

FOOD SHORTAGE IN SMALL FRAGMENTS: EVIDENCE FROM AN AREA-SENSITIVE PASSERINE

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Abstract. Many forest-interior songbirds are considered “area sensitive” because they are absent from smaller forest remnants in fragmented landscapes. Reductions in food abundance with fragment size could explain area sensitivity, but to date, only one empirical study has investigated this possibility. From 1995 to 1997, we tested the food abundance hypothesis in two small (~55-ha) and two large (>400-ha) forest fragments located in a matrix of agricultural land in northeastern New South Wales, Australia. We measured differences in food abundance by comparing the biomass of surface-dwelling invertebrates in large and small fragments. We also determined whether food supply was associated with foraging efficiency and reproductive performance in an area-sensitive, ground-foraging insectivore, the Eastern Yellow Robin (*Eopsaltria australis*), breeding at these same sites. Invertebrate biomass in the small fragments was about half of that in the large fragments. Incubating female robins received 40% less food from males, females left their nests more frequently to forage on their own, and nestlings were provisioned with less food in the small fragments. Females in the small fragments also had a shorter breeding season (by three weeks), laid eggs that were 7% lighter, and reared smaller nestlings. Because our measures of invertebrate biomass, foraging efficiency, and reproduction produced corresponding results, we conclude that Eastern Yellow Robins experienced relative food shortage in these small fragments. Therefore, food shortage probably influences area sensitivity in this species. We suggest that the role of food supply be given greater consideration in other fragmentation studies.

Key words: agricultural landscapes; area sensitivity; autecology; conservation biology; *Eopsaltria australis*; food limitation; forest fragmentation; impaired reproduction; limiting factors; passerines; songbirds.

INTRODUCTION

Forest-interior passerines are of conservation concern because many are adversely affected by forest loss and fragmentation. For example, many forest songbirds are considered to be area sensitive because they occur less often than expected in small than in large forest fragments (e.g., Ambuel and Temple 1983, Blake and Karr 1984, Barrett 1995, Bellamy et al. 1996). Investigations into the causes of area sensitivity have focused primarily on nest predators and brood parasites (reviewed in Paton 1994), with little attention given to food abundance (but see Blake et al. 1992, Burke and Nol 1998). Many studies, however, have documented adverse effects of food shortage on annual reproductive success and population densities of songbirds (reviews in Newton 1980, Martin 1987, Boutin 1990). Given that avian demography is often observed to be food limited, then area sensitivity could be due to chronic food shortage in small fragments.

Food supply may vary with fragment size as a result

of edge effects. As a forest is fragmented, interior habitat is lost but edge habitat increases. Invertebrates, especially surface dwellers, are prone to desiccation and may not survive well in edge habitat, which is warmer and drier than the forest interior (Greenslade 1964, Matlack 1993, Didham et al. 1996). Thus, lower invertebrate biomass may be expected in smaller fragments where edge habitat encompasses an increasing proportion of the fragment (Gibbs and Faaborg 1990, Wenney et al. 1995). On the other hand, some studies have documented increases in invertebrate abundance on edges, mainly due to increases in the number of invasive edge species that have replaced the original invertebrate community (see Didham 1997). Therefore, increases in invertebrate biomass in smaller fragments based on changes in species composition could be observed.

Before food supply can be considered as a possible mechanism influencing area sensitivity, it must be shown that food supply decreases with decreasing fragment size. In a study conducted in Ontario, Canada, on the Ovenbird (*Seiurus aurocapillus*), an area-sensitive songbird, Burke and Nol (1998) found lower invertebrate biomass in smaller fragments and concluded that less food was available to these birds. Relying solely on measures of food *abundance* to answer questions

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about food *availability* has been criticized, mainly because birds are likely to perceive the environment differently than does a researcher (Hutto 1990). To determine whether abundance measures obtained by the researcher affect the study organism, it is necessary to measure aspects of behavior and/or reproduction that vary with food supply. Fortunately, a good deal is known about how food influences the foraging behavior and reproduction of passerines. For instance, food provided to incubating females by males reduces the energetic stress associated with incubation (Yom-Tov and Hilborn 1981, Walsberg 1983, Lifjeld and Slagsvold 1986, Smith et al. 1989). In instances in which incubating females do not receive sufficient food from the male, females must leave the nest to forage for food on their own (Lyon and Montgomerie 1985, Smith et al. 1989). In addition, the amount of food altricial nestlings receive from their parents varies depending on how much food is in the environment (Nisbet 1973, Crossner 1977, Davies 1986, Lorentsen 1996). Similarly, initiation of egg-laying, length of the breeding season, clutch size, egg mass, and nestling size and mass all respond positively to natural and artificial increases in food supply (reviews in Newton 1980, Martin 1987, Boutin 1990).

Our goal was to determine whether food supply varies with fragment size, in order to assess food availability as a possible mechanism influencing sensitivity to area. We compared invertebrate biomass in two small and two large forest fragments set in an agricultural landscape in northeastern New South Wales, Australia. We also compared small and large fragments for several behavioral and reproductive measures taken from a ground-foraging, insectivorous songbird, the Eastern Yellow Robin (*Eopsaltria australis*). We chose the Eastern Yellow Robin as a model species because resident species that forage on the ground are particularly prone to anthropogenic disturbances in the Australian environment (Recher and Lim 1990, Garnett 1992). Also, this is considered to be an area-sensitive species because it is found most often in large, continuous habitat patches (>400 ha) and does not occur in fragments of <20 ha (Barrett 1995). The behavioral and reproductive measures that we used are known to be influenced by food abundance (reviews in Martin 1987, Boutin 1990). Therefore, we were able to verify whether our measures of prey biomass (food abundance) reflected food availability for our study species. We expected invertebrate biomass to be lower in the small fragments, and we expected food shortage to be associated with reduced foraging efficiency and impaired reproduction among Eastern Yellow Robins.

METHODS

Study area

We studied Eastern Yellow Robins during two breeding seasons between August 1995 and January 1997 at

four study sites on the Armidale Plateau in northeastern New South Wales, Australia (30°27' S, 151°13' E). The Armidale Plateau was settled in the early 1800s, when much of the forest was converted into pasture for sheep and cattle, resulting in an extremely fragmented landscape (Barrett 1995). The Armidale Plateau sits atop the Great Dividing Range, with an elevation ranging from ~730 to 1300 m a.s.l. Because of the relatively high elevation, the region has a temperate climate. Mean annual rainfall is 750 mm (average monthly rainfall ranges between 38 and 104 mm). The coldest month of the year tends to be July, when daily mean temperatures range from 1.3° to 12.9°C, whereas daily mean temperatures in the hottest month, January, vary from 21.0° to 27.3°C (1981–1996 data from the NSW Regional Office of the Bureau of Meteorology).

