Effects of Forest Edges on Ovenbird Demography in a Managed Forest Landscape

DAVID J. FLASPOHLER,*‡ STANLEY A. TEMPLE,* AND ROBERT N. ROSENFIELD†

*Department of Wildlife Ecology, University of Wisconsin–Madison, Madison, WI 53706, U.S.A.
†Department of Biology, University of Wisconsin–Stevens Point, Stevens Point, WI 54481, U.S.A.

Abstract: *We studied the reproductive ecology of Ovenbirds (*Seiurus aurocapillus*) for 3 years in a primarily forested landscape in northern Wisconsin. We searched for and monitored nests in large, closed-canopy northern hardwood forests adjacent to recent clearcuts (<6 years old) and measured the effect of proximity to edge on nest success, clutch size, and breeding pair density. Mayfield nest success was lower near the forest edge (0.44,* $N_{nests} = 42$*; <300 m) than in the forest interior (0.69,* $N_{nests} = 47$*; >300 m;* $\chi^2 = 4.43$*, df = 1,* $p \leq 0.04$*), and mean clutch size was higher (4.93) near the forest edge than in the forest interior (4.27;* $t = -3.83$*, df = 59,* $p \leq 0.0003$*). Edge effects on nest success and clutch size extended farther (300 m) into intact forest than has been documented previously. Using habitat-specific demographic parameters, we found that annual productivity per pair was similar in edge (3.37 fledglings) and interior (3.85 fledglings) habitat. We used our estimates of per capita annual productivity and published estimates of adult and juvenile survival to approximate the finite rate of growth (λ) for birds breeding in edge and interior locations. Based on published estimates of age-specific survival, both edge and interior habitats appear to be source habitats (where* $\lambda > 1$*) for Ovenbirds in the landscape we studied. Our assessment of population status, however, was extremely sensitive to variation in survival estimates. We used geographic information system data from the Nicolet National Forest to estimate population size in northern and mixed-hardwood forests in this region and to quantify annual productivity in this landscape. Ovenbirds near forest edges faced higher predation pressure but laid more eggs on average than birds in the forest interior. Our data suggest that Ovenbirds may make tradeoffs between the probability of nest success and the per-nest productivity as measured by clutch size. Our findings are consistent with the equilibrium state of the ideal free distribution model in that although individual demographic characteristics (nest success and clutch size) varied with distance from edge, an important correlate of fitness, finite rate of increase (λ) remained relatively similar.*

Efecto de los Bordes del Bosque en la Demografía del Chipe Suelero en un Paisaje de Bosque Manejado

Resumen: *Estudiamos la ecología reproductiva del chipe suelero (Seiurus aurocapillus) por tres años en un paisaje en su mayor parte forestal al norte de Wisconsin. Buscamos y monitoreamos nidos en bosques leñosos de dosel cerrado adjacentes a bosques talados recientemente (<6 años de edad) y medimos el efecto de la proximidad del borde sobre el éxito de nidación, el tamaño de la nidada y la densidad de parejas reproductoras. El éxito de nidos en Mayfield fue más bajo cerca de los bordes del bosque (0.44,* $N_{nidos} = 42$*) (<300 m) en relación con el interior del bosque (0.69,* $N_{nidos} = 47$*) (>300 m) (*$\chi^2 = 4.43$*, df = 1,* $p < 0.04$*), y el tamaño de nidada fue mayor (4.93) cerca del borde del bosque que en el interior del bosque (4.27) (*$t = -3.83$*, df = 59,* $p = 0.0003$*). Encontramos que los efectos de borde sobre el éxito de nidación y el tamaño de la nidada se extendió aún más (300 m) al interior del bosque de lo que ha sido documentado previamente. Mediante el uso de parámetros demográficos hábitat-específicos, encontramos que la productividad anual por pareja es similar en el borde (3.37 polluelos) que en el interior (3.85 polluelos) del hábitat. Usamos nuestras estimaciones de productividad anual per cápita y estimaciones publicadas de la supervivencia de adultos y juveniles para estimar la tasa finita de crecimiento (λ) para aves que se reproducen en localidades de borde y del interior.*

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‡*Current address: School of Forestry and Wood Products, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931-1295, U.S.A., email: djflaspo@mtu.edu*
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En base a estimaciones publicadas de supervivencia de edad específica, tanto el hábitat de borde como del interior parecen ser hábitats fuente (donde λ >1) para los chipes en el paisaje estudiado. Sin embargo, nuestras estimaciones del estado poblacional fueron extremadamente sensibles a la variabilidad en las estimaciones de supervivencia. Usamos datos del Sistema de Información Geográfica del Bosque Nacional Nicolet para estimar el tamaño poblacional en bosques del norte y bosques leñosos mixtos en esta región y para cuantificar la productividad en este paisaje. Los chipes cercanos a los bordes enfrentan una presión por depredación más alta, pero tienen más huevos en promedio que las aves del interior del hábitat. Nuestros datos sugieren que los chipes podrían tener una compensación entre la probabilidad del éxito de nidación y la productividad por nido, medida como el tamaño de la nidada. Nuestros resultados son consistentes con el estado de equilibrio del modelo ideal de distribución libre, en el que las características demográficas individuales (éxito de nidación y tamaño de la nidada) varían en relación con la distancia del borde. La tasa finita de incremento (λ), que es una importante asociación de adaptabilidad permaneció relativamente igual.

