well ($\chi^2 = 0·20$, d.f. = 1, $P = 0·66$) with little variation between years or replicates (Table 1). Just over half (56%) of the females successfully reared at least one offspring to independence, including 64% of females in the small and 41% in the large fragments (Fisher's exact test, $P = 0·086$).

A minimum of 93 fledglings survived to independence, but the fates of an additional seven were uncertain; one from S1, four from S2, and two from L2. To estimate the number that reached independence, I multiplied the number of fledglings of unknown fate by the survival rate calculated for each study plot which resulted in an additional 0·67 independent young at S1, 3·25 at S2, and 1·69 at L1. Therefore, overall, an estimate of 98·58 independent young were produced by 72 females resulting in 1·37 independent young per female year^{-1} (Table 1).

Per capita production of independent young was similar in the small and large fragments (M-W U, $z = 1·69$, $P = 0·09$) but differed between the replicates (Table 1). Females in S2 produced over twice as many young as those in S1 (M-W U, $z = 2·34$, $P =$ 0·019), and females in L2 produced over six times as many offspring as those in L1 (M-W U, $z = 2·11$, $P = 0·035$, Table 1). Overall, females produced a similar number of independent young per capita in 1995 as in 1996 (Mann–Whitney U-test, $z = 0·31$, $P = 0·76$).

The causes of mortality for robin fledglings were unknown. I observed two separate cases of moribund fledglings in S1, 2 days after they had left the nest in 1994. When found, these fledglings were inactive and both had lost weight. I also observed two cases of predation by pied currawongs (*Strepera graculina*, White). One of these occurred in S2 on day 4 in 1995. This fledgling's feet were severely malformed, suggesting that predation was the proximate rather than ultimate cause of mortality. The second case occurred in S1 in 1995 on a fledgling 5 days out of the nest, who had appeared to be in good health.

SURVIVAL OF ADULT FEMALES

Annual survival of breeding females averaged 0·72 and did not vary with fragment size in the breeding season (Log-rank Test, $z = 1·36$, $P = 0·17$, $n = 60$), overwinter (Fisher's Exact Test, $P = 0·71$), or overall (Fisher's Exact Test, $P = 0·78$, Table 2). Female survival rates were similar between years (Fisher's Exact Test, $P = 0·59$) and between the two small fragment replicates (Fisher's Exact Test, $P = 1·00$). However, survival in L1 was only half that in L2 (Fisher's Exact Test, $P = 0·03$), the difference being due primarily to poor survival over the breeding season in L2 (Table 2).

Female body mass was corrected for body size by regressing tarsus length on body mass to obtain resi-

Table 2. Survival values for adult females in two small (S1, S2) and two large (L1, L2) forest fragments over a 2 year period. Survival during the breeding season was calculated with the Kaplan–Meier staggered entry procedure and represented a 21-week period. Overwinter survival rates were based on the minimum number of birds observed in year t known to be alive in year $t + 1$. Annual survival probabilities were the product of the two survival estimates. n is the number of banded females monitored

	Breeding ± SE	Overwinter ± SE	Annual ± SE	n
Study site				
S1	0.944 ± 0.052	0.778 ± 0.100	0.735 ± 0.101	19
S2	0.826 ± 0.077	0.900 ± 0.071	0.744 ± 0.089	24
L1	0.566 ± 0.132	0.714 ± 0.161	0.404 ± 0.132	12
L2	0.909 ± 0.079	1.00 ± 0	0.909 ± 0.079	13
Fragment size				
Small	0.881 ± 0.050	0.842 ± 0.063	0.742 ± 0.067	43
Large	0.741 ± 0.091	0.900 ± 0.069	0.667 ± 0.105	25
Total				
1995	0.856 ± 0.057	0.818 ± 0.068	0.701 ± 0.074	38
1996	0.798 ± 0.072	0.920 ± 0.055	0.734 ± 0.080	30
95/96	0.832 ± 0.045	0.862 ± 0.045	0.717 ± 0.054	68

