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ABSTRACT.—Area sensitivity in songbirds is commonly attributed to increased nest predation in forest fragments. In 1995 and 1996, we tested whether the nest predators and nesting success of an area-sensitive forest bird, the Eastern Yellow Robin (*Eopsaltria australis*), varied with fragment size, and we also conducted an artificial nest experiment. The study occurred in two small (55 ha) and two large (>400 ha) forest fragments in a matrix of agricultural land in New South Wales, Australia. Predation accounted for 95% of all failures of 282 robin nests, and the survival of robin nests was negatively correlated with how frequently we observed avian nest predators near nests (i.e. nest-predator activity). Of 461 artificial nests, 84% were depredated, nearly all (99%) by birds. Thus, birds were important predators of nests. The abundance, species richness, and activity of avian nest predators were not related to fragment size. Survival of robin nests averaged 19%; nests in small fragments had a 22% chance of producing at least one fledgling compared with 15% in large fragments, but the difference was not significant. Survival of artificial nests averaged 12% in both small and large fragments. Nest-predator activity accounted for the most variation (68%) in the fate of robin nests, followed by the cumulative density of open-cup nesters (16%). The placement of robin nests had no influence on nest fate. We conclude that nest predation was not area dependent and propose food supply as an alternative hypothesis to explain area sensitivity. We suggest that, rather than being related to fragment size, nest predation increases with decreasing forest cover in a landscape. Increased nest predation in fragmented compared with contiguous landscapes may lower the population viability of songbirds in a region, and hence regional numbers. Therefore, the spatial scale at which fragmentation influences nest predation and songbird populations must be considered carefully. Received 16 February 1999, accepted 1 October 1999.

DEFORESTATION AND FRAGMENTATION have been implicated in local and regional declines of songbirds in many parts of the world (see Hagan and Johnston 1992), and many forest songbirds are now commonly found only in large tracts of forest (Ambuel and Temple 1983, Lynch and Whigham 1984, Bellamy et al. 1996). In agricultural landscapes, forest edges harbor a more abundant and species-rich assemblage of nest predators than do forest interiors (Møller 1989, Andrén 1992, Marini et al. 1995), and songbirds may suffer high nest predation at forest edges (Paton 1994). Because small fragments contain more edge than large fragments, low nesting success as a result of high nest predation could result in losses of area-

sensitive species from small fragments (Andrén and Angelstam 1988, Temple and Cary 1988). Nesting success often declines with decreasing fragment size (Møller 1988, Small and Hunter 1988, Telleria and Santos 1992, Hoover et al. 1995), lending support to this idea. However, area-dependent changes in nesting success have not been found in all studies (Nour et al. 1993, Haskell 1995, Gale et al. 1997). Furthermore, most studies of nest predation in forest fragments have used artificial nests, which may not experience the same predation pressure as do real nests (Ortega et al. 1998).

Nesting success may be affected by area-dependent changes in predator assemblages, but other factors also may be important. For instance, nesting birds may be attracted to edge-dominated environments, and higher nest densities may attract nest predators or improve their foraging efficiency (Gates and Gysel 1978). Therefore, low nesting success in fragments could be due to density-dependent mortality from predation. Nest placement also can

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influence the foraging efficiency of nest predators (Wray and Whitmore 1979, Sugden and Beyersbergen 1986). In this case, nesting success could vary with fragment size, even if the assemblage of nest predators remained constant, if nests in small fragments were in more or less conspicuous places. For instance, nest cover could be reduced by tree extraction and the selective removal of shrubs and woody debris, which can be intense in small fragments (Barrett 1995). Alternatively, increased solar radiation in small fragments may increase primary productivity, providing more nesting cover (Ranney et al. 1981, Martin 1992). Assessing correlates of nesting success should help to identify factors that are important in determining the fate of nests.

We examined the nesting success of Eastern Yellow Robins (*Eopsaltria australis*) in two small (55 ha) and two large (>400 ha) forest fragments that were surrounded by agricultural land. Eastern Yellow Robins (hereafter "robins") are area-sensitive songbirds that typically occur more than 25 m from the forest edge (Howe 1984, Barrett 1995). The goals of our study were to (1) assess whether nesting success varied with fragment size; (2) test whether small fragments possessed a higher abundance, richness, or activity level of potential nest predators; (3) determine whether the survival of robin nests depended on the assemblage of avian nest predators, the density of open-cup nesting songbirds, and/or nest placement; and (4) examine nesting success and the influence of nest predators on artificial nests in these same fragments.

STUDY AREA AND METHODS

Study area and species.—This study was conducted on the Northern Tablelands in northeastern New South Wales (30°27'S, 151°13'E). The area is in the Great Dividing Range at 730 to 1,300 m. The climate is temperate with a mean annual rainfall of 750 mm. Most of the original forests were converted into pastures between 1830 and 1930, and at present only 20% of the initial forest remains in patches of varying size. The four fragments that we studied included two small fragments of 55 ha each (S1 and S2) and two large fragments of 500 and 1,000 ha (L1 and L2, respectively). The size of fragments in the two categories was chosen *a priori* based on the known distribution of robins on the Northern Tablelands (Barrett 1995). Forest fragments of 55 ha were considered small because robins do not occur in fragments

smaller than 20 ha and occur in fragments less than 50 ha only when other forest tracts are within 100 m. Robins typically occur in fragments that exceed 400 ha in size.