The four study sites included two small fragments ~55 ha in size (termed S1 and S2) and two large fragments >400 ha (termed L1 and L2). The size of fragments in each category was chosen a priori, based on the known distribution of Eastern Yellow Robins on the Armidale Plateau (Barrett 1995; see *Study species*). The study sites were selected from among a larger pool (Barrett 1995) so as to minimize differences in vegetation and general geographical features. In both small fragments, the entire area was gridded with flagging tape at 100-m intervals. Plots of comparable size (55 ha) were gridded with flagging tape within each large fragment. In the large fragments, the plots were positioned as close to the center of the fragments as possible and >150 m from the boundary between the forest and pasture.

All four study areas consisted of remnant eucalyptus forest dominated by rough-barked tree species including New England stringybark (*Eucalyptus caliginosa*), red stringybark (*E. macrorhynca*), western New England blackbutt (*E. andrewsii*), rough-barked applebox (*Angophora floribunda*), white box (*E. albens*), and mugga ironbark (*E. sideroxylon*). Smooth-barked eucalypts including mountain orange gum (*E. prava*) and Blakely's red gum (*E. blakelyi*) were also present. The shrub layer was dominated by *Cassinia* spp., blackthorn (*Bursaria spinulosa*), and *Acacia* spp. No creeks, streams, or rivers ran through any of the study areas. We expected each area to receive comparable rainfall and temperatures, as the areas were separated from one another by no more than 11.8 km (range 1.8–11.8 km, mean 6.1 km).

Study species

Eastern Yellow Robins are 16–24 g passerines belonging to the endemic Australian flycatchers in the family Eopsaltriidae (formerly Petroicidae; Simpson and Day 1996). They are forest-interior songbirds (Howe 1984) that are considered to be sensitive to area. In an extensive survey of fragments on the Armidale Plateau (Barrett 1995), this species was not recorded in fragments <20 ha in size, but was found most often

in larger fragments (>400 ha). In addition, Eastern Yellow Robins seldom occur in fragments as small as 20–50 ha unless other forest tracts are nearby (i.e., separated by <100 m).

Eastern Yellow Robins are socially monogamous, year-round residents that generally breed between August and December. The sexes are distinguishable in the field only by differences in breeding behavior, but can be identified in the hand using morphological characteristics such as wing chord and body mass. This species has a reproductive life history similar to that of many forest-interior migrants in North America that have been of recent conservation concern (see Ehrlich et al. 1988, Anders et al. 1997). Eastern Yellow Robins lay relatively small clutches (2–3 eggs) and have a short nesting cycle that includes a 16-d incubation and 10–14 d brooding period. Adults potentially can rear up to three broods every season (Marchant 1984; L. Zanette, *personal observations*), but most produce only one brood (L. Zanette, *unpublished data*).

Females usually build their nests in tree forks and bushes from 1 m to 25 m above the ground (Marchant 1984), but most nests are <3 m from the ground (Marchant 1986). The female alone incubates the eggs and broods the nestlings. While the female is tending the nest, the male brings food to her (“incubation feeding”), but she leaves the nest occasionally to forage on her own (“incubation foraging trips”). The male also brings food to young nestlings, although the female also feeds the nestlings late in the nestling period. Only one food item is brought to the nest at a time.

On each plot, most breeding adults were captured using mist nets and were color-banded with a unique combination of four color bands and one numbered metal band. Care was taken to ensure that at least one member of the breeding pair was banded. We banded birds mainly in June and July (prior to breeding), but continued throughout the breeding season.

We monitored all pairs nesting on the study plots by searching each territory until a member of the breeding pair was located, at which time the bird was followed until it went to a nest site. The territories of breeding pairs were mapped in 1995 using three techniques. First, playbacks of the calls and songs of Eastern Yellow Robins were used. Once the female and/or male came in to the playback, the observer moved away from the bird in an attempt to draw the bird toward the edge of its territory. The territory border was assumed to be located where the bird turned around and flew back toward the center of its territory. This method is often the best and quickest way to mark out territories, but not all birds responded to the playback at all times (also see Krebs 1971). Second, an observer would follow a bird and attempt to “push” the bird as far as possible toward a territory border. Again, the point at which the bird turned around and flew toward the center of its territory was assumed to be the border. Third, the locations of border disputes were recorded. Border dis-

putes occurred frequently, and we continued to record them throughout the breeding season.

Invertebrates

Eastern Yellow Robins use a “sit and wait” foraging tactic to capture their invertebrate prey on the ground by pouncing from above (Marchant 1986; L. Zanette, *personal observations*). Consequently, we sampled the invertebrate fauna using pitfall traps, a technique extensively used to assess the relative abundance of cursorial, surface-dwelling invertebrates (Southwood 1992). Invertebrates were sampled three times between 6 October and 24 November 1996.

Six 0.04-ha sampling areas on six territories (one sampling area per territory) were chosen randomly in each grid. Within each sampling area, 10 pitfall trap sites were created using a cylindrical auger. PVC sleeves (10 cm long, 5 cm in diameter) were then placed within each trap site so that the lip of the sleeve was at the surface of the soil. The sleeves were left for 2.5 wk before collection began. The trap sites were evenly spaced along two 22-m transect lines running perpendicularly north–south and east–west. For collection, plastic cups (7.5 cm long and 5 cm in diameter), two-thirds filled with 70% alcohol, were placed within each PVC sleeve and were left for 1 wk, at which time the cups were removed and their contents were placed in plastic vials for sorting. The trap sites containing the PVC sleeves were then left for 2 wk before the next bout of collecting. As this procedure was labour intensive, for each trial, pitfall traps were distributed and later collected at two study sites (one large and one small fragment) on one day, and at the remaining two sites on the subsequent day. We varied the order of distribution at the study sites for each trial.

Macroinvertebrates (≥ 3 mm long) were sorted to order, and length \times width measurements were taken by S. Trémont. We calculated biomass in two ways: (1) volume was calculated using the formula, length \times (width)² \times $\pi/4$; and (2) invertebrates were dried in a 40°C oven for 48 h and were weighed on an electronic balance to the nearest 0.001 g.

We conducted nest watches from August to December 1995, between the hours of 0800 and 1700. In the incubation period, incubation feeding and incubation foraging trips were recorded. In the brooding period, nestling provisioning was recorded. We also attempted to collect data shortly after fledging, but this proved too difficult.