duals. The residuals were analysed in a one-way ANCOVA with study plot as the main effect and month of capture as the covariate. Only data from 1995 were analysed as there were insufficient data from 1996. There was no interaction between study plot and month (i.e. slopes for the two lines were parallel). Female body mass differed significantly across the four fragments ($F = 3.1$, d.f. $= 3$, 27, $P = 0.04$; covariate $F = 2.9$, d.f. $= 1$, 27, $P = 0.10$). Duncan's multiple range post hoc tests revealed that females weighed significantly less in L1 compared to the other fragments (means $\pm$ SE: L1 $= -2.0 \pm 0.5$, $n = 6$; L2 $= 0.1 \pm 0.8$, $n = 8$; S1 $= 0.4 \pm 0.4$, $n = 5$; S2 $= 0.8 \pm 0.6$, $n = 13$).

POPULATION VIABILITY

Models

In total, 26% and 34% of breeding females were lost per year from the small and large fragments, respectively (Table 2). Therefore, females needed to produce at least 0.26 and 0.34 independent female young per female year^{-1} in these fragments to maintain population numbers. Because females actually produced 0.79 independent female young in the small fragments and 0.52 young in the large fragments, reproduction was sufficient to balance adult female losses.

To ensure replacement, 33% and 66% of subadult females were required to survive in the small and large fragments, respectively. Subadult female survival was estimated at 0.36 ($\pm$ 0.08, SE) because 14 independent young from S1 and S2 in 1995 were subsequently seen in these sites as yearlings in 1996. Thus, populations in the small fragments produced a 2% surplus of first-year females per year while populations in the large fragments had a 15% deficit

in the number of female yearlings produced per year (Table 3, Fig. 1a). When each year was considered separately, similar results were obtained for the large fragments. In the small fragments, populations showed a 2% decline in 1995 and a 6% increase in 1996 (Table 3).

To investigate the demography of these populations more fully, I examined each study plot separately. A clear pattern emerged, but it did not coincide with fragment size. Breeding females were lost from S1, S2, L1, and L2 at annual rates of 27, 26, 60, and 9%, respectively. The numbers of independent female offspring produced per capita in each of these fragments were 0.47, 1.07, 0.15, and 0.91. Therefore, all fragments produced a sufficient number of independent female young to maintain their populations, with the exception of L1 where the population was expected to decline. As for the remaining fragments, 57%, 24%, and 10% of subadult females were needed to survive to ensure full replacement. Using the estimate of 0.36, therefore, resulted in declining populations in S1 and L1 and increasing populations in S2 and L2 (Table 3, Fig. 1b). These results suggest that the populations in S1 and L1 needed some immigration to persist.

When each year was considered separately, similar results were obtained for all of the fragments with the exception of S1, which had a decreasing population growth rate in 1995 but an increasing rate in 1996 (Table 3). To gain further insight into the viability of the population in S1, I analysed the data I collected there in 1994. In this case, $\lambda = 0.82 \pm 0.17$ ($S_f = 0.667$, $N_i = 0.417$, $S_i = 0.355$), indicating that females in S1 produced 18% fewer young than were needed to sustain the population. Thus, in 2 of 3 years, the birth rates were lower than the death rates in S1.

Table 3. Population viability models for Eastern yellow robins in two small (S1, S2) and two large (L1, L2) forest fragments