Introduction

Research on the nesting success of forest songbirds and the persistence of their populations in highly fragmented landscapes has identified two mechanisms that reduce reproductive success: edge-related increases in rates of nest predation (Robinson et al. 1995; Hartley & Hunter 1998) and brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) (Brittingham & Temple 1983; Robinson 1992; Robinson et al. 1995). Some studies have reported higher nest densities near forest edges (Gates & Gysel 1978; Hanowski et al. 1995, 1996), suggesting that the combination of reduced nest success and high nest density could magnify the impact of local edge effects on regional populations as predicted by the "ecological trap" hypothesis (Gates & Gysel 1978; Donovan et al. 1997). To test these ideas, researchers have used demographic data to build models to predict how songbird populations respond to landscape structure and composition (Temple 1986; Temple & Cary 1988; Thompson 1993; Donovan et al. 1995*a*).

These songbird models suggest that local populations subjected to high rates of nest predation and brood parasitism may become sink populations that to persist must be subsidized by immigrants from source populations (Temple & Cary 1988; Robinson 1992; Porneluzi et al. 1993; Donovan et al. 1995*b*). The majority of these models focus on agricultural landscapes containing woodlots of various sizes. Less is known about the effects of anthropogenic forest edges on nesting density, reproductive success, and other demographic parameters that also may affect birds in landscapes dominated by forest cover (King et al. 1996, 1998*a*; Donovan et al. 1997; Morse & Robinson 1999).

To understand the dynamics of songbird populations breeding in heterogeneous landscapes, it is crucial to quantify the effects of varying habitat quality on reproductive success and per capita annual productivity (Bernstein et al. 1991; Bowers 1994). The reproductive ecology of the Ovenbird (*Seiurus aurocapillus*) has been studied extensively (Hann 1937; Bond 1957; Brittingham & Temple 1983; Smith & Shugart 1987; Van Horn & Donovan 1994; King et al. 1996; Burke & Nol 1998), and relationships between Ovenbird reproduction and landscape patterns have been described (Bond 1957; Brittingham & Temple 1983; Gibbs & Faaborg 1990; Porneluzi et al. 1993; Villard et al. 1993; Burke & Nol 1998). The Ovenbird is considered to be sensitive to forest fragmentation (Whitcomb et al. 1981; Temple 1986; Robbins et al. 1989) because it is often absent from smaller patches of forest (Whitcomb et al. 1977; Robinson 1992) and its nesting success (King et al. 1996; Flaspohler 1998) and male pairing success (Gentry 1989; Van Horn 1990; Villard et al. 1993) are lower near forest edges than in the forest interior.

In a heterogeneous landscape, species-specific habitat quality varies, a potential consequence of which is that population attributes such as density, reproductive success, and per capita annual productivity vary across the landscape. For example, clutch size often varies between habitats (Lack 1966). Forest edges can influence these aspects of forest songbird demographics (Gates & Gysel 1978; Brittingham & Temple 1983; Wilcove 1985) and therefore may influence local population dynamics. The dynamics of Ovenbird populations nesting in a forested landscape that includes edge habitat may be disrupted by mechanisms related to anthropogenic edges such as increased nest predation (Paton 1994). We predicted that Ovenbirds nesting near forest edges would experience different predation rates than those nesting far from forest edges. We tested this prediction in an extensively forested landscape in northern Wisconsin, where forest edges are the result of clearcutting. We used local demographic data and spatially explicit modeling techniques to infer the population status of the Ovenbird in this region. We discuss the implications of our findings for population dynamics, models of breeding distribution, and conservation of songbirds.

Methods

Study Area

We gathered data on Ovenbird clutch size, reproductive success, and nest density over three summers across a broad region of northern Wisconsin (Fig. 1). Data were collected on nine study plots (mean size, 19.3 ha; range, 10.2–28.5 ha) in Nicolet National Forest in Vilas and Forest Counties, Wisconsin, and the Northern Highland–American Legion State Forest, Vilas County, Wisconsin (Fig. 1). The northern portion of the Nicolet National Forest encompasses 195,199 ha and is relatively uniform in terms of topography, forest cover composition, and management patterns. (For a complete description of the study plots, see Flaspohler et al. 2001.)

Each study plot was embedded in a large, contiguous forest stand adjacent to a recent clearcut (≤6 years old) that was at least 10 ha in size (mean clearcut size, 18.34 ha; range, 10.2–28.5 ha). The clearcuts were relatively large openings with sharp boundaries adjacent to intact forest. All these edges (hereafter referred to as *forest edges*) could be classified as hard edges because there was an abrupt transition between the clearcuts and the adjacent forest.