Each fragment contained a 55-ha study plot marked in intervals of 100 m. Plots in the large fragments were at least 150 m from the boundary between the forest and pasture. Vegetation in plots was dominated by rough-barked trees such as New England stringybark (*Eucalyptus caliginosa*), Western New England blackbutt (*E. andrewsii*), mugga ironbark (*E. sideroxylon*), and rough-barked applebox (*Angophora floribunda*). The shrub layer was dominated by *Cassinia* spp., *Bursaria* spp. and *Acacia* spp. Plots were 1.8 to 11.8 km from one another (\bar{x} = 6.1 km).

Eastern Yellow Robins are small (ca. 20 g) flycatchers that are endemic to Australia. They are socially monogamous and hold all-purpose territories year-round. Breeding generally occurs between August and December. Females build new open-cup nests following nest failures or three weeks after a previous brood fledges. Most nests are placed in tree forks and bushes less than 3 m above ground, the median nest height being 1.75 m (Marchant 1984, 1986). Robin clutches have two to three eggs, with most three-egg clutches being laid in the middle of the breeding season. One egg is laid every 27 h (Marchant 1986), and incubation generally begins with the second egg. Females desert their nests if the clutch size is reduced to one egg by partial predation, but they do not desert nestlings.

Robin nests.—We monitored all robin pairs that nested on the four study plots for the entire breeding season in 1995 (n = 38 pairs) and 1996 (n = 34 pairs). At least one member of each breeding pair was captured in a mist net and banded with a unique combination of four color bands and one numbered metal band. We found nests by following behavioral cues of adults and relocated them from compass bearings and distances from grid points.

Most nests were checked at intervals of one or two days either directly or by using a pole and mirror that could reach up to 5.0 m. To monitor higher nests, we sat 15 m from the nest tree and considered the nest inactive if it remained unattended for 15 min. No nests were misclassified by this procedure. We never approached a nest if a potential predator was nearby, and our activities did not appear to increase predation risk. On 94 occasions after monitoring a nest in the S1 fragment in 1994, we walked at least 20 m from the nest and observed it for 20 min. No cases of predation were recorded during this interval.

Artificial nest experiment.—Artificial nests and eggs (two per nest) resembled those of robins to increase the chance that they would show the same patterns of predation as natural nests. Tennis balls were cut in half and bark from stringybark trees was glued to

all surfaces (following R. E. Major pers. comm.). The nests were decorated with lichen and moss. We made robin-sized eggs (22 × 16 mm) using a mixture of green, white, and brown plasticine. Varnish gave the eggs the glossy sheen of robin eggs and also prevented the plasticine from melting. Finally, the eggs were speckled with reddish-brown paint. We used plasticine eggs because nest predators ranging in size from small mammals to large birds routinely attempt to prey on these eggs (e.g. Møller 1988, Nour et al. 1993, Haskell 1995).

To facilitate the identification of predators, we designed a method that allowed predation to occur without egg removal. Both eggs were glued to wooden disks that were 2 cm in diameter. Each disk had a 1 cm hole in the center so that we could tie two pieces of durable string, approximately 60 cm in length, onto opposite sides of the disk. The leads were threaded through a small hole at the bottom of the artificial nest. When the nests were distributed for the experiment, the leads were tied to the nest tree or bush, thereby securing the disk.

We conducted artificial nest experiments once per month from September to November 1995 and then again from August to December 1996. For each trial, 15 nests were distributed per plot along grid lines separated by 200 m. Within each grid line, nests were placed every 200 m in 1995 and every 100 m in 1996. To distribute nests, we went to preassigned grid markers and walked a minimum of 5 m to the NW, NE, SW, or SE (direction determined randomly). Nests were attached to tree forks or bushes with cable ties (28.6 cm long) threaded through two small holes that we drilled into one side of the artificial nests. Nests were placed 20 cm to 2 m above ground, which is within the height range typically used by robins. No attempt was made to conceal nests because robin nests generally are not concealed and because we wished to avoid any potential bias from differences in concealment effort. We left the nests out for 16 days and checked them on days 3, 6, 9, and 16. We used a larger interval at the end of the experiment because most nests (>70%) were depredated by day 9. When at least one egg from a nest was disturbed, we removed the nest to avoid the possibility of further predation. Predation was attributed to birds (which left peck marks), mammals (which left tooth imprints), or unknown causes.

Activity indices and bird censuses.—Birds are important members of the nest-predator assemblage in agricultural landscapes (e.g. Ambuel and Temple 1983, Angelstam 1986, Andrén 1992). The potential avian nest predators that we monitored were Laughing Kookaburras (*Dacelo novaeguineae*), Pied Currawongs (*Strepera graculina*), Grey Butcherbirds (*Cracticus torquatus*), Australian Magpies (*Gymnorhina tibicen*), and Australian Ravens (*Corvus coronoides*). At each study site, we plotted the location of all nest predators seen or heard relative to robin nests. After the

breeding season ended, we divided the grids at each study site into 1-ha blocks and counted the number of blocks that contained at least one robin nest. Within each nesting block, we tallied the number of avian nest predators observed. Activity indices per plot were the number of nest predators observed divided by the total number of nesting blocks. If more than two sightings of the same species of nest predator occurred in a study plot on the same day, we counted only the first sighting unless the sightings were separated by at least 400 m.