	Year					
	95		96		95/96	
	Lambda $\pm$ SE	Change year^{-1}	Lambda $\pm$ SE	Change year^{-1}	Lambda $\pm$ SE	Change year^{-1}
Study site						
S1	0.76 ± 0.16	-0.24	1.09 ± 0.15	0.09	0.90 ± 0.12	-0.10
S2	1.17 ± 0.18	0.17	1.05 ± 0.17	0.05	1.12 ± 0.14	0.12
L1	0.61 ± 0.19	-0.39	0.23 ± 0.13	-0.77	0.46 ± 0.14	-0.54
L2	1.08 ± 0.20	0.08	1.38 ± 0.18	0.38	1.23 ± 0.11	0.23
Fragment size						
Small	0.98 ± 0.13	-0.02	1.06 ± 0.12	-0.06	1.02 ± 0.10	0.02
Large	0.86 ± 0.15	-0.14	0.89 ± 0.18	-0.11	0.85 ± 0.12	-0.15
Total	0.94 ± 0.10	-0.06	0.98 ± 0.11	-0.02	0.96 ± 0.08	-0.04
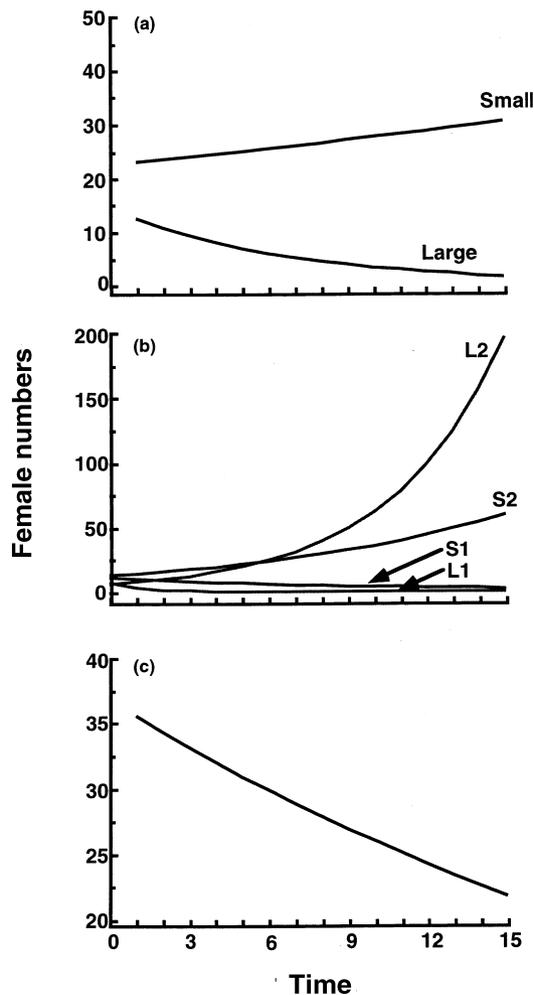
Fig. 1. Population projection models using the per capita birth rate and death rate of robins inhabiting two small (S1, S2) and two large (L1, L2) forest fragments. The models were run to help assess the viability of populations in the (a) small vs. large fragments; (b) four study sites considered separately; and (c) four study sites combined.

Table 4. Number of female breeding vacancies that were filled by new recruits compared to the number that remained empty in the four forest fragments from 1995 to1997. Breeding vacancies occurred when a banded, previously breeding female disappeared from a study plot

| | Female breeding vacancies | | |
| | Filled | Unfilled | |
	n	n	%
Study site			
S1	2	3	60
S2	6	0	0
L1	6	2	25
L2	1	0	0
Fragment size			
Small	8	3	27
Large	7	2	22
Total	15	5	25

Observed recruitment and population size

I observed the dispersal of one banded young. A female born in S1 in 1994 emigrated overwinter and recruited into the S2 population about 2·5 km away. Between 1995 and 1997, 20 females disappeared from the four fragments (Table 4). Recruits replaced most but not all female breeding vacancies, and the numbers of breeding pairs declined an average of 8% year^{-1} with all fragments combined (Tables 4 & 5). Recruitment fell short by 27% in the small fragments and 22% in the large ones (Table 4). In addition, the number of breeding pairs declined 5% year^{-1} and 8% year^{-1} in the small and large fragments, respectively (Table 5). Examining the four study sites separately, recruitment fully compensated

I estimated whether the two potential source populations (i.e. positive population growth rates, S2 and L2) produced enough female young to balance female losses in the four populations as a whole, by combining the data for all four fragments. Twenty-eight per cent of breeding females disappeared from the four fragments per year but each female produced 0·68 independent females per year, which was enough to sustain the population. However, 41% of subadult females were required to survive to ensure replacement. Using the subadult survival estimate of 0·36 resulted in $\lambda = 0.96 \pm 0.14$, which means that females in these fragments produced 4·0% fewer first-year females year^{-1} than were needed to compensate for female losses (Table 3, Fig. 1c). Similar results were obtained when each year was examined separately (Table 3).