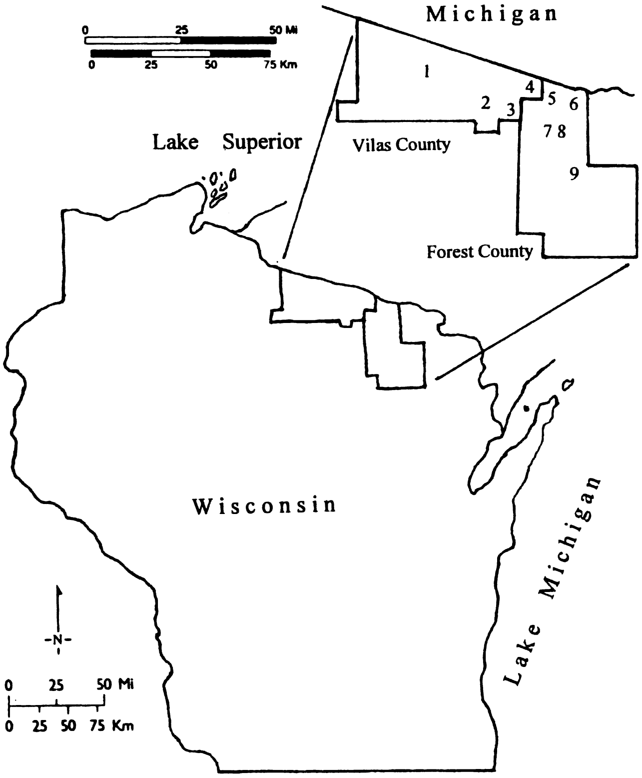

Figure 1. Map of nine study sites in northern Wisconsin: site 1, Northern Highland–American Legion State Forest (Vilas County); sites 2–9, Nicolet National Forest (Vilas and Forest Counties). Site names are as follows: (1) Camp 2, (2) Pine Sap, (3) Anvil Lake, (4) Bear, (5) Kaine Lake, (6) Brule River, (7) Huff Creek, (8) Holt Road, (9) Popple River.

Ovenbird Populations

Plots were searched for nests from mid-May to late July in 1995, 1996, and 1997. Flaspohler et al. (2001) and Martin and Geupel (1993) provide a complete description of nest searching and monitoring protocols. We estimated nest success on a per-nest basis using the Mayfield (1961, 1975) method. Exposure days were calculated according to Mayfield's midpoint assumption. We assumed that daily survival was constant within the incubation and nestling periods and calculated daily survival values for each period. Because incubation and nestling periods can vary geographically (Van Horn & Donovan 1994), we used data from several nests on our study sites for which we had precise period lengths (incubation = 12 days, nestling = 9 days). We separated the nesting period into incubation and nestling periods to more precisely examine the timing of any predation-mediated edge effect.

In 1997 we estimated the density of Ovenbirds on each plot by using a modified spot-mapping protocol, focusing on singing male Ovenbirds (International Bird Census Committee 1970). Using the 50-m alphanumeric grid on each plot, workers plotted the location and movements of singing Ovenbirds on a map of the plot. Workers stopped and made observations for three minutes at each 50-m interval. This procedure was repeated once by another worker on each plot, and the two maps were merged into a single map of Ovenbird detections. We used the spot maps to generate density estimates, locate the approximate center of each territory, and count the number of Ovenbird territories centered in edge and interior habitats. Our modified spot-mapping protocol, although not as reliable as the standard protocol (8–10 visits), provided estimates of relative differences in density within our plots. We were able to reinforce these density estimates with data from actual nest locations. Because we were working in a forested landscape, we assumed that each singing male represented a breeding pair (King et al. 1996), although some males may not have been mated (Gentry 1989; Porneluzi et al. 1993).

Landscape-Scale Modeling

Previous analyses of these data revealed that Mayfield nest success was positively correlated with distance to forest edge and that the effect of distance resembled a threshold function (Flaspohler et al. 2001). In short, for the full nesting period (prehatching and posthatching periods combined), logistic regression models containing a distance-to-edge parameter, either actual distance or $\log_{10}$(distance), provided the best fit to data on nest fate. Logit models of edge-related nest failure resembled a rather flat sigmoid curve with an inflection point between 200 and 400 m. Thus, a threshold edge effect on nest success appears to exist for the Ovenbird at approximately 300 m. We defined forest edge in our model as 0–300 m from edges and forest interior as >300 m from edges. We used forest cover data from the Nicolet National Forest to estimate breeding population size, annual productivity, and population trends in two discrete types of habitat: (1) mature forest (>30 years old) within 300 m of a forest edge (hereafter referred to as edge habitat) and (2) mature forest more than 300 m from a forest edge (hereafter referred to as interior habitat). We assumed homogeneity of all population parameters within these two habitats.

All spatial data were from the March 1997 National Forest Vegetation Resource Inventory of the Chequamegon-Nicolet National Forests (U.S. Forest Service 1997). The "extent" of our model (sensu Wiens 1989) was chosen to approximate the area within which our plots were arranged (approximately 152,000 ha) (Fig. 1). We used the landscape characteristics of this region in our model. The "grain" of our model (sensu O'Neill et al. 1986; Wiens 1989) was dictated by the spatial scale at which we studied and were able to detect differences in local population attributes such as nesting density and success (i.e., about 20 ha).

We used 15 years as an estimate of the persistence time of the edge effects we were modeling. Growth rates for aspen vary with soil quality, site suitability, and other factors (Laidly 1990), but the difference in tree height between mature northern hardwoods and regenerating aspen is reduced to about half at 15 years in northern Wisconsin (Carmean 1978; Laidly 1990). Although some edge effects may persist beyond 15 years, we believe that this criterion is a conservative approach to estimating the duration of edge effects on songbird reproduction. We identified all clearcuts in the model landscape that were <15 years old (in 1997).

