EFFECT OF EDGE ON BREEDING FOREST BIRD SPECIES

ROGER L. KROODSMA

The clearing of forests often creates forest edges where an edge effect reportedly causes increased densities and diversities of birds and other wildlife (Lay 1938, Johnston 1947, Anderson et al. 1977, McElveen 1979, Strelke and Dickson 1980). The clearing also causes loss of forest habitat and often results in forest fragmentation. In addition to the effects of habitat loss, forest fragmentation may be responsible for an observed decline in abundance of certain bird species in the remaining forest fragments (Robbins 1979, Whitcomb et al. 1981). The decline of birds in the forest fragments theoretically could result from the small size and isolation of the forest islands (MacArthur and Wilson 1967), increased predation on nestlings near edges (Gates and Gysel 1978), negative responses of forest interior birds to edges (Kroodsma 1982a), brood parasitism by cowbirds (Molothrus sp.) near edges (Brittingham and Temple 1983) or from disturbances other than forest clearing itself (e.g., human activity, industrial facilities) (Robbins 1979).

The present paper examines the effects of power-line corridor edges on the density of individual breeding bird species of forests, including several of the species that have apparently declined in forest fragments (Whitcomb et al. 1981). The study is based on a total of four territory-mapping censuses, each in a different year, on two large forest plots adjacent to power-line corridors. An earlier paper (Kroodsma 1982a) examined edge effect on forest birds at the community level rather than at the species level and covered only 2 years of censusing on one plot. The purpose of the current paper is twofold: (1) to determine the sensitivity of individual bird species to edges and to forest fragmentation; and (2) to study edge effect based on territory mapping from edges to deeper forest. Previous studies of birds along edges did not examine the density of territories from the edges to deep habitat interior. Most studies were either based on frequencies of observations or registrations rather than on territories (Lay 1938, Anderson et al. 1977, Strelke and Dickson 1980) or involved little or no forest interior (Johnston 1947, McElveen 1979). The results of this study will be useful in assessing the effects on various forest bird species of creating power-line corridors and other clearings (e.g., wildlife clearings) in forests.
STUDY AREAS

Two hardwood forest plots were selected at the Department of Energy's Oak Ridge Reservation in eastern Tennessee. The Reservation occupies about 15,000 ha in the Ridge and Valley Province. About 72% (10,800 ha) is forested, 13% (1950 ha) is pasture, and about 15% (2250 ha) consists of three industrial complexes. The forested areas consist of 37% hardwoods, 20% hardwood-pine (Pinus spp.), 17% planted pine, 16% natural pine, and 10% various mixtures of cedar (Juniperus sp.) with hardwood and pine. Areas surrounding the Reservation contain proportionately more cleared lands in pasture and crops.

One study plot was located on the Reservation and the other was on Haw Ridge adjacent to the eastern end of the Reservation. Both plots consisted primarily of oak (Quercus spp.)-hickory (Carya spp.) forest and were rectangular, with one of the longer sides being the forest edge along a power-line corridor (Fig. 1). The remaining plot edges were bounded by additional extensive hardwood or hardwood-pine forest. The major topographic features (ridges and a stream valley) and vegetational features of the plots were perpendicular to the power-line corridors rather than parallel. Thus, any effect of the corridor edge on birds should not be confounded by ecological gradients (e.g., a gradient from ridge top to stream) associated with these other environmental features. Prior to about 1935, the forests were probably dominated by American chestnut (Castanea dentata), which is now absent from the plots as a mature tree due to the chestnut blight. Elevations on the plots range from 245-350 m above mean sea level. Both power-line corridors were initially cleared in 1964 and 1965 and are oriented roughly north and south. The Reservation corridor was widened in 1969. Both corridors are maintained by mechanical cutting with a large rotary blade on a tractor usually once every 4 years. Cutting is conducted up to the forest edges, which are thus very narrow and distinct.