Table 5. Number of breeding pairs observed at the beginning of the breeding season from 1995 to 1997. Proportion change is the degree to which populations increased or decreased relative to their initial population size

| | Year | | | |
	1995	1996	1997	Proportion change year^{-1} $\pm$ SE
Study site				
S1	12	9	9	− 0.14 ± 0.20
S2	12	11	13	0.04 ± 0.18
L1	6	6	4	− 0.20 ± 0.29
L2	6	6	6	0.00 ± 0.00
Fragment size				
Small	24	20	22	− 0.05 ± 0.11
Large	12	12	10	− 0.08 ± 0.14
Total	36	32	32	− 0.08 ± 0.06

for female losses in the S2 and L2 study plots, but in S1 and L1, recruitment fell short by 60% and 25%, respectively (Table 4). The number of breeding pairs declined only in the S1 and L1 fragments (Table 5).

Discussion

Studying an area-sensitive, forest-interior songbird species, the Eastern yellow robin, I found no evidence of reduced reproductive success in small fragments. While females in small fragments produced more fledglings on average than females in large fragments, there were no differences in the number of independent young produced per capita. Area-dependent effects on female survival also were absent. Finally, I found no evidence that populations in small fragments produced fewer yearling females than were needed to balance adult female losses. In the small fragments, 2% more yearlings survived annually than were needed for replacement. There was a 15% annual deficit in the number of yearlings that survived in the large fragments. Thus, reproductive success, adult survival, and population viability did not decline with decreasing fragment size.

My findings are consistent with an experimental study of fragmentation using small mammals. After reducing a landscape to 30% remaining habitat, Wolff, Schauber & Edge (1997) found no significant differences in the reproduction and survival of female gray-tailed voles (*Microtus canicaudus*, Miller) in small compared with large fragments.

I know of no other studies that have directly measured the reproductive success and survival of area-sensitive songbirds in fragments of varying size. Donovan *et al.* (1995a, b) found that the females of three neotropical migrant species breeding in fragments averaging 550–600 ha produced an average of 0·66 female fledglings per female in landscapes with about 30% remaining forest. The fragments in Donovan *et al.*'s study were similar in size to the large fragments in my study where 0·70 female robin fledglings per female were produced in a landscape with about 20% remaining forest. Similarly, using the demography data presented by Donovan *et al.*, I estimated that $\lambda = 0.82$ for the populations they studied (female survival = 0·62, fledglings per female = 0·66, fledgling survival to their first year = 0·31). This value compares closely with the estimate of population growth calculated in my large fragments where $\lambda = 0.85$. The similarities in per capita reproduction and population growth rates between these two studies suggest that forest fragmentation may have similar net effects on populations of several forest-interior songbird species.

Fragment size was not associated with fledgling survival to independence. Average survival was 0·75, and ranged from 0·63 to 0·82 across the four frag-

ments. I had assumed that all fledglings observed ≥ 11 days out of the nest reached independence, based on data obtained in 1994. This assumption seemed to hold for the present study. Of 93 fledglings known to have survived ≥ 11 days, 91 were subsequently seen ≥ 22 days post-fledge, which would alter the survival estimates minimally. Few accounts of survival to independence are available for passerines (but see Sullivan 1989). However, my estimate of yearling survival was 0·28 (0·75 × 0·36), which is the same value found for yearlings of the closely related Western yellow robin (*Eopsaltria georgiana*, Quoy & Gainard; R. & M. Brown, unpublished data as cited in Rowley & Russell 1991). My estimate is also similar to other published accounts of yearling survival for songbird species both in Australia and elsewhere (e.g. 0·31 for neotropical migrants in the US, Temple & Cary 1988, and Donovan *et al.* 1995b; Australian birds, reviewed in Rowley & Russell 1991).