We calculated the abundance and richness of birds in the study plots from censuses. After distributing artificial nests, we conducted one census in one of the four study plots per day between 0600 and 0930 over four consecutive days, weather permitting. Each study plot was censused once per month between September and November 1995 and between August and December 1996. Each census consisted of five transect lines (each 200 m long and 50 m wide) placed 200 m apart. We spent 20 min in each transect and used a mixture of the strip line and point count techniques (Recher 1988). We recorded all birds seen or heard on the transect and also stopped for approximately 1 min every 10 m along the transect to count birds. Every 50 m, or in areas with dense vegetation, we walked 10 to 15 m perpendicular to the transect line to increase the chances of observing cryptic species. Within each year, the same transects were sampled each month but a different set of transects was sampled in 1995 and 1996. Birds were categorized as nest predators, small open-cup nesters (8.5 to 20 cm in length; data from Slater et al. [1993]), or other. Only the first two categories were used in data analyses.

Nest placement.—We measured nest-placement variables after the nests were inactive. In total, we measured 205 nests built by 51 breeding pairs (109 nests by 27 pairs in the small fragments and 96 nests by 24 pairs in the large fragments) in 1995 and 1996. Measurements were taken at two spatial scales, the nest site and the nest patch. Nest-site variables included: (1) substrate height (m); (2) nest height (m); (3) nest: substrate height; (4) distance of nest from the main stem (m); (5) percent plant cover in the shrub layer (0.5 to 3 m); (6) percent plant cover in the subcanopy layer (3 to 8 m); (7) percent plant cover in the canopy layer (>8.0 m); and (8) nest concealment. Height was measured with a meter stick or calculated using a clinometer. Percent plant cover was quantified by walking 1 m from the nest and recording whether vegetation at each layer was present when looking through a 14-cm ocular tube. Eight points were taken at compass directions around the nest, so the percentage was calculated by dividing the number of hits by eight. Concealment was quantified by scoring how much of the nest was covered by vegetation when looking from a distance of 2.5 m. The scoring system was 1 = no cover; 2 = less than 50%; 3 = more

than 50% but less than 100%; and 4 = complete cover. The concealment index was an average of eight compass points taken around the nest and one score from directly below the nest. We were confident that repeatable measures of concealment were taken only for nests that were less than 4 m above the ground, so analyses were restricted to these nests.

We measured nest-patch characteristics in 0.002-ha circles centered around each nest. Variables included the number of stems and percent plant cover in the shrub, subcanopy, and canopy layers. Percent plant cover was calculated by walking around the census circle and at each step ($n = 16$) recording the number of times vegetation at each layer occurred in the ocular tube.

Statistical analyses.—We considered that a robin nest failed from predation when the entire contents were removed or when a nest was abandoned after partial predation. A successful nest fledged at least one young (fledging defined as leaving the nest). The nesting period was 29 days, including 1 day preincubation, 16 days incubation, and a 12-day median brood-rearing period (range 10 to 14 days). An artificial nest was considered depredated if at least one of the two plasticine eggs was disturbed and successful if undisturbed after 16 days. For both types of nests, daily survival rates and standard errors were calculated using the maximum-likelihood estimator of Bart and Robson (1982). We tested whether daily nest survival rates varied between groups (e.g. small vs. large fragments) using chi-square analysis (Sauer and Williams 1989).

We analyzed nest-predator activity with goodness-of-fit tests. For the census data, we calculated a single mean per transect line for each year ($n = 5$ transects per study plot per year) by averaging monthly counts on each line and used these means in our statistical models ($n = 40$). We looked for differences in the abundance of nest predators using Mann-Whitney U -tests corrected for ties. We analyzed the abundance of open-cup nesters with a mixed-model two-way nested ANOVA (McKone 1993, Krebs 1998). Fragment size and year were the fixed effects, and study plots were the random replicates. S1 and S2 were nested within the "small fragment" size category and L1 and L2 within the "large fragment" category to increase statistical power (McKone 1993). We considered 1995 to be independent of 1996 because the five transects sampled per plot differed between the two years of study (see above). Means for open-cup nesters were log transformed to approximate a normal distribution (tested with Shapiro-Wilks' statistic). All results are presented on their original scales.

We used stepwise discriminant function analysis (DFA) to compare unsuccessful and successful nests to determine whether nest placement was associated with the success of a nest. The model included all nest-placement variables except concealment be-

cause only nests below 4 m had a concealment index. Wilks' lambda and F -tests revealed the combination of variables that best discriminated the two groups of nests. To assess the effectiveness of a given DFA, we calculated Cohen's kappa statistics (Z -scores) for the classification matrix. This statistic indicates whether the model classified observations into their respective groups (unsuccessful vs. successful nests) significantly better than by chance (Titus et al. 1984). Concealment was analyzed separately with a univariate logistic regression. Each nest-placement variable was averaged for each breeding pair and transformations were applied when necessary.