The cover-type classifications used by the U.S. Forest Service include four categories that correspond with the forest types on our study plots: mixed hardwoods, sugar maple, sugar maple–basswood, and sugar maple–yellow birch. Because all four of these cover types correspond to the forests in our study plots and all are used more or less evenly by breeding Ovenbirds (Van Horn & Donovan 1994), we combined them into a single cover type, which we refer to hereafter as northern hardwoods. We calculated area coverage for clearcuts using ArcView (Environmental Systems Research Institute 1996). We then buffered all clearcuts by 300 m and generated estimates for the area of northern hardwoods within the total buffered areas using ArcInfo (Fig. 2). We calculated forest-cover statistics from tables generated by ArcInfo.

We used our estimates of nest success and clutch size to calculate per capita annual productivity. We calculated the mean number of female offspring per breeding female per year based on the number of female offspring per successful nest (assuming a 1:1 sex ratio). We calculated per capita annual productivity according to the following equation in which F is per capita annual productivity, p is probability that a nest is successful, and y is mean clutch size of successful nests:

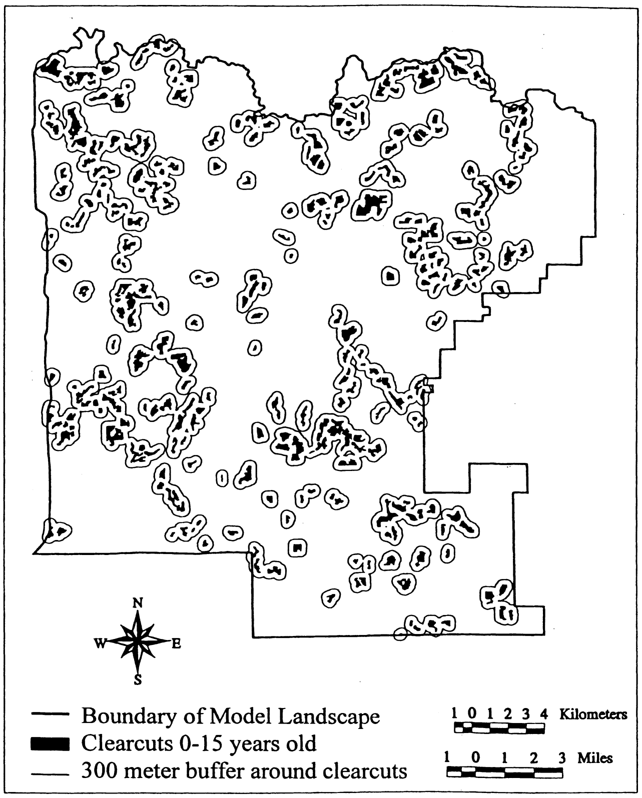

Figure 2. Model landscape corresponding to the Florence District (approximately one-quarter of the entire Nicolet National Forest) showing recent aspen clearcuts (<15 years old) and 300-m buffer.

$$F = p^*y + (1-p)^*p^*y = p^*y(2-p). \qquad (1)$$

With this equation, we assume that all pairs that fail in their first nesting attempt will renest with the same probability of success but cannot attempt a third brood if the first two nests fail. We assumed an equal sex ratio, so per capita annual productivity of females was one half of per capita annual productivity.

Information on crucial parameters contributing to per capita annual productivity is lacking for most songbirds—in particular, the frequency of double-brooding (Ricklefs 1973). Female Ovenbirds will replace initial clutches lost to predation or other causes, but they rarely renest following successful nesting attempts (Van Horn & Donovan 1994; King et al. 1996).

We examined differences in nest success and clutch size across the breeding season and between years using logistic regression. Statistical analyses of density and clutch size and seasonal patterns of nest success were done with SYSTAT (Wilkinson 1997). We compared

Mayfield nest success values in edge and interior habitat using the computer program Contrast (Hines & Sauer 1989). Comparisons of nest density values and clutch sizes in edge habitat versus interior habitat were done with two-sample *t* tests.

To explore the relation between distance to edge and clutch size, we compared linear regression models containing a parameter for clutch size using Mallow's C_p, which provides an objective method of comparing models with different numbers of parameters (Draper & Smith 1981; Burnham & Anderson 1992). Factors that varied with year or between plots could mask a relationship between distance to edge and clutch size. To control for such factors, we included year and plot as categorical variables in the analysis.

For our baseline population model, we assumed pairs that were successful in their initial nest attempt did not attempt a second brood. The frequency distribution of nest initiation dates, however, suggests that there is a small cluster (5–10% of all nests) of nesting starts late in the breeding season (Fig. 3), which could represent double-brooding by some pairs but also may represent renesting attempts after initial nest failure. Therefore, as a means of assessing the importance of renesting on per capita annual productivity, we also calculated per capita annual productivity assuming that either 5% or 10% of successful females renest. Furthermore, we analyzed the sensitivity of our model to changes in estimates of adult and juvenile survival rate. To compare rates of per capita annual productivity with and without second brooding, we held clutch size constant for edge habitat (mean = 4.93 eggs) and interior habitat (mean = 4.27 eggs), even though clutch size may decline throughout the breeding season for many species of passerines (Perrins 1965). We modified Eqn. 1 for calculating per capita annual productivity by including a constant (q) representing the percentage of females that attempt a second nest after a successful first nest (i.e., either 0.05 or 0.10):

$$F = p^{*}y(2-p) + q(p^{*}y). \tag{2}$$

We calculated the finite rate of increase (λ) for populations using Eqn. 3, in which N_t is the population size at time t, F is an estimate of per capita annual productivity (as female offspring), and S_a and S_j are adult and juvenile survival estimates, respectively:

$$\lambda = N_t(S_a) + N_t(F)(S_j) = S_a + (F)(S_j). \tag{3}$$

We used published estimates of annual survival for adults (S_a) and juveniles (S_j) for Ovenbirds and for other similarly sized passerines (Ricklefs 1973; Karr et al. 1990) and assumed that S_j was one-half of S_a (Ricklefs 1973; May & Robinson 1985). Based on previous modeling exercises by Temple and Cary (1988) and published estimates of Ovenbird survival, our baseline model uses annual survival rates of 0.60 and 0.30 for adults and juveniles, respectively.