The observer waited 25–45 m from the nest tree for 3 min before beginning a 45-min nest watch. All observations were recorded on a voice-activated cassette recorder for later transcription. The number of watches per nest varied from one to three, but a nest was never watched more than once on the same day. To control for seasonal changes in behavior, we ensured that the number of nest watches each month varied similarly in each study plot. Chi-square tests showed that our at-

tempt to balance the observations was successful (incubation, $\chi^2 = 17.45$, $df = 12$, $P > 0.10$; brooding, $\chi^2 = 2.40$, $df = 3$, $P > 0.40$). All behavioral observations were carried out by P. Doyle.

Incubation feeding and incubation foraging trips.—We recorded the number of food items brought to the incubating female during each nest watch. We did not determine the size of prey items brought to females, because females often left the nest and went to a nearby perch to receive food. Although females were visible on these occasions, the size of food in their bills was too difficult to assess. We also recorded the number of times an incubating female left the nest to forage for herself. Again, these females stayed in view of the observer, so foraging behavior could be confirmed. We calculated the probability that females would leave the nest to take an incubation foraging trip. We divided the number of nest watches when at least one foraging trip was observed by the total number of nest watches conducted. We also calculated the rate of incubation foraging trips by dividing the total number of times females left the nest to forage by the number of nest watches conducted.

In instances when a female was off the nest and out of view, even briefly, more than once during a nest watch, we cancelled the session. Similarly, we abandoned a session if the female was off the nest and out of view for more than four consecutive minutes. Only complete sessions were used in the data analyses.

Nestling provisioning.—We recorded the number of food items brought to nestlings during each nest watch. In addition to the quantity of food items brought to nestlings, the size of each prey item was classified as small (smaller than the bill length of the adult) or large (as large as or larger than the bill). We could not follow the movements of the female while watching the nest to record feeding events to nestlings. Consequently, no data on the provisioning of food to females during the brooding period were recorded.

Reproduction

Initiation date, length of the breeding season, and nesting intervals.—We located nests over two breeding seasons between August 1995 and January 1997. In each year, the first egg laid by each female was assigned a Julian date using 20 July as day 1. We found a significant effect of year on initiation date, with birds initiating breeding 17 d earlier in 1996 than in 1995 (medians were 23 August 1995, $n = 28$, vs. 6 August 1996, $n = 23$; Mann-Whitney U test, $z = 4.99$, $P = 0.0001$). Therefore, to compare initiation date between small vs. large fragments, we corrected for this effect by reassigning the Julian dates based on the initiation dates observed in each year (i.e., 3 August was assigned as day 1 in 1995 and 20 July as day 1 in 1996).

In multibrooded species such as the Eastern Yellow Robin, birds should begin breeding as early as possible and breed for as long as possible (Arcese and Smith

1988, Crick et al. 1993). Therefore, we estimated the total number of nesting days for each female by summing the number of days from the first egg in the first clutch to the first egg in the last clutch. Females that disappeared during the breeding season were not included. No differences between year were detected (Mann-Whitney U test, $z = 1.24$, $P = 0.216$), so data for 1995 and 1996 were combined for analyses.

We calculated the interval between successful and unsuccessful nesting attempts by summing the number of days between fledging date, or failure date, respectively, and the date of egg-laying for the subsequent nest. The median interval between successful nests was 19.5 d in 1995 and 33 d in 1996, a significant difference (Mann-Whitney U test, $z = 2.39$, $P = 0.017$). Thus, each year was considered separately in our analyses. We did not detect a year effect for the interval between unsuccessful nests ($z = 0.50$, $P = 0.617$), so these data were combined.

Clutch size.—Only complete clutches were included in our analyses. A two-egg clutch was considered complete when no new eggs were added for 27 h (Marchant 1984). Clutches of three were recorded as a full clutch whenever they were encountered. There were no differences in clutch size (two- vs. three-egg clutches) between 1995 and 1996 ($\chi^2 = 0.11$, $df = 1$, $P = 0.743$), so data from both years were combined for comparison of small and large fragments.

Egg and nestling measures.—All eggs and nestlings were measured ≥ 5 m from the nest and were handled while wearing surgical gloves. Eggs were weighed to the nearest 0.05 g using a Pesola spring balance. For eggs of known age weighed > 1 d into incubation, we estimated the initial mass, given that the eggs of Eastern Yellow Robins lose 1.23% of their initial mass per day (L. Zanette, unpublished data). The age of eggs at weighing was known either from the laying date or from back-dating from the hatching date.

We measured nestling head–bill length (from the external occipital protuberance to the tip of the bill) to the nearest 0.1 mm using vernier calipers. Nestling body mass was measured to the nearest 0.1 g using an electronic balance. We measured most nestlings three times during the brooding period, once after hatching (0–3 d), then again in the middle (4–6 d), and at the end (7–12 d) of the brooding period. Nestlings were not measured after day 12 to avoid inducing premature fledging. The first time a nestling was measured, we marked one or both of its legs with a unique combination of colors using a nontoxic, odor-free marker to allow for individual recognition.

Statistical analyses

Transformations were applied to data that were not normally distributed. Log transformations were applied to the invertebrate biomass data, and data on incubation feeding and nestling provisioning were square-root transformed. All results are presented in their original

TABLE 1. Summary results of mixed-model nested ANOVA for log-transformed invertebrate volume (cubic millimeters) and dry mass (g) in two replicate forest fragments, each small (55 ha) or large (>400 ha) in size (see Fig. 1). The study area was in northeastern New South Wales, Australia.

Factor	df	SS	MS	F	P
Volume					
Fragment size	1	0.50	0.50	8.90	0.007
Replicate (nested subgroup)	2	0.21	0.10	1.83	0.186
Error	27	1.12	0.06		
Dry mass					
Fragment size	1	0.27	0.27	12.11	0.002
Replicate (nested subgroup)	2	0.01	0.00	0.20	0.824
Error	27	0.45	0.02		

scale. Nonparametric statistics (corrected for ties when necessary) were used where the data were not normally distributed and could not be normalized with a transformation.

We used mixed-model nested ANOVAs to analyze data on invertebrate biomass, incubation feeding, nestling provisioning, and egg mass. Treatment and year were the fixed effects and study sites were the random replicates. The study sites S1 and S2 were nested within the Small-fragment treatment, whereas the study sites L1 and L2 were nested within the Large-fragment treatment.

To compare the small and large fragments for invertebrate biomass, we calculated a single mean per sampling area (total $n = 24$) by first calculating a mean per sampling area for each trial (biomass per number of pitfall traps) and then averaging over trials. When comparing small vs. large fragments for the behavior and reproduction variables, we used data calculated on a per female basis. Therefore, when there was more than one observation per nest (e.g., more than one nest watch or egg per nest), we obtained a single value per female by: (1) pooling the observations and calculating a mean, resulting in one datum point for each nest; and then (2) averaging over nests for each female. Where there was only one observation per nest, we applied only step 2. When we examined the data for effects of time, we plotted the time variable (e.g., month, age of eggs, etc.) against the data obtained for each nest and presented correlation coefficients as descriptive statistics.