I did not calculate a local survival estimate for subadults in the large fragments because I predicted that this value would be seriously underestimated (see Methods). In fact, only 14% of 14 independent young born in 1995 were observed in the large fragments in 1996, which means that yearling survival would only be 11% in the large fragments (0·79 × 0·14). I know of no reason why yearling survival would be 2·5 times lower in the large than small fragments. Also, 11% yearling survival is called into question because it is much lower than that found for other passerines, as discussed above. Therefore, I presume that applying my estimate of subadult survival to large fragments was reasonable even though it was based on data from the small fragments. Estimating subadult survival for birds that are sampled on plots smaller than the entire tract is a methodological problem which, as yet, has no solution that is fully adequate (Tanaka 1972).

The average annual survival rate of female Eastern yellow robins in this study was 0·72 and is comparable with the 0·75 found by Marchant (1986), in a study of Eastern yellow robins breeding in southeastern NSW. In addition, a survival value of 0·78 was calculated for the Western yellow robin (R. & M. Brown, unpublished data as cited in Rowley & Russell 1991). Females in all of the fragments that I studied had relatively high annual survival rates except for those in L1, who had low survival especially during the breeding season. These data must be interpreted with caution. Female numbers in L1 were not high, so the loss of any single female represents a large proportion of the population, thereby artificially inflating mortality rates. Keeping this proviso in mind, I suggest that the females in L1 were lost from the study plot at such a high rate because they were in poor condition and died. I base this conclusion on the fact that these females were lighter than those in the other fragments.

Alternatively, poor survival in L1 could be due to high rates of emigration. For example, poor nesting success can induce emigration (Greenwood & Harvey 1982; Roth & Johnson 1993), and of the four fragments, nesting success was lowest in L1 (8%, Zanette & Jenkins 2000). However, whether or not a female robin bred successfully in one season was unrelated to whether she survived or disappeared in the following season (L. Zanette, unpublished). A complete search of the entire L1 fragment, or the use of radio-tags would be required to assess the causes of female losses there.

In a previous study in these same fragments, Zanette *et al.* (2000) reported area-dependent changes in food availability, with food being in short supply in the small compared with the large fragments. Robins in the small fragments responded to decreased food availability by exhibiting impaired foraging efficiency and reproduction (i.e. low egg and nestling mass). However, despite low food supply and its negative consequences on individual reproduction, I found none of the population effects expected given the food-limitation that is commonly observed in birds (reviews in Martin 1987 and Boutin 1990). Similarly, others have found increased nest predation rates in small fragments (Hoover *et al.* 1995), which have been expected to translate into decreased reproductive success and poor population performance (Wilcove 1985; Andrén & Angelstam 1988; Robinson *et al.* 1995; Gale, Hanners & Patton 1997). My results underscore the necessity of measuring demographic parameters directly whenever possible, and caution against relying solely on these indirect measures to draw conclusions about annual reproductive success and population viability.

Breeding densities were another inadequate indicator of population performance (Zanette *et al.* 2000). Densities were about two times higher in S1 and S2 than in L1 and L2. Yet my population viability models showed positive population growth rates in S2 and L2, and negative rates in S1 and L1. Because neither reproductive success nor adult female survival varied consistently with fragment size, then higher densities in the small fragments were unlikely to be related to these demographic parameters. Instead, male dispersal may play a role (Zanette *et al.* 2000; L. Zanette, unpublished). Male robins tend to recruit locally (L. Zanette, unpublished data). However, male natal dispersal may have been further discouraged in the small fragments because they were completely surrounded by pasture (e.g. Stamps, Buechner & Krishnan 1987). Low male emigration may result in strong competition for territories which can raise population densities (Knapton & Krebs 1974).