We used Pearson correlation coefficients to assess the relationship between daily nest survival rates, aspects of the nest-predator assemblage, and the abundance and richness of open-cup nesters. In all cases, the sample sizes were eight because we calculated one mean for each study plot in each year. A stepwise logistic regression (F to enter = 4) identified the factors that were most strongly associated with the survival of robin nests. Variables were transformed when necessary as above, but results are presented on their original scales.

RESULTS

Nesting success.—On average, we sampled 12 territories per year in each of the small fragments and 6 per year in each of the large ones. Pairs in each territory produced an average of $3.9 \pm \text{SE of } 0.2$ nests per season, including 3.8 ± 0.2 and 4.2 ± 0.4 nests per year in the small and large fragments, respectively. In total, we located 282 active robin nests in the four study plots, and 98% were found during nest building or incubation. Nest predation was the main cause of failure for robin nests overall (95%) and in small (96%) and large (92%) forest fragments. Nests also failed owing to infertile clutches (1%), weather (1%), and unknown causes (3%).

The overall survival probability of robin nests was 19%, ranging from 15% in the large fragments to 22% in the small fragments (Table 1). Daily nest survival rates were not significantly different between the small and large fragments overall, and when each year was considered separately (χ^2 tests, $0.16 < P < 0.35$; Table 1). However, significant variation in daily nest survival occurred among the four study plots when both years were combined ($\chi^2 = 24.61$, $df = 3$, $P < 0.0001$) and in 1995 ($\chi^2 = 20.58$, $df = 3$, $P < 0.001$), but not in 1996 ($\chi^2 = 5.47$, $df = 3$, $P = 0.14$). Daily survival rates of

TABLE 1. Daily survival rate (DSR) and nesting success of Eastern Yellow Robin nests and artificial nests in two small (55 ha) and two large (>400 ha) forest fragments. Nesting success is the chance of surviving the entire nesting period, which was 29 days for robin nests and 16 days for artificial nests. Values are $\bar{x} \pm SE$.

Fragment	1995			1996			Both years		
	DSR	Success	n	DSR	Success	n	DSR	Success	n
	Real nests								
Small	0.945 ± 0.006	0.20 ± 0.07	94	0.952 ± 0.006	0.24 ± 0.08	77	0.949 ± 0.004	0.22 ± 0.08	171
Large	0.933 ± 0.100	0.14 ± 0.04	50	0.942 ± 0.009	0.18 ± 0.05	46	0.937 ± 0.007	0.15 ± 0.05	96
Total	0.941 ± 0.005	0.17 ± 0.06	144	0.949 ± 0.005	0.22 ± 0.08	123	0.945 ± 0.004	0.19 ± 0.08	267
	Artificial nests								
Small	0.882 ± 0.014	0.13 ± 0.05	85	0.876 ± 0.011	0.12 ± 0.04	145	0.878 ± 0.009	0.12 ± 0.05	230
Large	0.888 ± 0.013	0.15 ± 0.04	87	0.870 ± 0.012	0.11 ± 0.05	144	0.877 ± 0.009	0.12 ± 0.05	231
Total	0.885 ± 0.010	0.14 ± 0.05	172	0.873 ± 0.009	0.11 ± 0.04	289	0.878 ± 0.006	0.12 ± 0.05	461

TABLE 2. Activity indices of potential avian nest predators around Eastern Yellow Robin nests in two small (S1 and S2) and two large (L1 and L2) forest fragments.

Site	1995	1996	Both years
S1	3.71	2.54	3.16
S2	1.26	1.59	1.43
L1	2.73	1.92	2.37
L2	1.45	1.37	1.42
Total	2.26	1.84	2.05

robin nests in S2 ($\bar{x} = 0.966 \pm 0.005$) and L2 ($\bar{x} = 0.948 \pm 0.008$) generally were higher than those of nests in S1 ($\bar{x} = 0.927 \pm 0.008$) and L1 ($\bar{x} = 0.917 \pm 0.013$). Daily nest survival did not vary significantly between years (1995, $\bar{x} = 0.941 \pm 0.005$; 1996, $\bar{x} = 0.949 \pm 0.005$; $\chi^2 = 1.0$, $df = 1$, $P = 0.317$) or between the incubation and brood-rearing periods (incubation, $\bar{x} = 0.947 \pm 0.005$; brood rearing, $\bar{x} = 0.941 \pm 0.007$; $\chi^2 = 0.38$, $df = 1$, $P = 0.54$).

We distributed 461 artificial nests in the forest fragments, of which 84% were depredated. Survival probabilities of artificial nests were 12% in both the small and large fragments (Table 1). Not surprisingly, daily survival rates of artificial nests were similar in fragments of different size (χ^2 tests, $0.71 < P < 0.96$; Table 1). In addition, daily survival rates were comparable across the four study plots (1995, $\chi^2 = 4.94$, $df = 3$, $P = 0.16$; 1996, $\chi^2 = 0.19$, $df = 3$, $P = 0.98$; overall, $\chi^2 = 1.59$, $df = 3$, $P = 0.66$) and between years ($\chi^2 = 0.87$, $df = 1$, $P = 0.35$).