We analyzed data for incubation foraging trips using frequency tests. The observed data were tested against the expectation that incubation foraging trips would occur in proportion to the number of nest watches conducted.

We assessed nestling size by fitting a common logistic growth curve to all of the head-bill measures using nonlinear parameter estimation (SYSTAT 1992). From the population curve, we calculated average residuals for each individual and then averaged over nest mates to obtain a mean residual for each nest (following Ricklefs 1983). The residuals were analyzed in a two-way ANOVA in which the main effects were treatment

and year. Mean residuals from the S2 and L1 study plots were used because we had sufficient data only from these two sites over the 2-yr study. Mean residuals from two-nestling broods were analyzed because there were not enough three-nestling broods. We also fitted a logistic growth curve to nestling body mass data using data from days 0–10 only. Body mass recession (i.e., decrease in mass shortly before fledging) occurs in this species and can be observed as early as day 11 (L. Zanette, *unpublished data*). Again, from the population curve, residuals were averaged for each nest and mean residuals from two-nestling broods measured in S2 and L1 were analyzed in a two-way ANOVA.

RESULTS

Invertebrates

We sorted 7743 invertebrates from 712 pitfall traps. Total abundance was represented mainly by nine orders, including Coleoptera (33.3%), Araneae (18.7%), Hymenoptera (15.3%), Diptera (9.8%), Hemiptera (9.4%), Blattodea (3.6%), Acarina (2.7%), Coleoptera larvae (2.3%), and Orthoptera (2.1%).

In addition to invertebrates, we also captured a few small vertebrates, including skinks and frogs. Eastern Yellow Robins prey upon skinks, but they do not appear to eat frogs (Marchant 1986, Barker and Vestjens 1990; L. Zanette, *personal observations*), so frogs were removed from the biomass analyses. Volume was significantly lower in the small than in the large fragments, whereas no significant differences were detected between the replicates (Table 1, Fig. 1a). Our second biomass measure, dry mass, showed similar results. Dry mass varied between fragments of different sizes but not between fragments within the same size class (Table 1, Fig. 1b). Volume and dry mass were 2.0 times and 1.6 times greater, respectively in the large fragments.

The small fragments were not missing any of the nine main orders of invertebrates, and the proportion of each of these orders varied in a similar way in the small and large fragments (Fig. 2a). Therefore, the biomass differences did not result from differences in the composition of the invertebrate fauna between frag-

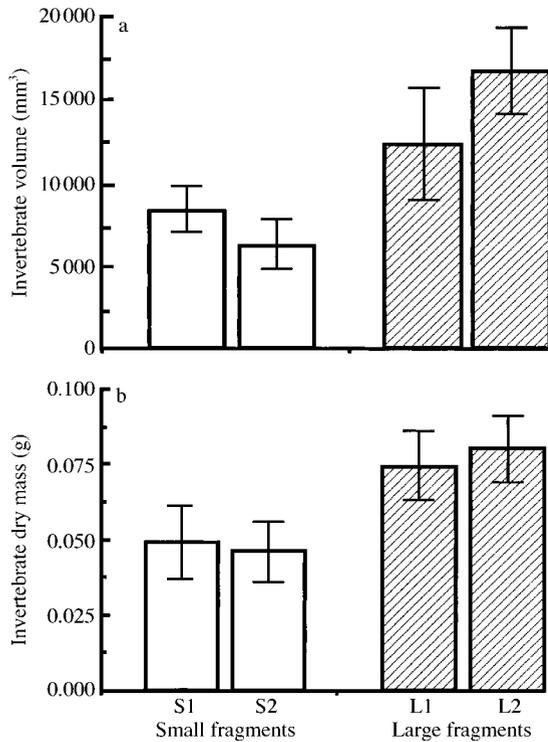


FIG. 1. Mean (\pm 1 SE) volume and dry mass of invertebrates in the small (S1, S2) and large (L1, L2) forest fragments, collected from 712 pitfall traps on 24 Eastern Yellow Robin territories (six per study site) over three trials. Each bar represents a sample size of six replicates.

ments, but from changes in the abundance and size of invertebrates (Fig. 2b). Total volumes in the small and large fragments were similar for the smallest (3–10 mm long) and largest (>30 mm) invertebrates (Fig. 2b). However, total volumes for invertebrates 11–29 mm long were higher in the large than in the small fragments (Fig. 2b).

Behavior

Incubation feeding and incubation foraging trips.— In 1995, we monitored 26 and 12 pairs of Eastern Yellow Robins in the small and large fragments, respectively. In 1996, we monitored 21 pairs in the small fragments and 13 pairs in the large ones. We carried out 245 nest watches at 93 nests in 1995. Rates of incubation feeding varied significantly with fragment size, with little variation between the replicates (one-way nested ANOVA, treatment $F_{1,27} = 7.2, P = 0.012$; nested $F_{2,27} = 2.53, P = 0.098$). Incubating females in the small fragments received 40% fewer incubation feeding visits (0.051 ± 0.006 visits/min, mean \pm 1 SE; $n = 20$) than did those in the large fragments (0.071 ± 0.006 visits/min; $n = 11$).

Incubation foraging trips also varied with fragment size (Table 2). In the small fragments, females were two times more likely to take at least one incubation

foraging trip during a nest watch than were females in the large fragments ($\chi^2 = 7.56, df = 1, P = 0.006$). Females in the small fragments also left the nest to engage in incubation foraging significantly more often than did females in the large fragments ($\chi^2 = 16.69, df = 1, P < 0.0001$; Table 2). Variation between the replicates was not significant for the first measure (nest watches with incubation foraging: S1 vs. S2, $\chi^2 = 0.01, df = 1, P = 0.928$; L1 vs. L2, $\chi^2 = 1.51, df = 1, P = 0.219$), and no differences between the small fragments were detected for the second measure (number of trips per nest watch: $\chi^2 = 0.00, P = 0.986$; Table