Population modeling requires that unknown parameters be estimated in order to gauge the sensitivity of the population to parameter variation (Starfield & Bleloch 1991). To gauge the sensitivity of our population assessment to variation in S_a and S_j, we explored the relationships between variability in survival estimates and values of λ. First, we retained the assumption that $S_j = S_a/2$ and explored how λ is affected by our calculated values for per capita annual productivity. We also incorporated habitat-specific population estimates to generate annual increments of growth using the given parameters. Next, we relaxed the assumption that $S_j = S_a/2$ and provided values for λ under a variety of combinations of age-specific survival. We generated a landscape-specific value for per capita annual productivity by taking productivity values for edge and interior habitat and multiplying them by the proportional representation of each habitat in the northern Nicolet National Forest. This provided a weighted average of per capita annual productivity for our model landscape.

Results

Clutch Size

The mean clutch size during the incubation period was greater in edge habitat (4.93 ± 0.09 SE, $n = 39$) than in interior habitat (4.27 + 0.14 SE, $n = 40$) ($t = -3.83$, df = 59, $p = 0.0003$). Mean brood size during the nestling period was also greater in edge habitat (4.74 ± 0.10 SE, $n = 27$) than in interior habitat (4.27 + 0.12 SE, $n = 34$) ($t = -2.99$, df = 77, $p = 0.004$) (Table 1).

Linear regression models using clutch size as the dependent variable and distance to edge as the independent variable provided the best fit to the data (based on Mallow's C_p criterion) when year and plot were included. Clutch size also varied with initiation date (day the first egg is laid; $p \leq 0.002$). After observing that our data contained many late-season nests near the forest edge and few in the forest interior (Fig. 3), we explored the possibility that this pattern may have actually reduced the real magnitude of the differences in clutch size between edge and interior zones. When we analyzed nests only up to and including 19 June, clutch size within 300 m of the forest edge was larger (4.97 ± 0.08 SE, $n = 27$) than in the forest interior (4.55 ± 0.09 SE, $n = 29$), but the difference was less than when all data were used in the analysis.

Nest Success and Per Capita Annual Productivity

Brown-headed Cowbirds were extremely rare on all plots in all three years of this study, and only two Ovenbird nests were parasitized. Mayfield nest success in edge habitat (43.8%, $n = 51$, daily predation rate = 0.033) was significantly lower ($\chi^2 = 4.43$, df = 1, $p \leq 0.04$) than in in-

Table 1. Spatially specific population parameters used in Ovenbird modeling exercise.

Parameter	*Edge habitat*	*Interior habitat*
Breeding density (pairs/ha)	0.36	0.28
Available breeding habitat (ha)[a]	6,034	18,826
Population size (females only)	2,172	5,271
Mean nest success[b] ± SE (N_{nests})	0.438 ± 0.08 (51)	0.685 ± 0.09 (38)
Mean clutch size ± SE (N_{nests})	4.93 ± 0.09 (39)	4.27 ± 0.14 (40)
Median clutch size	5	4
Mean per capita annual productivity per pair[c]	3.37	3.85
Mean female per capita annual productivity per pair	1.69	1.93
Annual adult survival (baseline)	0.60	0.60
Annual juvenile survival (baseline)	0.30	0.30
λ[d]	1.11	1.18
Total female production immediately after breeding	3,671	10,173
Annual female increment to breeding population	239	949

[a] *Amount of mature northern hardwoods (>30 years old) in the northeastern portion of the Nicolet National Forest.*
[b] *Mayfield (1961, 1975) nest success calculated from exposure.*
[c] *Per capita annual productivity* $= F = p * y + (1 - p) * p * y$.
[d] $\lambda = S_a + FS_j$.

terior habitat (68.5%, $n = 39$, daily predation rate = 0.015) (Table 1). There was no significant relationship between nest success and initiation date ($p = 0.59$).

Female Ovenbirds nesting in edge habitat produced an average of 1.69 females per nesting attempt, whereas those nesting in interior habitat produced an average of 1.93 females per nesting attempt (Table 1). Thus, per capita annual productivity in interior habitat was 14.2 % greater than in edge habitat.

Density

Density estimates from spot mapping of singing males on our nine study plots ranged from 0.13/ha to 0.47/ha and averaged 0.31/ha (13 pairs/40 ha). Our estimate of nesting density in edge habitat (0.36 pairs/ha) was not significantly different ($t = 1.17$, df = 7, $p = 0.28$) than in interior habitat (0.28 pairs/ha) (Table 1). As a separate index of relative density within the plots, nests from all 3 years were grouped into 50-m zones relative to distance from edge, and the number of nests in each zone was expressed as nests per hectare (Flaspohler et al. 2001). Results from this analysis suggest that Ovenbirds may nest in higher densities near forest edges than in forest interior locations.