The Reservation plot covered 21.4 ha and was censused in 1977 and 1979. It extended 800 m along a 79-m-wide corridor and 268 m from the corridor edge into the forest. Aerial photographs taken in 1935 showed that at that time about an eighth of the plot was a cleared pasture and the remainder consisted of forest with a highly broken canopy, which possibly resulted from selective logging and a die-off of American chestnut. A small permanent stream with a gradual gradient of 2% runs through the south half of the plot, perpendicular to the corridor. A long narrow pine plantation, 55 m wide, is located about 40 m from and parallel to the stream. The north half of the plot is on a low ridge with gentle slopes and has two small stands of immature forest totaling about 2 ha adjoining the corridor. The remainder of the plot is medium-aged forest.

The Haw Ridge plot was censused in 1980 and 1981. The plot extends 948 m along a 107-m-wide corridor. In 1980 the plot extended 213 m into the forest and covered 20.2 ha. In 1981 it was enlarged to extend 488 m into the forest and covered 46.3 ha. On 1935 aerial photos, the entire plot consisted of medium- to old-aged hardwood forest with a slightly broken canopy. The northern half of the plot is on a highly dissected ridge with steep slopes. The southern half is an upland area at a lower elevation than the ridge and has a few small intermittent streams and primarily gentle slopes.

METHODS

Census procedure.—Breeding birds were censused by the territory mapping technique (IBCC 1970, Robbins 1978, Svensson 1978). To provide for systematic coverage, I divided the Reservation plot lengthwise into two halves, with one half adjacent to the corridor and the other half in deeper forest. Down the middle of each half and parallel to the corridor edge, I marked a line with grid points 30 m apart. I mapped bird locations as I moved
slowly down the lines and stood for an equal time at each grid point. Singing or calling males within each entire half of the plot (i.e., within 67 m of each grid line) could be easily heard from the grid points. Further details on censusing procedure in this plot are given elsewhere (Kroodsma 1982a). On Haw Ridge I established eight grid lines that were 122 m apart and perpendicular to the power-line corridor. Grid points on the lines were 30 m apart in 1980, but 61 m apart in the larger 1981 plot. The outermost grid points were 30 m outside the plot. Equal time was spent at each point. No part of the plot was more than 61 m from the grid lines.

The Reservation plot was visited 13 times in 1977 and 12 times in 1979. The Haw Ridge plot was visited 13 times in 1980 and 11 times in 1981. The large size of the Haw Ridge plot in 1981 required two mornings for a complete visit. Visits were conducted between 05:45 and 09:30 EDT, 10 May–15 June. They began at different places on the plots to avoid time-of-day bias and were not conducted during rainy or windy conditions. The vast majority of registrations were songs and calls rather than sightings. The occurrence of contemporary registrations of singing males played a major role in my identification of separate territories. The degree to which forest bird territories extended into the power-line corridors was determined by territory mapping on the Haw Ridge corridor in 1980 and 1981, on the Reservation corridor in 1976 and 1980, and on several other corridors in a previous study (Kroodsma 1982b).

Bird registrations recorded on the visit maps during censusing were later transferred to species maps (one map for each species in each year). Territorial boundaries were drawn with curved lines (convex and concave) that closely fit the clusters of registrations. Lone registrations that appeared to be outliers of a territory were connected to the main body of the territory by drawing narrow territorial extensions. Thus, the contribution of outlier registrations to territory size was minimized so that any estimated territory tended to be a used territory rather than a maximum territory as defined by Odum and Kuenzler (1955). Because the location and configuration of each territory with respect to the edge were of primary interest in this study rather than territory size, it was not important to use one of the standard methods (e.g., the minimum convex polygon method, Ford and Myers 1981) of delineating territories for the purpose of estimating territory size. However, it was important not to include large intraterritorial spaces without registrations in order to avoid inaccurate estimates of territory location and configuration. Densities were calculated as the
number of males per 40 ha, including only the estimated fractions of territories within the study plots.