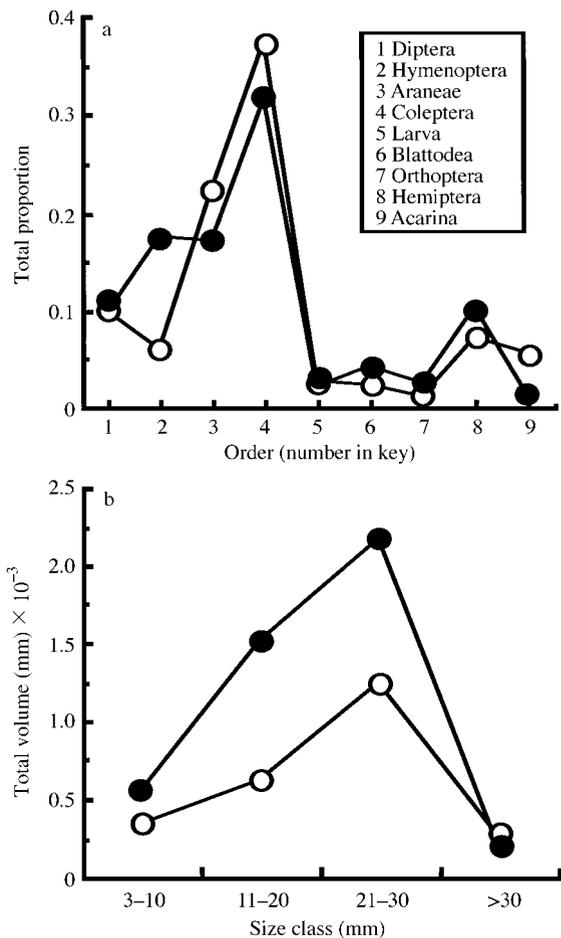


FIG. 2. (a) Assemblage of the nine main invertebrate orders in the small fragments (S1 and S2, open circles) and large fragments (L1 and L2). To calculate total proportions, we summed the number of invertebrates captured in each order across the two replicates and divided by total abundance. This measure was corrected for the number of pitfall traps used in the fragments ($n=354$ and 358 traps for the small and large fragments, respectively). (b) Total volumes of invertebrates captured in the two small (open circles) and two large (solid circles) fragments are presented by different invertebrate size classes. Total volumes were calculated by summing the volume in each invertebrate size class (corrected for the number of pitfall traps collected) across the two replicates.

TABLE 2. Incubation foraging trips by the Eastern Yellow Robin in the small (S1, S2) and large (L1, L2) forest fragments.

Site or fragment size	No. nest watches	Nest watches with incubation foraging		No. incubation foraging trips	
		Counts†	Proportion‡	Counts§	Trips/nest watch
Site					
S1	44	18	0.409	36	0.818
S2	36	16	0.444	28	0.777
L1	37	5	0.135	6	0.162
L2	40	11	0.275	18	0.450
Fragment size					
Small	80	34	0.425	64	0.800
Large	77	16	0.207	24	0.312

† The number of nest watches with at least one incubation foraging trip.

‡ This measure (counts/number of nest watches) gives the likelihood that a female would leave the nest during the watch.

§ The total number of times females left the nest to forage.

|| The rate at which females left the nest to forage (counts/number of nest watches).

2). However, females in L2 took more foraging trips per nest watch than did females in L1 ($\chi^2 = 5.1$, $df = 1$, $P = 0.024$; Table 2).

We found a general decline in incubation feeding in both small ($r = -0.35$, $n = 36$) and large ($r = -0.32$, $n = 37$) fragments as the season progressed, but incubation feeding was not related to the age of the eggs ($r = 0.126$, $n = 143$), to the time of day at which nest watches were performed ($r = 0.077$, $n = 112$), or to clutch size (logistic regression, $\chi^2 = 1.83$, $df = 1$, $P = 0.176$). We detected seasonal changes in foraging trips in both the small ($\chi^2 = 9.61$, $df = 4$, $P = 0.048$) and large ($\chi^2 = 12.98$, $df = 4$, $P = 0.011$) fragments. Foraging trips were more frequent early (August to September) than late (October to December) in the season (contingency table analysis: small fragments, $\chi^2 = 6.08$, $df = 1$, $P = 0.014$; large fragments, $\chi^2 = 4.65$, $df = 1$, $P = 0.031$).

Nestling provisioning.—The number of food items brought to each nestling did not vary with fragment size and was consistent across the replicates (one-way nested ANOVA, treatment $F_{1,20} = 0.98$, $P = 0.333$; nested $F_{2,20} = 2.09$, $P = 0.149$; Table 3). The sizes of food items, however, did differ between the small and large fragments (Table 3). Nestlings in the small fragments received large prey items at a lower rate (one-way nested ANOVA, $F_{1,13} = 11.60$, $P = 0.005$), and

they received a smaller proportion of large prey items (large prey/total prey) (Mann-Whitney U test, $z = 2.47$, $P = 0.013$) than did nestlings in the large fragments. In neither case were differences across replicates significant (large prey, nested term, $F_{2,13} = 0.28$, $P = 0.761$; proportion of large prey, S1 vs. S2, $z = 0.99$, $P = 0.322$; L1 vs. L2, $z = 1.06$, $P = 0.289$).

All of these measures were correlated with nestling age in the large, but not in the small, fragments (Figs. 3a–c: (a) number of prey per nestling, large and small fragments, $r = 0.516$, $n = 28$ and $r = 0.112$, $n = 48$; (b) number of large prey per nestling, $r = 0.647$, $n = 22$ and $r = 0.342$, $n = 24$; (c) proportion of large prey, Spearman rank correlation coefficient, $z = 2.22$, $n = 22$, $P = 0.026$ and $z = 1.67$, $n = 26$, $P = 0.094$). As nestlings in the large fragments aged, they received food at an increasing rate (Fig. 3a), received an increasing number of large prey (Fig. 3b), and were provisioned with an increasing proportion of large prey items (Fig. 3c). The number of nest watches conducted in the small and large fragments between days 0–4 vs. days 5–10 was similar ($\chi^2 = 0.52$, $df = 1$, $P = 0.473$). Also, feeding rates of nestlings in the different-sized fragments did not change over the breeding season (large fragments, $r = -0.011$, $n = 28$; small fragments, $r = -0.012$, $n = 48$), and they were not correlated

TABLE 3. Mean nestling provisioning in the small (S1, S2) and large (L1, L2) forest fragments.

Site or fragment size	No. feedings·(nestling) ⁻¹ ·min ⁻¹		No. large prey·(nestling) ⁻¹ ·min ⁻¹		Proportion of large prey	
	Mean ± 1 SE	<i>n</i>	Mean ± 1 SE	<i>n</i>	Mean ± 1 SE	<i>n</i>
Site						
S1	0.072 ± 0.012	6	0.007 ± 0.007	3	0.062 ± 0.062	4
S2	0.049 ± 0.005	10	0.003 ± 0.001	7	0.083 ± 0.035	7
L1	0.066 ± 0.006	4	0.012 ± 0.001	3	0.199 ± 0.024	3
L2	0.069 ± 0.006	4	0.019 ± 0.004	4	0.252 ± 0.030	4
Fragment size						
Small	0.058 ± 0.006	16	0.004 ± 0.002	10	0.076 ± 0.030	10
Large	0.067 ± 0.004	8	0.016 ± 0.002	7	0.229 ± 0.021	7

Notes: Means and standard errors were calculated based on the number of individual females sampled through the 1995 breeding season. Sample sizes are denoted by *n*.