We estimated the population size of Ovenbirds breeding in our model landscape (northern hardwoods in the northern portion of the Nicolet National Forest). In

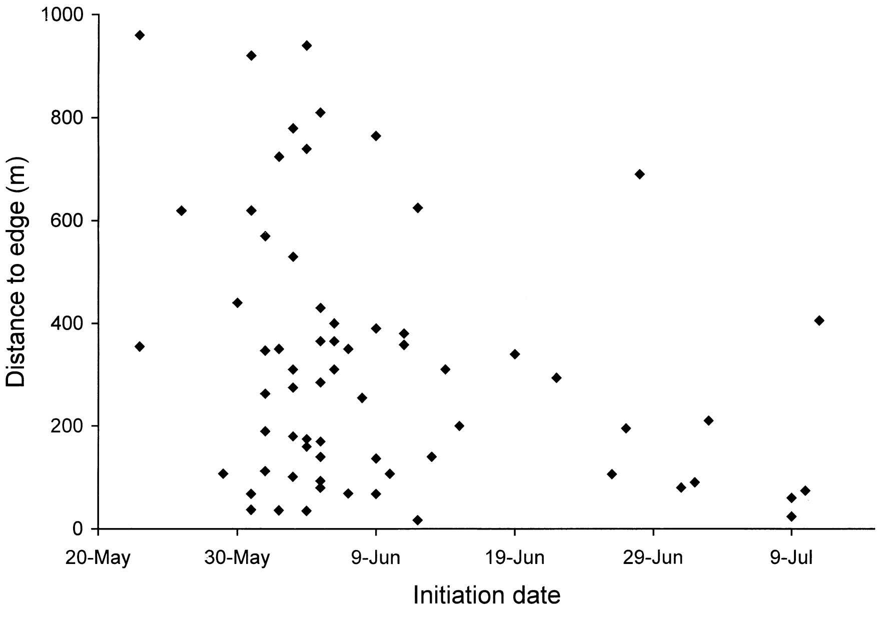

Figure 3. Ovenbird nest-initiation dates plotted against distance to forest edge for data from 1995 to 1997.

1997, 6034 ha of mature northern hardwood forest were within 300 m of a clearcut, whereas 18,826 ha were farther than 300 m from a recent cut. The population size within mature northern hardwoods was calculated as the product of our density estimates and the area of available edge and interior habitat (Table 1). Using our estimates of habitat-specific Ovenbird density, we estimated that the breeding population in our model landscape was 2172 pairs in edge habitat and 5271 pairs in interior habitat.

Model Results

We used estimates of density to make inferences about the distribution and size of Ovenbird populations in the Nicolet National Forest. Because nest density in edge habitat was 28.6% higher than in interior habitat, an average 40-ha stand of northern hardwoods forest composed entirely of edge habitat would contain 14.4 Ovenbird pairs, whereas the same size stand of interior habitat would contain 11.2 pairs. On average, birds nesting in edge habitat laid clutches that were 15.5% larger than clutches in interior habitat. The apparent "ecological trap" resulting from the combination of relatively high nest density and low nest success in edge habitat was largely offset by the difference in mean clutch size between edge and interior habitat. Based on our estimates of S_a (0.60) and S_j (0.30), both edge and interior habitats are source habitats ($\lambda > 1.0$) (Table 2). The population in our model landscape would therefore produce a surplus of 1188 females each year (Table 1).

Our baseline model for per capita annual productivity assumed a single brood for all successful nests, but the possibility of double-brooding exists (Holmes et al. 1991, 1992; Rodenhouse & Holmes 1992). An analysis of the sensitivity of per capita annual productivity to double-brooding yielded the following results. If 5% of females renested, per capita annual productivity would increase by 0.06 female offspring per breeding attempt in edge habitat (3%) and 0.08 females in interior habitat (4%). If 10% of females renested, per capita annual productivity would increase by 0.11 in edge habitat (7%) and by 0.15 in interior habitat (8%). Although we cannot definitively separate renests from second broods, most nest initiations late in the breeding season were within 200 m of the forest edge, where nest failure rates were relatively high (Fig. 3). This pattern indicates that these are incidences of renesting rather than second broods.

Survival estimates from our baseline model ($S_a = 0.60$, $S_j = 0.30$) yield values for λ in edge habitat (1.13) and interior habitat (1.18) that indicate an increasing population (Tables 2 & 3). Still, the extreme sensitivity of our model to variation in survival can be demonstrated by setting $\lambda = 1.0$ and calculating a value of S_a that would generate a stable population (assuming $S_j = S_a/2$): 0.54 in edge habitat and 0.51 in interior habitat. Thus, although our best assessment of population status indicates that Ovenbirds in this region produce an annual surplus, a relatively small decline in adult and juvenile survival (10% in edge habitat, 15% in interior habitat) could transform regional populations from increasing populations to declining populations.

We examined the behavior of λ in edge and interior habitat when S_a and S_j vary (Tables 2 & 3). Both edge and interior habitats maintained $\lambda \geq 1.0$, except when either S_a or S_j dropped below some threshold. In general, in both edge and interior habitat, values for S_a below 0.60 and values for S_j below 0.30 were associated with a declining population ($\lambda \leq 1.0$).