In the habitat fragmentation literature, small fragments are generally expected to be demographic sinks and large fragments potential sources (Temple & Cary 1988; Porneluzi *et al.* 1993; Donovan *et al.* 1995a,b; Hoover *et al.* 1995). Contrary to this expectation, wood thrushes (*Hylocichla mustelina*, Gmelin) breeding in fragments of 1100–2200 ha in the US Midwest had negative population growth rates (Trine 1998), while this same species breeding in a small, 15-ha fragment in Delaware had a stable population (Roth & Johnson 1993). In my study, source–sink relations also did not follow the expected pattern because, on average, populations in the small fragments were potential demographic sources while the large fragments were demographic sinks. For robins, however, averaging across fragments within the same size class masked the variability in population performance that was evident between the replicates. This variability was related to the rates of nest predation within each fragment because S2 and L2 had high rates of nest predation and were demographic sinks, while S1 and L1 had low rates of nest predation and were potential sources (Zanette & Jenkins 2000). Nest predation is frequently cited as an important factor limiting songbird populations in fragmented landscapes (e.g. Wilcove 1985; Robinson *et al.* 1995), and my comparisons of nest predation rates with population viability are consistent with this idea.

Robins are found infrequently in fragments of < 50 ha and are absent from fragments of ≤ 20 ha (Barrett 1995). I found that demographic performance did not decline with fragment size, so I am unable to explain this pattern of distribution with my data. My results, however, are consistent with the random sampling hypothesis. Andrén (1994) proposed that in fragmented landscapes with 10–30% remaining habitat, isolation among fragments becomes extreme, resulting in low colonization rates and a decline in the occupancy of suitable habitat. Extinction probabilities are expected to increase with decreasing fragment size as a result of stochastic events. Thus, low colonization would be particularly detrimental to the persistence of populations in small fragments (i.e. < 50 ha in this study), resulting in decreased occupancy there. In my study area, 20% of the forest remains in fragments of varying size, so this scenario may apply.

Alternatively, population growth rates for robins may become strongly and consistently negative only in fragments smaller than 50 ha, where robins usually do not occur. Food supply could be responsible for such a demographic threshold. Food availability declines with decreasing fragment size (Burke & Nol 1998; Zanette *et al.* 2000). In fragments under 50 ha, food may fall to a critical threshold where it is too scarce to allow for adequate survival and/or reproduction. In this case, one of two scenarios may apply. First, songbirds may settle in such fragments and exhibit declining population growth rates and eventual extinction in the absence of immigration. Alternatively, rather than settle in these resource-poor fragments, songbirds could avoid

them altogether (Lynch & Whigham 1984), as has been found for ovenbirds, an area-sensitive, forest-dependent songbird from North America (Burke & Nol 1998). Songbirds could avoid such resource-poor fragments by direct sampling of the invertebrate fauna or by using some other cue associated with food abundance such as litter depth (Burke & Nol 1998).

Whether birds settle in or avoid fragments below a demographic threshold may depend on how common the species is on a regional scale. Forest-dependent species that are regionally abundant are likely to be found in most forest fragments, even if the habitat is suboptimal (e.g. Haila, Hanski & Raivio 1993). On the other hand, species that are regionally uncommon should distribute themselves only among the fragments in which survival and reproduction are possible. I propose that robin numbers were depressed in the fragmented landscape in which I worked, and that the remaining birds avoided fragments < 50 ha in size.

Low robin numbers in fragmented landscapes may not be surprising. Regional numbers will decline with decreases in forest cover (Andrén 1994). Because so little of the initial forests remain in the region where I worked, robin numbers have probably suffered. Also, in agricultural landscapes, the forest fragments left behind were usually left standing because they were unsuitable for agriculture, being on less fertile soils, steep slopes, etc.... (Robinson & Traill 1996). In turn, the habitat left for songbirds may be of poor quality. Robins experience higher nest predation rates in fragmented compared to more forested landscapes (Zanette & Jenkins 2000), as has been found for some songbirds in the US (Robinson *et al.* 1995). In addition, food supply for robins may be lower in more disturbed regions, though this hypothesis requires testing. When I combined the demographic variables for all four robin populations, I found a 4% annual decline as estimated from the population models, and an 8% annual decline as estimated from the observed data on population numbers. My estimates of population change did not differ from stable populations. However, populations in fragmented landscapes may be performing poorly relative to those in contiguous landscapes. For instance, in the US Midwest, population models for three neotropical migrant species revealed that at least two species had decreasing population growth rates in fragmented landscapes (30% forest), while all three species had increasing rates in contiguous landscapes (90% forest, Donovan *et al.* 1995b).