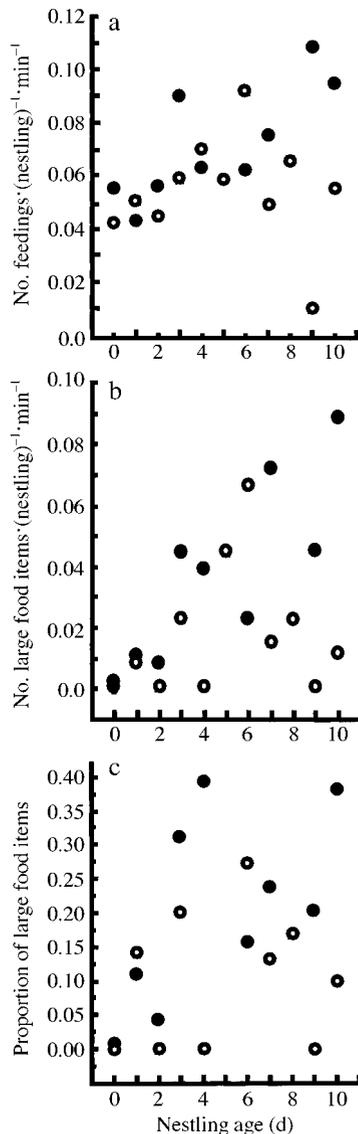


FIG. 3. Three aspects of nestling provisioning in relation to nestling age in small fragments (open circles) and large fragments (solid circles): (a) mean number of food items received by nestlings; (b) mean number of large prey items received by nestlings; (c) proportion of food items that were large in size ([number of large prey]/[total prey]).

with time of day (large fragments, $r = 0.159$, $n = 28$; small fragments, $r = -0.194$, $n = 48$).

Reproduction

Initiation date, length of the breeding season, and nesting intervals.—We located 282 nests over two breeding seasons, including 151 nests in 1995 and 131 in 1996. Of these nests, 23% produced at least one fledgling; the principal cause of total nest failure was predation at all sites in both years (Zanette and Jenkins 2000).

Over both years, the median date of initial egg-laying

was 18 August, and females spent 111.3 d breeding. No effect of fragment size on initiation date was detected (Mann-Whitney U test, $z = 1.04$, $P = 0.298$), but the replicates tended to vary. The median breeding date was 4 d earlier in S1 than in S2 ($z = 1.95$, $P = 0.052$), whereas females in L2 began breeding 5.5 d earlier than those in L1 ($z = 1.76$, $P = 0.078$). Although females in the small and large fragments began breeding at about the same time, the total length of the breeding season differed ($z = 2.32$, $P = 0.020$). Females in the large fragments bred for 128 d (median), whereas their counterparts in small fragments bred for 107 d, a 3-wk difference. No differences between the replicates were detected for this measure (S1 vs. S2, $z = 0.45$, $P = 0.651$; L1 vs. L2, $z = 0.05$, $P = 0.958$). We found no significant differences between small and large fragments for the interval between either successful or unsuccessful nests, and we detected no differences between the replicates for either measure (Mann-Whitney U tests, $P > 0.05$ for all comparisons).

Clutch size.—Overall, the number of two-egg vs. three-egg clutches produced did not vary with fragment size ($\chi^2 = 0.003$, $df = 1$, $P = 0.959$). We found seasonal variation in clutch size, as is commonly seen in multibrooded species (e.g., Ludvig et al. 1995). Females in both the small and large fragments tended to lay their three-egg clutches in the middle of the breeding season. Consequently, we pooled the data for August and December and for September to November and compared the number of two- and three-egg clutches produced in the different-sized fragments, while controlling for the season effect using the Mantel-Haenszel chi-square statistic (SYSTAT 1992). Again, clutch size did not vary significantly with fragment size ($\chi^2 = 0.262$, $P = 0.608$). Clutch sizes were also similar between S1 and S2 ($\chi^2 = 0.78$, $df = 1$, $P = 0.376$) and between L1 and L2 ($\chi^2 = 0.10$, $df = 1$, $P = 0.755$).

Egg mass.—A three-way nested ANOVA showed a significant effect of fragment size ($F_{1,50} = 9.21$, $P = 0.004$), a nonsignificant decreasing trend in egg mass with increasing clutch size ($F_{1,50} = 3.32$, $P = 0.07$; two-egg vs. three-egg clutches, 2.88 ± 0.04 g, $n = 41$, vs. 2.78 ± 0.06 g, mean ± 1 SE; $n = 23$), with no effect of year, no nested effect, and no interactions ($P > 0.05$). Eggs in the large fragments (2.96 ± 0.05 g, $n = 27$) averaged 7% heavier than those in the small fragments (2.76 ± 0.04 g, $n = 37$). Egg mass did not vary over the breeding season in either fragment (large fragments, $r = 0.175$, $n = 41$; small fragments, $r = 0.105$, $n = 50$).

Nestling body size and body mass.—The logistic growth curve provided a good fit to both the head-bill data ($r^2 = 0.997$, $df = 3$, $n = 201$) and the nestling body mass data ($r^2 = 0.984$, $df = 3$, $n = 186$). Head-bill length varied with fragment size (two-way ANOVA, $F_{1,20} = 4.86$, $P = 0.039$), and year ($F_{1,20} = 8.20$, $P = 0.01$), with no interaction ($F_{1,20} = 0.01$, $P = 0.939$). Head-bill lengths were greater in the large than in the