Nest predators and open-cup nesters.—The activity indices of nest predators did not vary with fragment size (1995, $\chi^2 = 0.59$, $P = 0.44$; 1996, $\chi^2 = 1.37$, $P = 0.24$; overall, $\chi^2 = 1.81$, $P = 0.18$), but predator activity was slightly higher in 1995 than in 1996 ($\chi^2 = 3.20$, $P = 0.07$; Table 2). The activity indices also differed across the four study plots, generally being higher in S1 and L1 than in S2 and L2 ($\chi^2 = 24.84$, $df = 3$, $P < 0.001$; Table 2). Of the five avian nest predators sampled, Pied Currawongs and Laughing Kookaburras were encountered the most frequently near robin nests and together accounted for 64% of all observations (Table 3).

The relative abundance of avian nest predators ranged from 0.08 to 0.56 birds per ha in small fragments and 0.12 to 0.27 per ha in large fragments, but the differences were not significant (Mann-Whitney tests, 1995, $z = 0.04$, $P = 0.97$; 1996, $z = 0.88$, $P = 0.38$; overall, $z = 0.69$,

TABLE 3. Total number of potential avian nest predators seen in the nesting area of Eastern Yellow Robins in two small (S1 and S2) and two large (L1 and L2) forest fragments.

Site	Kookaburra	Currawong	Butcherbird	Magpie	Raven
1995					
S1	8	38	13	5	9
S2	11	11	4	1	3
L1	11	18	8	0	8
L2	7	9	2	1	5
1996					
S1	10	16	7	9	5
S2	7	19	1	12	2
L1	2	11	6	0	6
L2	14	5	1	1	2
Total (%)	70 (22.8)	127 (41.2)	42 (13.6)	29 (9.4)	40 (13.0)

$P = 0.49$). We found no significant difference in the relative abundance of nest predators between years ($z = 0.16$, $P = 0.87$) or among study plots (Kruskal-Wallis test, $H = 2.88$, $P = 0.41$). In a nested ANOVA on the relative abundance of open-cup nesters, only the nested term (fragment size) was significant (Table 4). More open-cup nesting songbirds occurred in S2 ($\bar{x} = 12.6 \pm 1.7$) than in S1 ($\bar{x} = 7.7 \pm 1.1$) and in L2 (8.9 ± 1.4) than in L1 (6.9 ± 0.8 ; $n = 10$ for each plot).

Correlates of nesting success.—Thirteen vegetation measures were used in the DFA, but the models could not differentiate between successful and unsuccessful nests in 1995 or 1996. The overall model was significant (Wilks' lambda = 0.95, $F = 4.02$, $P = 0.049$), but it provided only a 4.4% improvement in classification over chance (observed probabilities = 0.61, chance probabilities = 0.57; Cohen's Kappa, $Z = 0.81$, $P > 0.10$). Nest concealment was not related to nest fate (univariate logistic regressions, $P > 0.51$ for 1995, 1996, and both years combined).

Daily survival rates of robin nests were negatively correlated with nest-predator activity ($r = -0.83$, $n = 8$, $P = 0.011$; Fig. 1A) and posi-

tively correlated with the abundance of all open-cup nesters ($r = 0.77$, $n = 8$, $P = 0.026$; Fig. 1B). Daily nest survival was not related to the abundance of nest predators ($r = -0.25$, $n = 8$, $P = 0.55$) or to any of the measures of species richness (nest predators, $r = -0.12$, $n = 8$, $P = 0.78$; open-cup nesters, $r = 0.07$, $n = 8$, $P = 0.86$). A stepwise linear regression using all relative abundance and species richness variables as predictors found that only nest-predator activity ($r^2 = 0.68$) and the abundance of open-cup nesters ($r^2 = 0.16$) contributed significantly to the daily survival of robin nests ($r^2 = 0.85$, $df = 2$ and 5 , $P = 0.009$).

Lace monitors (*Varcinus varius*) and red-bellied black snakes (*Pseudechis porphyriacus*) occurred in all study plots and may have depredated some robin nests. We calculated activity indices for lace monitors in the same manner as for avian nest predators, and the indices were significantly correlated with the survival of robin nests ($r = -0.76$, $n = 8$, $P = 0.028$). We assessed their relative importance by recalculating the stepwise linear regression using avian activity, the abundance of open-cup nesting songbirds, and lace monitor activity as predictors. Lace monitor activity contributed signifi-

TABLE 4. Summary of mixed-model ANOVA for the abundance of open-cup nesters (log transformed) observed in two replicate small (55 ha) or large (>400 ha) forest fragments, 1995 and 1996.

	df	SS	MS	F	P
Fragment size	1	0.10	0.10	2.50	0.123
Year	1	0.01	0.01	0.33	0.569
Fragment size \times year	1	0.02	0.02	0.61	0.441
Replicate (fragment size)	2	0.27	0.13	3.38	0.047
Replicate (fragment size) \times year	2	0.02	0.01	0.23	0.799
Error	32	1.26	0.04		