I showed that population viability for Eastern yellow robins was not related to fragment size, yet this species is area-sensitive and so clearly affected by forest fragmentation. Alternatives to the traditional argument that reproductive success and population viability decline with decreasing fragment size must

be proposed. I suggested that a demographic threshold exists below which robin populations are never viable, but above which populations may or may not be viable, depending on factors not related to fragment size (i.e. nest predation). In addition, spatial scale must be taken into consideration. Instead of being negatively related to fragment size, as is usually expected, it is possible that reproductive success and population viability decline with decreases in the amount of forest cover in a landscape. In this case, reductions in songbird numbers on a regional scale would be expected in fragmented as compared to heavily forested areas. Regional numbers may be further compromised if the threshold size of fragment acceptable to area-sensitive species increases over time in fragmented landscapes. Due to a high edge:interior habitat ratio, small fragments are prone to a variety of edge effects (reviews in Saunders, Hobbs & Margules 1991; Paton 1994), which could degrade the quality of the fragment as time passes (see Janzen 1986; Robinson & Traill 1996). Thus, fragments that were formerly productive (i.e. 55 ha in this study) may become progressively degraded and subsequently uninhabitable.

References

Ambuel, B. & Temple, S.A. (1983) Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology*, **64**, 1057–1068.

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different pro-

portions of suitable habitat: a review. *Oikos*, **71**, 355–366.

Andrén, H. & Angelstam, P. (1988) Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecology*, **69**, 544–547.

Barrett, G.W. (1995) *Woodland bird assemblages on the New England Tablelands, Northeastern New South Wales.* PhD Thesis, University of New England, Australia.

Beissinger, Z.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.

Bellamy, P.E., Hinsley, S.A. & Newton, I. (1996) Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology*, **33**, 249–262.

Blake, J.G. & Karr, J.R. (1984) Species composition of bird communities and the conservation benefit of large versus small forests. *Biological Conservation*, **30**, 173–187.

Boutin, S. (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. *Canadian Journal of Zoology*, **68**, 203–220.

Burke, D.M. & Nol, E. (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk*, **115**, 96–104.

Donovan, T.M., Lamberson, R.H., Kimber, A., Thompson, F.R. III & Faaborg, J. (1995a) Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds.

Donovan, T.M., Thompson, F.R. III, Faaborg, J. & Probst, J.R. (1995b) Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology*, **9**, 1380–1395.

Gaillard, J.-M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology and Evolution*, **13**, 58–63.

Gale, G.A., Hanners, L.A. & Patton, S.R. (1997) Nesting success of worm-eating warblers in a forested landscape. *Conservation Biology*, **11**, 246–250.

Garnett, S. (1992). *Threatened and Extinct Birds of Australia.* Report No. 82. Royal Australasian Ornithologists Union, Melbourne.

Greenwood, P.J. & Harvey, P.H. (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.

Haila, Y., Hanski, I.K. & Raivio, S. (1993) Turnover of breeding birds in small forest fragments: the 'sampling' colonization hypothesis corroborated. *Ecology*, **74**, 714–725.

Hoover, J.P., Brittingham, M.C. & Goodrich, L.J. (1995) Effects of forest patch size on nesting success of wood thrushes. *Auk*, **112**, 146–155.

Howe, R.W. (1984) Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. *Ecology*, **65**, 1585–1601.

Janzen, D.H. (1986) The eternal external threat. *Conservation Biology: the Science of Scarcity and Diversity* (ed. M.E. Soulé), pp. 286–303. Sinauer Associates, Inc. Sunderland, Massachusetts.