Data analysis. — The potential effects of the forest edges on birds were examined by plotting bird density vs distance from the edge and testing statistically for significant trends. To calculate density at various distances from the edge, I divided the species maps lengthwise into strip transects representing approximately 11-m-wide strips through the forest plots (the width differed slightly between plots). Thus, a 264-m-wide plot would have 24 strip transects. The first strip transect for each plot was adjacent to the power-line corridor, and the remaining transects were successively deeper into the forest. The fraction of each territory in each transect was determined. Population density in each transect was calculated by summing the territorial fractions located within the transect and converting to numbers of territories per 40 ha, and plotted on distance from the edge. Thus, each transect yielded one coordinate (data point) for each species in each year that the species was present. Forest bird territories rarely extended into the corridor. Therefore, in calculating density I assumed that all forest bird territories near the corridor edge lay completely within the plot.

Although the territory mapping method is traditionally used for estimation of bird density on entire plots rather than on narrow transects as in this study, I feel that my more specialized application of the method is valid. Because I mapped territories on large plots and only subdivided the plot maps into narrow transects after censusing and delineation of territories were completed, boundary effects experienced in sampling small plots (Marchant 1981, Verner 1981) were not a factor in this more specialized approach. I should also point out that each density estimate for a transect is by itself of no significance in this paper and is not meant to indicate the bird density at a particular distance from the forest edge. Rather, the density estimates are used only to identify trends in density from the edge to forest interior.

Differences in bird density between near-edge and deep-forest areas were tested statistically in two steps. First I used linear regression to test for trends in each species' density from the corridor edge to 268 m into the forest. The density data for each species were pooled over the 4 years during which censusing was conducted. Differences between years and between plots were not tested because of inadequate sample sizes (i.e., the numbers of territories) in each year or each plot. Regression analysis was performed on the pooled data. Species not showing significant trends in pooled density from the edge to deep forest were deleted from further testing, because, if the pooled sample size were sufficient and real trends did exist, the trends should have shown up at this stage of testing.

This regression analysis could not be used to determine which species actually responded to edge, because the density values for the strip transects were not independent; i.e., a high density in one strip transect was likely to be associated with a high density in adjacent strip transects, because each territory covered portions of many strip transects. For example, all 24 strip transects in the Reservation plot were intersected by three territories of Red-bellied Woodpeckers in 1979 (see tables for scientific names). Although the resulting 24 density values showed a significant trend, a sample size of only three territories does not justify inferring that there is a response at the species level.

Therefore, data for each species whose density showed a statistically significant regression were then analyzed by individual year to determine whether the trend was consistent among years and plots. Each plot was divided into equal rectangular quarters, two quarters adjacent to the power-line corridor (edge quarters) and two in deeper forest (interior quarters) (excluding the portion of the Haw Ridge plot from 268–488 m into the forest in 1981) (Fig. 1). Density was calculated for each quarter in each year. The density estimates for an interior quarter and the estimate for the adjacent edge quarter formed one pair of observations. A total of eight pairs of observations (N = 16) were available for each species that occurred
in each pair of edge and interior quarters in each of the 4 years. The differences in density between edge and interior quarters were tested by analysis of variance with paired comparisons after transforming the data to natural logarithms, and by the Wilcoxon signed-ranks test, a nonparametric method (Sokal and Rohlf 1969:328, 399). The log transformation improves the normality of the data, independence of the variance and the mean, and the additivity of the effects (Snedecor and Cochran 1967:325–330). For the Acadian Flycatcher, whose territories were relatively small, each plot was divided into six rectangles instead of four, and the mean density value for each pair of interior rectangles was used in the statistical comparison with the respective edge rectangle.

For both analysis of variance and the signed-ranks test, the pairs of observations must be independent. I feel that this requirement was adequately satisfied because: (1) the habitats of the north and south halves of each plot were different, and (2) the plot quarters were relatively large. Thus, I believe that, apart from any effect of the forest edge, the locations of territories within one half of each plot had inconsequential effect on, or correlation with, the locations of territories in the other half. Both tests have the paired comparisons design. This design was more efficient than completely randomized analysis of variance because of the often large differences in density between north and south halves of the plots.