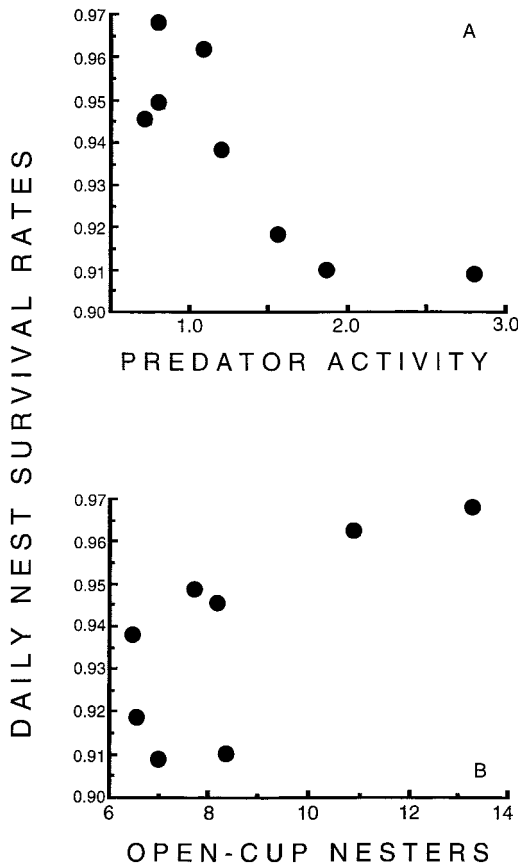


FIG. 1. Correlations between (A) avian nest-predator activity around Eastern Yellow Robin nests and daily nest survival rates, and (B) the abundance of open-cup nesters in forest fragments and daily nest survival rates.

cantly to the model ($r^2 = 0.93$, $P = 0.009$) and accounted for an additional 8% of the variation in daily survival rates. Red-bellied black snakes were encountered too infrequently to calculate activity indices.

We determined the identity of the predator for 363 depredated artificial nests. Of these, 99% were birds and 1% were mammals. Mammalian predation occurred only in the large fragments (two in L1 and one in L2). Daily survival rates of artificial nests were not associated with the abundance of nest predators ($r = -0.59$, $P = 0.12$), with the abundance of open-cup nesters ($r = -0.20$, $P = 0.63$), or with any of the measures of species richness (nest predators, $r = 0.38$, $P = 0.35$; open-cup nesters, $r = 0.22$, $P = 0.61$).

DISCUSSION

Nest predation accounted for most of the nest failures, and birds were the principal predators of both robin and artificial nests. However, the numbers, species richness, and activity levels of nest predators did not vary with fragment size, nor did daily survival rates for robin nests and artificial nests. Two other studies have used the active nests of area-sensitive songbirds to estimate nest survival in fragments of varying size. Hoover et al. (1995) detected lower success rates in small fragments in their study of Wood Thrushes (*Hylocichla mustelina*) in Pennsylvania, but Gale et al. (1997) found no effect of fragment size for Worm-eating Warblers (*Helmintheros vermivorus*) in Connecticut. Gale et al. attributed their findings to the low level of fragmentation in the landscape where they worked, which was 70% forested. A forested landscape with minimal edge habitat may contain relatively few nest predators, resulting in low rates of nest predation across all forest fragments. Only 20% of the forest is extant in the fragmented landscape where we worked, ruling out this possibility for our study.

Our results for artificial nests were consistent with those of Nour et al. (1993) and Haskell (1995), whereas other studies have found that survival of artificial nests was lower in small fragments than in large fragments (Wilcove 1985, Møller 1988, Small and Hunter 1988, Tellería and Santos 1992). Both Nour et al. and Haskell attributed their results to area-dependent changes in the types of nest predator involved. Birds were the main nest predators in small fragments, and nest predation by small mammals became increasingly important in larger fragments. Each type of predator compensated for the other in fragments of varying size, resulting in no overall effect of fragment size. This explanation does not apply in our case. We did not observe a switch in predator type on artificial nests in our fragments. Potential mammalian nest predators such as common brush-tailed possums (*Trichosurus vulpecula*) and house mice (*Mus musculus*) were present in all plots, but the dominant nest predators always were birds.

Nest predation did not vary with fragment size primarily because nest predation and nest predators did not vary consistently between fragments within the same size class. Robins

could find refuge from intense nest predation in small fragments, whereas large fragments offered no guarantee of high nesting success. Other studies of area-dependent changes in nest predation have yielded similar results (e.g. Wilcove 1985, Small and Hunter 1988, Tellería and Santos 1992). Spatial heterogeneity in predation pressure among replicates also has been reported at forest edges (Marini et al. 1995, Hanski et al. 1996) and has been found even among similar-sized plots in heavily forested areas (Reitsma et al. 1990, Leimgruber et al. 1994). Thus, spatial heterogeneity in predation pressure is common in both fragmented and contiguous landscapes.