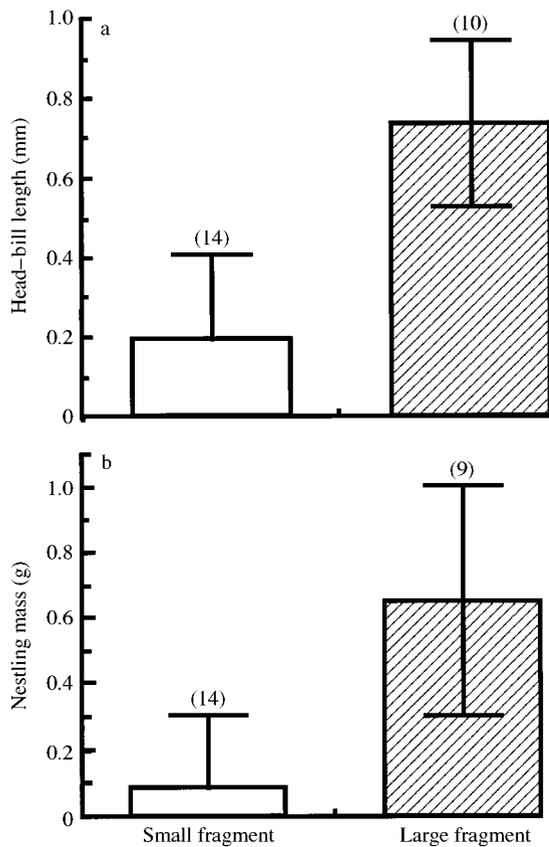


FIG. 4. Mean residual (± 1 SE) for (a) head-bill length and (b) mass of nestlings in one small (S2, open bars) and one large (L2, hatched bars) fragment. Values in parentheses indicate sample sizes.

small fragments (Fig. 4a), and they were larger in 1995 (0.761 ± 0.185 , mean residual ± 1 SE; $n = 13$) than in 1996 (0.019 ± 0.221 , $n = 11$). In addition to being structurally larger, nestlings in the large fragments were also heavier (Fig. 4b), although the difference in body mass was not significant (two-way ANOVA, $F_{1,19} = 3.38$, $P = 0.082$). Nestlings were significantly heavier in 1995 (0.622 ± 0.265 , mean residuals ± 1 SE; $n = 12$) than in 1996 (-0.022 ± 0.256 , $n = 11$; $F_{1,19} = 3.78$, $P = 0.032$), with no treatment-by-year interaction ($F_{1,19} = 1.01$, $P = 0.246$).

DISCUSSION

Our results demonstrate that our model area-sensitive songbird, the Eastern Yellow Robin, experienced relative food shortage in the breeding season in small vs. large fragments. Prey biomass was significantly lower in small fragments. Incubating females were provided with food less frequently and foraged on their own more frequently in the small fragments, suggesting that they were more food stressed. Females in the small fragments laid lighter eggs and had a shorter breeding season. Food shortage in the brooding period also was

evident. Although nestlings were fed equally often, nestlings in the small fragments received fewer large prey items. Nestlings in the small fragments had smaller head-bill lengths and also tended to have lower body mass.

We found differences between large and small fragments in the mass of eggs produced, but not in the number of eggs produced. Clutch size can be food limited to some extent, but Boutin (1990) reported increases in clutch size after food addition in only four of 13 avian studies reviewed. Also, the range of clutch sizes for Eastern Yellow Robins is small because females lay only two or three eggs per nest. They rarely lay very small clutches of one egg, even in drought years, which presumably have low food abundance (see Blake et al. 1992). Therefore, changes in clutch size with food supply may be difficult to detect.

Weather conditions varied considerably between 1995 and 1996. Rainfall was 819 mm in 1995, but 1080 mm in 1996, well above the average for the area (1981–1996 data, 750 ± 163 mm, mean ± 1 SD). Rainfall of this magnitude occurs infrequently in our study region and last occurred in 1983, when 1029 mm of rain fell. Despite this difference in the macroclimate, we detected no significant fragment size by year interactions in our analyses. Therefore, relative differences in Eastern Yellow Robin reproduction between the small and large fragments were similar over the 2-yr study, suggesting that food supply was chronically low in the small fragments.

Differences in the microclimate of fragments due to edge effects could explain variation in food abundance with fragment size. Evapotranspiration is greater in edge than in interior habitat, resulting in desiccated soil and litter (Ranney et al. 1981, Matlack 1993). Small fragments exhibit the characteristics of edge habitat (Ranney et al. 1981). Therefore, surface-dwelling invertebrates that are prone to desiccation may be excluded from small fragments (Greenslade 1964), resulting in changes in composition or abundance. We found no evidence that the composition of invertebrate assemblages in small and large fragments differed, but we did find lower invertebrate biomass in the small fragments. Burke and Nol (1998) also found lower invertebrate biomass in the leaf litter of smaller fragments in Canada. In a study looking at beetle and ant abundance in forest fragments in Brazil, however, Didham (1997) found a trend of decreasing beetle abundance with increasing fragment size, although no differences in ant abundance were detected (biomass was not assessed).

Most area-sensitive passerines are insectivorous in the breeding season (Hagan and Johnston 1992) and, therefore, could be adversely influenced by edge effects on food supply. On the other hand, edge effects may promote food for bird species in other guilds. The density and diversity of plant species tend to be higher on the edge (Ranney et al. 1981, Lovejoy et al. 1986), and

edge vegetation is often structurally complex (Thompson and Willson 1978) and productive (Ranney et al. 1981). Thus, the amount of nectar, seed, and/or berries produced on the edge could be higher than in the interior (e.g., Strelke and Dickson 1980, Green 1984). Consequently, nectivores, granivores, and frugivores may be less likely to experience food shortage in small fragments. In Brazil, Stouffer and Bierregaard (1995) documented the abundance of different hummingbird species before forested habitat was fragmented, and continued their monitoring for nine years post-isolation. No hummingbird species disappeared from the fragments after isolation and, depending on the species involved, their abundance was either unaffected or increased twofold. These results were in sharp contrast to those for insectivores, which showed a 60% decline in abundance post-isolation and frugivores who showed a 40% decline.

Although microclimate may explain low invertebrate biomass in small fragments (Gibbs and Faaborg 1990, Burke and Nol 1998), this hypothesis is untested and plausible alternatives exist. In our study, for example, about two times as many Eastern Yellow Robin pairs nested on the grids in the small fragments, so Eastern Yellow Robins there may have been depleting their own food resources. Similarly, an increase in the richness or abundance of other species in the ground-foraging insectivore guild in small fragments could result in lower invertebrate biomass. At our sites, we had 5–8 different ground-foraging species, with no obvious differences in species composition or richness. However, if abundances of these birds were to increase in small fragments, as occurred with Eastern Yellow Robins, then invertebrate biomass could be reduced.

Higher breeding densities of Eastern Yellow Robins could increase agonistic interactions between conspecific neighbors, which could reduce the amount of time males have to forage. This hypothesis may explain our results concerning behavior and reproduction, but it cannot explain why invertebrate biomass was reduced in the small fragments. Increased vegetation density in the herb and/or shrub layer, as is seen on forest edges (e.g., Ranney et al. 1981), could also reduce foraging efficiency in smaller, more edge-dominated fragments. Eastern Yellow Robins forage by perching on some substrate above the ground, such as tree trunks and stumps. They watch the ground and wait until they detect a prey item before pouncing. Thus, increased vegetation density near the ground could interfere with prey detection.