Table 2. Habitat-specific (forest edge and forest interior) values for per capita annual productivity and λ for Ovenbirds with varying estimates of adult and juvenile survival.

	λ in edge habitat when S_j is			*λ in interior habitat when S_j is*		
Adult survival (S_a)	*0.20*	*0.30*	*0.40*	*0.20*	*0.30*	*0.40*
0.40	0.74	0.91	1.08	0.79	0.98	1.17
0.50	0.84	1.01	1.18	0.89	1.08	1.27
0.60	0.94	1.11	1.28	0.99	1.18	1.37
0.70	1.04	1.21	1.38	1.09	1.28	1.47
0.80	1.14	1.31	1.48	1.19	1.38	1.57

Discussion

Our model of habitat-specific population demography indicates that Ovenbirds breeding in northern hardwood forests are producing an annual surplus of off-

Table 3. Landscape-weighted values for λ with different estimates of adult (S_a) and juvenile (S_j) survival based on per capita annual productivity of ovenbirds.[a]

Adult female survival rate[b]	*Juvenile female survival rate*				
	0.20	*0.25*	*0.30*	*0.35*	*0.40*
0.40	0.77	0.87	0.96	1.05*	1.14
0.45	0.82	0.92	1.01*	1.10	1.19
0.50	0.87	0.97	1.06	1.15	1.24
0.55	0.92	1.02*	1.11	1.20	1.29
0.60	0.97	1.07	1.16	1.25	1.34
0.65	1.02*	1.12	1.21	1.30	1.39
0.70	1.07	1.17	1.26	1.35	1.44
0.75	1.12	1.22	1.31	1.40	1.49
0.80	1.17	1.27	1.36	1.45	1.54

[a] *Values of λ calculated from average per capita annual productivity of edge and interior habitat (unweighted mean per capita annual productivity = 1.81) weighted by percent coverage of each habitat in our model landscape (weighted mean per capita annual productivity = 1.86). Values on the diagonal (*) represent approximately stable population conditions. Values above the diagonal represent declining population conditions. Values below the diagonal represent increasing population conditions.*

[b] *Survival rates are assumed to be constant after the first year.*

spring. This is consistent with the hypothesis that areas dominated by contiguous forest are source habitats for some area-sensitive bird species (Terborgh 1989; Donovan et al. 1995*b*; Robinson et al. 1995). Although the finite rate of increase was approximately 6% greater in interior habitat ($\lambda = 1.18$) than in edge habitat ($\lambda = 1.11$), the most striking result of our parameterized model is the similarity of λ values in edge and interior habitats.

Breeding Distribution and Demography

Habitat-specific differences in reproductive success and other fitness correlates are common among birds, including raptors (Newton 1986), resident passerines such as parids (Krebs 1971; Dhondt et al. 1992) and corvids (Goodburn 1991), and migrant passerines (Holmes et al. 1996), including the Ovenbird (Gibbs & Faaborg 1990; Porneluzi et al. 1993). Many studies have compared habitats that contrasted strongly in terms of vegetation structure and composition or fragment size. Few studies have examined how proximity to edge influences habitat quality in a relatively unfragmented forest landscape (although see King et al. 1996, 1998*a*; Morse & Robinson 1999).

Two key population parameters—clutch size and nest success—differed between edge habitat and interior habitat in our study, but because of compensation between these parameters, λ was >1.0 and similar in both edge and interior forest habitat. Several factors could explain observed differences in clutch size and nest success.

Although distance to forest edge was the proximate factor associated with variability in clutch size and nest success for the Ovenbird, it is almost certainly not proximity to edge per se that is important but rather factors associated with edge. Some researchers have found that nest predators are more abundant near edges (Gates 1991; King et al. 1998*b*). In western U.S. forests, microclimatic gradients extend up to 240 m from clearcut edges into intact forest (Chen et al. 1995). Such physical gradients could affect the attractiveness of forest edges to breeding birds and/or nest predators. A warmer microclimate near the forest edge early in the breeding season could stimulate plant growth and associated herbivorous insects, making such areas more attractive to breeding birds in search of food and nest cover. Alternatively, in some fragmented landscapes, forest edges are prone to greater desiccation, possibly reducing arthropod density and diversity (Burke & Nol 1998).

Forest edges often contain greater vegetative heterogeneity than interiors (Chen et al. 1992), which may be associated with more foraging or singing sites (Morgan & Gates 1982) or denser nesting cover (Bowman & Harris 1980; Redmond et al. 1982). The lack of great variation in topography on any of our nine study sites suggests that the relatively deep penetration of edge effects that we found is not attributable directly to topographic variation. Plainly stated, the mechanism responsible for reduced nesting success near edges is a predator-prey dynamic, and we can only speculate as to the mechanism behind edge-related variation in clutch size. Because there were over two dozen potential nest predators on our study sites (unpublished data), we will refrain from further speculative discussion of the effects of edges on individual predator species.