Spatial heterogeneity among replicates indicates that detecting area-dependent changes in predator pressure may be difficult without large sample sizes. We had two replicates of each treatment, so the power of our tests was fairly low. More important, however, spatial heterogeneity in predation pressure suggests that fragment size alone generally is not sufficient to explain differences in nesting success (Small and Hunter 1988). In our study, avian nest predators were present at low densities in all plots, but their activity near robin nests explained 68% of the variation in successful nesting. Thus, only when the distribution of nest predators overlapped with the nesting area of robins did nesting success suffer. Similarly, Møller (1988) found that the nesting success of Eurasian Blackbirds (*Turdus merula*) decreased nearly 50% when they nested near a pair of breeding Black-billed Magpies (*Pica pica*), irrespective of fragment size.

Why the distribution of nest predators should overlap extensively with prey in some fragments but not others is unknown. Of the five nest predators that we sampled, all but the Australian Magpie bred in each of the four fragments. The overlap in the distribution of nest predators and robins may have been a function of habitat suitability for breeding nest predators. In this case, the habitat in S1 and L1 perhaps was more suitable for nest predators than was that in S2 and L2.

Nest predators did not prefer areas with higher densities of prey, given that S2 and L2 had lower nest-predator activity levels but higher densities of open-cup nesting songbirds. In fact, the survival of robin nests was positively correlated with the density of open-

cup nesters (also see Marini et al. 1995). Therefore, instead of suffering from density-dependent mortality as suggested by Gates and Gysel (1978), songbirds may accrue a net benefit from the presence of other nesting songbirds. This benefit may result from increased vigilance (Krebs and Davies 1986), or from the antipredator behavior of other species (Andersson and Wicklund 1978). For example, Willy Wagtails (*Rhipidura leucophrys*) are open-cup nesters that bred in all study plots, and this species, unlike robins, actively mobbed large avian nest predators. Nest survival also may have increased with increasing nesting densities through a dilution effect (Pulliam and Caraco 1984) if higher densities decreased the probability that any particular nest or the nests of a particular species would be depredated. Alternatively, if the low predation rates on robin nests in S2 and L2 applied to other open-cup nesting species, then open-cup nesters may have been attracted to these study sites, resulting in increased densities.

We found no evidence that rates of nest predation were area dependent. By contrast, in another study conducted in these same plots, Zanette et al. (2000) found that food supply for robins was consistently lower in the smaller fragments. If the causes of area sensitivity can be judged by weighing the evidence for different possibilities (Caughley and Gunn 1996), then current evidence suggests that food supply is the primary proximate mechanism for area sensitivity in Eastern Yellow Robins (Zanette 2000).

Even if differential nest predation is only weakly related to fragment size, nest predation may remain a significant problem for songbirds. The spatial scale at which fragmentation influences nest predation must be considered. Specifically, the extent of fragmentation in a region may have a greater influence on nesting success than the size of the fragments. For example, a fragmented region with more edge habitat may contain more nest predators than a contiguous area (Andrén et al. 1985). Robinson et al. (1995) found a negative relationship between nest survival of several Neotropical migrant species and the regional degree of fragmentation in the midwestern United States. The region where we worked was extremely fragmented, with 20% forest cover remaining. Robin nesting success was 23% (64/282 nests),

which was significantly lower than the 32% found by Marchant (1986) for robins in a more contiguous forested area in southeastern New South Wales ($\chi^2 = 5.7$, $df = 1$, $P = 0.017$). The levels of nest predation experienced by robin populations are negatively related to population viability (birth rate/death rate; Zanette 2000). Therefore, high rates of nest predation in fragmented landscapes should reduce regional viability and hence regional numbers. Accordingly, we suggest that patterns of nest predation, and the responses of songbird populations to nest predation, emerge only at large landscape scales.

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LITERATURE CITED

- AMBUEL, B., AND S. A. TEMPLE. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057-1068.
- ANDERSSON, M., AND C. G. WICKLUND. 1978. Clumping versus spacing out: Experiments on nest predation in Fieldfares (*Turdus pilaris*). *Animal Behaviour* 26:1207-1212.
- ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation: A landscape perspective. *Ecology* 73:794-804.
- ANDRÉN, H., AND P. ANGELSTAM. 1988. Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69:544-547.
- ANDRÉN, H., P. ANGELSTAM, E. LINDSTRÖM, AND P. WIDÉN. 1985. Differences in predation pressure in relation to habitat fragmentation: An experiment. *Oikos* 45:273-277.
- ANGELSTAM, P. 1986. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. *Oikos* 47:365-373.
- BARRETT, G. W. 1995. Woodland bird assemblages on the New England Tablelands, northeastern New South Wales. Ph.D. dissertation, University of New England, Armidale, Australia.
- BART, J., AND D. S. ROBSON. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* 63:1078-1090.
- BELLAMY, P. E., S. A. HINSLEY, AND I. NEWTON. 1996. Factors influencing bird species numbers in small woods in south-east England. *Journal of Applied Ecology* 33:249-262.
- CAUGHLEY, G., AND A. GUNN. 1996. Conservation biology in theory and practice. Blackwell Science, Sydney, Australia.
- GALE, G. A., L. A. HANNERS, AND S. R. PATTON. 1997. Nesting success of Worm-Eating Warblers in a forested landscape. *Conservation Biology* 11:246-250.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- HAGAN, J. M. III, AND D. W. JOHNSTON (Eds.). 1992. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C.
- HANSKI, I. K., T. J. FENSKE, AND G. J. NIEMI. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. *Auk* 113:578-585.
- HASKELL, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* 9:1316-1318.
- HOOVER, J. P., M. C. BRITTINGHAM, AND L. J. GOODRICH. 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.
- KREBS, C. J. 1998. Ecological methodology, 2nd ed. Benjamin/Cummings, Menlo Park, California.
- KREBS, J. R., AND N. B. DAVIES. 1986. An introduction to behavioural ecology. Sinauer Associates, Sunderland, Massachusetts.
- LEIMGRUBER, P., W. J. MCSHEA, AND J. H. RAPPOLE. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58:54-260.
- LYNCH, J. F., AND D. F. WHIGHAM. 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*. Pages 231-240 in *Birds of eucalypt forests and woodlands: Ecology*