Knapton, R.W. & Krebs, J.R. (1974) Settlement pattern, territory size and breeding density in the song sparrow (*Melospiza melodia*). *Canadian Journal of Zoology*, **52**, 1413–1420.

Krebs, C.J. (1999). *Ecological Methodology*, 2nd edn. Benjamin/Cummings, Menlo Park, CA.

Lande, R. (1988) Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia*, **75**, 601–602.

Lynch, J.F. & Whigham, D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation*, **28**, 287–324.

Marchant, S. (1984) Nest-records of the Eastern yellow robin *Eopsaltria australis*. *Emu*, **84**, 167–174.

Marchant, S. (1986) Breeding of the Eastern yellow robin *Eopsaltria australis*. *Birds of Eucalypt Forests and Woodlands: Ecology, Conservation, Management* (eds A. Keast, H.F. Recher, H. Ford & D. Saunders), pp. 231–40. Royal Australasian Ornithologists Union and Surrey Beatty & Sons, Australia.

Martin, T.E. (1987) Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics*, **18**, 453–487.

Martin, T.E. (1992) Breeding productivity considerations: what are the appropriate habitat features for management. *Ecology and Conservation of Neotropical Migrant Landbirds* (eds M. Hagan III, & D.W. Johnston), pp. 455–473. Smithsonian Institution Press, Washington DC.

Paton, P.W.C. (1994) The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology*, **8**, 17–26.

Pease, C.M. & Grzybowski, J.A. (1995) Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. *Auk*, **112**, 343–363.

Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. (1989) Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management*, **53**, 7–15.

Porneluzi, P., Bednarz, J.C., Goodrich, L.J., Zawada, N. & Hoover, J. (1993) Reproductive performance of territorial ovenbirds occupying forest fragments and a continuous forest in Pennsylvania. *Conservation Biology*, **7**, 618–622.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.

Robinson, D. & Traill, B.J. (1996) Conserving woodland birds in the wheat and sheep belts of southern Australia. RAOU Conservation Statement No. 10. *Wingspan Supplement*, **6**, 1–15.

Robinson, S.K., Thompson, F.R. III, Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.

Roth, R.R. & Johnson, R.K. (1993) Long-term dynamics of a wood thrush population breeding in a forest fragment. *Auk*, **110**, 37–48.

Rowley, I. & Russell, E. (1991) Demography of passerines in the temperate southern hemisphere. *Bird Population Studies: Relevance to Conservation and Management* (eds C.M. Perrins, J.-D. Lebréton & G.J.M. Hirons), pp. 235–250. Oxford University Press, Oxford.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Simpson, K. & Day, N. (1996). *Field Guide to the Birds of Australia.* Penguin Books Australia Ltd, Australia.

Stamps, J.A., Buechner, M. & Krishnan, V.V. (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist*, **129**, 533–552.

Sullivan, K.A. (1989) Predation and starvation: age-specific mortality in juvenile juncos (*Junco phaenotus*). *Journal of Animal Ecology*, **58**, 275–286.

Tanaka, R. (1972) Investigation into the edge effect by use of capture–recapture data in a vole population. *Researches on Population Ecology*, **13**, 127–151.

Temple, S.A. & Cary, J.R. (1988) Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology*, **2**, 340–347.

Trine, C.L. (1998) Wood thrush population sinks and implications for the scale of regional conservation strategies. *Conservation Biology*, **12**, 576–585.

Wenney, D.G., Clawson, R.L., Faaborg, J. & Sheriff, S.L. (1993) Population density, habitat selection and minimum area requirements of three forest-interior warblers in Central Missouri. *Condor*, **95**, 968–979.

Wilcove, D.S. (1985) Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, **66**, 1211–1214.

Wolff, J.O., Schauber, E.M. & Edge, W.D. (1997) Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. *Conservation Biology*, **11**, 945–956.

Zanette, L., Doyle, P. & Trémont, S. (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology*, **81**, in press.

Zanette, L. & Jenkins, B. (2000) Nesting success and nest predators in forest fragments: a study using real and artificial nests. *Auk*, **117**, 445–454.