Distribution of Breeders in Relation to Habitat Quality

Interpretation of population status based solely on any one of the three parameters we studied could have led to inconsistent conclusions. Based on a larger mean clutch size, edge habitat would appear to be of higher quality than interior habitat; based on nest-success estimates, edge habitat appears to be of lower quality than interior habitat. Based on density, edge habitat may have been better than interior habitat, but van Horne (1983) and Vickery et al. (1992) suggest caution in using density as an indicator of habitat quality. Per capita annual productivity and λ were similar in both habitats. Thus, there appears to be compensation, with higher relative predation risk but higher mean clutch size in edge habitat, and lower relative risk of predation but lower mean clutch size in interior habitat. Similarly, King et al. (1996) reported that Ovenbirds near edges compensate for increased predation by renesting. In contrast, Morse and Robinson (1999) found that Kentucky Warbler (*Oporornis formosis*) productivity is lower in agricultural edge than interior areas.

These results are consistent with the equilibrium state of the ideal free-distribution model (Fretwell & Lucas 1970; Rosenzweig 1985), which predicts that individuals choose habitat patches that maximize per-capita benefit in terms of access to resources, reproductive success, or some other measure of fitness. It is assumed that individuals are free to settle in any place they choose and that they have perfect knowledge of variation in realized habitat quality (Cody 1985). Although the intrinsic quality of various habitat patches may vary, the realized quality of all patches for individuals using them is the same. Thus, "at equilibrium, the suitability of all habitats will be the same, so that individuals, regardless of habitats, will have equal fitness, or equal success, as measured by a proximate correlate of fitness" (Bernstein et al. 1991:321). The ideal free distribution is frequently assumed to exist, yet evidence for its existence in patchy environments is not well documented (Parker 1978; Milinski 1979), and its general utility has been questioned (Kennedy & Gray 1993). Although the territorial nature of Ovenbirds would predict a despotic model, substantial research (reviewed by Parker & Southerland 1986) suggests that mixed free and despotic models may best explain animal distribution within habitats of varying quality.

Application of Local-Scale Demography to Populations

By limiting our model to the region in which we gathered our data, we sought to minimize errors associated with extrapolation of population data. We are confident that our estimates of the location and extent of clearcuts and northern hardwoods were accurate. Local population parameters, however, were gathered in relatively homogeneous forest plots. The application of these data to larger and more heterogeneous landscapes increases the risk that other factors may complicate the use of a general model. For example, our land-cover data indicate that 24.3% of our model landscape falls within 300 m of a recent clearcut. This proportion would be higher if we included edges created by things other than clearcutting, such as road corridors. Also, Ovenbirds may reach their highest nesting density in northern hardwoods, but they do nest in other common forest types in the upper Great Lakes region (e.g., lowland conifer) (Howe et al. 1996).

Many spatially explicit models of animal populations have not incorporated the effects of dynamic vegetation changes (Pulliam & Dunning 1995). We assumed that edge effects on clutch size and reproductive success end abruptly when the regenerating clearcut reaches approximately one-half of the stature of the intact forest at approximately 15 years. The transition from edge effect to no edge effect is more likely to be gradual over time.

Conservation Implications

In many forested areas, timber harvesting represents the most common form of habitat alteration on the landscape, in both frequency and extent. Models that incorporate habitat selection and habitat-specific demographics are necessary for predicting the effects of these forest manipulations on natural populations (Kennedy & Gray 1993). Detailed information on the status of local populations in heterogeneous landscapes is also needed to complement large-scale population trend data from the Breeding Bird Survey (Robinson 1992).

Perhaps our most interesting finding is that Ovenbirds appeared to make tradeoffs between clutch size and the probability of nest success. Dunning et al. (1995) and others have suggested that species that are poor discriminators of habitat quality face the greatest threat from population sinks when physical boundaries between sources and sinks are subtle (McKelvey et al. 1992). Our findings support the hypothesis that relatively unfragmented forests of the upper Great Lakes support growing populations of Ovenbirds. In this respect, they may be important source populations that subsidize sink populations in the more heavily fragmented forests to the south (Robinson et al. 1995).

Our study also suggests that edge effects have complex implications for Ovenbirds breeding in forested landscapes. More broadly, our findings suggest that classifications such as "forest interior species" may be landscape-specific. This is not surprising, given that the proximate causes of deleterious edge effects are a host of species (e.g., Brown-headed Cowbird, Blue Jay [*Cyanocitta cristata*], raccoon [*Procyon lotor*]), each with its own geographic distribution and habitat needs. If landscape condition proves a good predictor of whether edge effects have negative, positive, or neutral effects on forest-breeding songbirds (e.g., Donovan et al. 1997), then it is important to know what levels of forest clearcutting create conditions associated with declining populations (e.g., $\lambda < 1.0$). The determination of this "population trend threshold" will depend on how populations of nest predators and cowbirds respond to increases in landscape-scale fragmentation. It will also be influenced by songbird response to the changing appearance and connectivity of the forest landscape.

A more complete understanding of the factors that control populations of Ovenbirds and other forest-nesting songbirds on their breeding grounds will require information on responses to habitat features at many scales. Ovenbird population parameters have been shown to respond to habitat variation in the immediate vicinity of the nest (i.e., nest concealment; Flaspohler 1998), the local patch of habitat (i.e., forest edge; Kroodsma 1984), and the pattern of forest and interstitial land use in the surrounding landscape (Brittingham & Temple 1983; Gibbs & Faaborg 1990; Villard et al. 1993). Two key areas that remain poorly understood for most songbirds are rates of annual survival and dispersal (Payne 1990). Long-term studies of the relationship between demographics and vegetative succession are also needed to measure the duration of habitat alterations related to land management.

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