- conservation, management (A. Keast, H. F. Recher, H. Ford, and D. Saunders, Eds.). Royal Australasian Ornithologists' Union and Surrey Beatty and Sons, Sydney, Australia.
- MARINI, M. A., S. K. ROBINSON, AND E. J. HESKE. 1995. Edge effects on nest predation in the Shawnee National Forest, southern Illinois. *Biological Conservation* 74:203–213.
- MARTIN, T. E. 1992. Breeding productivity considerations: What are the appropriate habitat features for management. Pages 455–473 in *Ecology and conservation of Neotropical migrant landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington D.C.
- MCKONE, M. J. 1993. Statistical analysis of experiments conducted at multiple sites. *Oikos* 67:184–186.
- MØLLER, A. P. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: A study of magpies and blackbirds. *Oikos* 53:215–221.
- MØLLER, A. P. 1989. Nest site selection across field-woodland ecotones: The effect of nest predation. *Oikos* 56:240–246.
- NOUR, N., E. MATTHYSEN, AND A. A. DHONDT. 1993. Artificial nest predation and habitat fragmentation: Different trends in bird and mammal predators. *Ecography* 16:111–116.
- ORTEGA, C. P., J. C. ORTEGA, C. A. RAPP, AND S. A. BACKENSTO. 1998. Validating the use of artificial nests in predation experiments. *Journal of Wildlife Management* 62:925–932.
- PATON, P. W. C. 1994. The effect of edge on avian nest success: How strong is the evidence? *Conservation Biology* 8:17–26.
- PULLIAM, H. R., AND T. CARACO. 1984. Living in groups: Is there an optimal group size? Pages 122–147 in *Behavioural ecology: An evolutionary approach* (J. R. Krebs and N. B. Davies, Eds.). Blackwell Scientific Publications, Oxford.
- RANNEY, J. W., M. C. BRUNER, AND J. B. LEVENSON. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–95 in *Forest island dynamics in man-dominated landscapes* (R. L. Burgess and D. M. Sharpe, Eds.). Springer-Verlag, New York.
- RECHER, H. F. 1988. Counting terrestrial birds: Use and application of census procedures in Australia. *Australian Zoological Reviews* 1:25–45.
- REITSMA, L. R., R. T. HOLMES, AND T. W. SHERRY. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: An artificial nest experiment. *Oikos* 57:375–380.
- ROBINSON, S. K., F. R. THOMPSON III, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- SAUER, J. R., AND B. K. WILLIAMS. 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *Journal of Wildlife Management* 53:137–142.
- SLATER, P., P. SLATER, AND R. SLATER. 1993. The Slater field guide to Australian birds. Lansdowne, Sydney, Australia.
- SMALL, M. F., AND M. L. HUNTER. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76:62–64.
- SUGDEN, L. G., AND G. W. BEYERSBERGEN. 1986. Effect of density and concealment on American Crow predation of simulated duck nests. *Journal of Wildlife Management* 50:9–14.
- TELLERÍA, J. L., AND T. SANTOS. 1992. Spatiotemporal patterns of egg predation in forest islands: An experimental approach. *Biological Conservation* 62:29–33.
- TEMPLE, S. A., AND J. R. CARY. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conservation Biology* 2:340–347.
- TITUS, K., J. A. MOSHER, AND B. K. WILLIAMS. 1984. Chance-corrected classification for use in discriminant analysis: Ecological applications. *American Midland Naturalist* 111:1–7.
- WILCOVE, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* 66:1211–1214.
- WRAY, T. II, AND R. C. WHITMORE. 1979. Effects of vegetation on nesting success of Vesper Sparrows. *Auk* 96:802–805.
- ZANETTE, L. 2000. Fragment size and the demography of an area-sensitive songbird. *Journal of Animal Ecology* 69: in press.
- ZANETTE, L., P. DOYLE, AND S. M. TRÉMONT. 2000. Food shortage in small fragments: Evidence from an area-sensitive passerine. *Ecology* 81: in press.

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