Our results showing higher numbers of Eastern Yellow Robins in small fragments are consistent with those of Gates and Gysel (1978), who found more forest songbirds nesting in forest edges than in the interior. Also, Hoover et al. (1995) found higher densities of Wood Thrush (*Hylocichla mustelina*) nests in small than in large fragments. Other studies have reported similar results (e.g., Howe 1984), but the reverse pat-

tern has also been observed (e.g., Burke and Nol 1998). It is not surprising to find conflicting results for songbird densities in the fragmentation literature. Density is a difficult variable to measure and different researchers tend to use different techniques; hence, studies usually are not directly comparable. However, high densities of birds have been associated with decreased seasonal fecundity, ultimately resulting from food shortage (e.g., Arcese and Smith 1988). Therefore, the role of avian population density in influencing food abundance in fragments of varying size could be important, but requires closer attention.

The reasons for higher densities of Eastern Yellow Robins in small fragments are unclear. Our small fragments contained more birds but less food. Higher densities in poor-quality habitat have been reported in other studies (e.g., Van Horne 1983). However, it is also possible that Eastern Yellow Robin densities were affected by factors other than resource abundance. For instance, Stamps et al. (1987) suggested that insular patches of habitat with "hard edges" (e.g., surrounded by inhospitable habitat) may discourage local emigration. Increases in breeding numbers may result as local offspring compete for territories (see Knapton and Krebs 1974, Stamps 1990). This scenario may apply in our case. Our small fragments were surrounded by pasture, but the grids in the large fragments were surrounded by forest. Thus, birds may have perceived the small fragments as having hard edges.

We found that nestlings received less food in the small fragments, which may explain why these nestlings had smaller head–bill lengths and tended to have lower body mass. We also found that the pattern of food provisioning through the nestling stage varied with fragment size. Adults in large fragments fed their nestlings at an increasing rate and fed them an increasing proportion of large food items as the nestlings aged. Birds in small fragments, on the other hand, did not vary either the rate or the size of food items that they provided. Birds in small fragments probably did not bring more food to older nestlings because there was less food in the environment (Nisbet 1977, Quinney et al. 1986). In Common Terns (*Sterna hirundo*), however, males that provided the most food to nestlings were the ones that switched most successfully from low- to high-quality food items (Nisbet 1973), suggesting that parental quality may also be important. In birds, parental quality is often related to the age or experience of the individual or breeding pair (Perrins 1970). Age and experience influence reproductive parameters (Furness 1983, Desrochers and Magrath 1993) at least partly because younger parent birds acquire less food (Källander 1974, Desrochers 1992). Therefore, although food shortage in small fragments may ultimately result from low invertebrate biomass (Quinney et al. 1986), the problems of food shortage may be compounded if younger or less experienced birds are more often found in smaller fragments.

The age or experience of breeding songbirds may vary with fragment size as a result of habitat selection. Older or more experienced birds may establish their territories in large fragments with better food resources (Burke and Nol 1998), thereby relegating younger birds to suboptimal habitat (Krebs 1971). We compared the number of first-time breeders observed in the small and large fragments in 1996. First-time breeders were defined as unbanded birds or banded natal recruits (L. Zanette, *unpublished manuscript*). There were 26.5% ($n = 34$) first-time breeders in the small fragments we studied, compared with 17.4% ($n = 23$) in the large fragments (L. Zanette, *unpublished data*). Therefore, age or experience had only a small effect on Eastern Yellow Robins in 1996. Also, other data on Eastern Yellow Robins at the same study sites showed that the survival of breeding females did not vary with fragment size (Zanette 2000). Therefore, new or younger birds were probably entering the different populations at similar rates.

Reductions in prey in small fragments were associated with poor foraging performance and impaired reproduction throughout the breeding cycle in this study. However, food supply could also influence other aspects of reproduction, including nest survival and brood parasitism. Hoover et al. (1995) found that higher nest predation in small fragments was associated with an increased abundance of nest predators. We suggest that low food supply in small fragments could interact with nest predators to increase predation risk beyond what would be expected from increases in nest predator abundance alone. For instance, adults spend less time guarding their nests when food is in short supply so nest predation and brood parasitism occur more frequently (Yom-Tov 1974, Arcese and Smith 1988, Ward and Kennedy 1996). Nestlings that are not well fed beg for food more vigorously than sated nestlings, which increases the risk of nest predation (Price and Ydenberg 1995, Leech and Leonard 1997). Also, reduced food can prolong the incubation period as well as the nestling period (Schifferli 1973, Lyon and Montgomerie 1985, Sanz 1996), thereby increasing predation risk. Although food supply may elevate rates of nest predation or brood parasitism in small fragments, this hypothesis requires study.

In view of our results for Eastern Yellow Robins and those of Burke and Nol (1998) for Ovenbirds, we suggest that food supply may play a significant role in influencing the area sensitivity of ground-foraging, insectivorous songbirds. Although these two studies cannot be the sole basis for general conclusions, they indicate that food shortage should be given greater consideration in other fragmentation studies. Fortunately, many techniques are available for measuring relative food abundance in addition to relative food availability (e.g., Southwood 1992; see references in Newton 1980, Martin 1987, Boutin 1990), so these tasks can be readily accomplished in the field.

In addition to understanding whether food supply varies with fragment size, we need to know why it may vary. For instance, a clear connection between microclimate and invertebrate biomass needs to be made. Also, we need to know the impact of food shortage on the demography of populations breeding in fragmented landscapes. Area-sensitive species are expected to show low seasonal fecundity in small fragments (e.g., Temple and Cary 1988, Pease and Grzybowski 1995). Food shortage can directly influence seasonal fecundity through reduced clutch or brood size (e.g., Holmes et al. 1986, Boland et al. 1997). Alternatively, food shortage may have indirect effects. For example, incubation feeding, nestling provisioning, and egg size influence hatching success and/or the growth and survival of nestlings as well as fledglings (Nisbet 1973, Schifferli 1973, Crossner 1977, Lyon and Montgomerie 1985, Amundsen and Stokland 1990, Magrath 1991, Wiebe and Bortolotti 1995). Also, females in our large fragments had a longer breeding season, whereas the interval between nests was comparable with that in small fragments. Thus, females in large fragments appeared to have the capacity to produce relatively more nests per season, which would increase their chances of fledging at least one brood. Finally, Burke and Nol (1998) found that food abundance was positively associated with the pairing success of male Ovenbirds. These demographic problems could have serious repercussions for population numbers of birds breeding in fragmented landscapes, which highlights the need to examine the possible role of food supply.

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