RESULTS

The plots of population density on distance from the power-line corridor are presented in Fig. 2. Several of the species plots are characterized by more or less regularly spaced peaks and lows of density (e.g., Acadian Flycatcher, Scarlet Tanager, Blue-gray Gnatcatcher, Blue Jay). The peaks may represent the location of the core areas of territories, and the lows may represent the buffer areas between territories. A core area is a central location in the territory where most singing occurs and where the birds are observed most often, and a buffer zone is the space between song territories where virtually no singing occurs (Stenger and Falls 1959, Zach and Falls 1979). The fact that the plots are characterized by distinct peaks rather than by straight or irregularly fluctuating lines indicates that territories tended to line up in rows parallel to the edge of the corridor (Kroodsma 1982a). One row of territories adjacent to but not extending into the corridor formed the first peak, and a second row of territories deeper into the forest formed the second peak. This result would be expected if birds tended to use all available space in the forest and if the corridor edge neither attracted nor repelled the birds. The territories of forest birds other than the cardinal and towhee, both edge species, did not extend into the corridor. These results suggest that the corridor/forest edge forms a natural border that affects the location of territories, both near the edge and deeper into the forest.

Several of the same species that showed density peaks had low densities at the edge of the corridor. This may have resulted from the tendencies of the territories delineated on species maps to be more circular than rectangular and to average less territorial area per registration at the pe-
Fig. 2. Plots of bird density (pairs/40 ha) from the corridor/forest edge into deeper forest.

...riphery than in the center of the territory (Kroodsma 1982a). Thus, on a per unit area basis, smaller fractions of forest bird territories would be expected to lie along a natural border (i.e., the forest-corridor edge) than slightly removed from the border (i.e., closer to the territorial core area).
TABLE 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size (N)</th>
<th>0-268 m (N₁)</th>
<th>268-488 m (N₂)</th>
<th>Total N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellow-billed Cuckoo (Coccyzus americanus)</td>
<td>21</td>
<td>4</td>
<td></td>
<td>23</td>
</tr>
<tr>
<td>Hairy Woodpecker (Picoides villosus)</td>
<td>11</td>
<td>3</td>
<td></td>
<td>13</td>
</tr>
<tr>
<td>Downy Woodpecker (P. pubescens)</td>
<td>13</td>
<td>4</td>
<td></td>
<td>16</td>
</tr>
<tr>
<td>Carolina Chickadee (Parus carolinensis)</td>
<td>22</td>
<td>8</td>
<td></td>
<td>29</td>
</tr>
<tr>
<td>Wood Thrush (Hylocichla mustelina)</td>
<td>35</td>
<td>5</td>
<td></td>
<td>37</td>
</tr>
<tr>
<td>Hooded Warbler (Wilsonia citrina)</td>
<td>7</td>
<td>0</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>Scarlet Tanager (Piranga olivacea)</td>
<td>29</td>
<td>6</td>
<td></td>
<td>32</td>
</tr>
<tr>
<td>Blue-gray Gnatcatcher (Polioptila caerulea)</td>
<td>18</td>
<td>6</td>
<td></td>
<td>24</td>
</tr>
</tbody>
</table>

* N is the number of territories measured, some of which were not located completely within the plots. Because some territories extended into both distance categories of the Haw Ridge plot and were counted in the sample size of both categories, the total N frequently is less than the sum of N₁ and N₂. N₁ represents 4 years of censusing whereas N₂ represents only 1 year.

Correspondingly, the density estimates, which were based on fractions of territories in narrow strip transects, would be less along the edge.

In several species (Blue Jay, chickadee, titmouse, Wood Thrush, gnatcatcher, Black-and-white Warbler), the core areas of territories adjacent to the corridor appeared to be shifted toward the edge. However, the density of territories was not significantly greater (P > 0.10) near the edge than in deeper forest.

Regression analyses based on data pooled over plots and years indicated that densities of about a third of the bird species did not depend on distance from the edge. These species are listed in Table 1. Pooled densities of each of the 14 remaining species (Table 2) showed significant (P < 0.05) trends from the corridor edge to deeper forest. These species were therefore further tested for year-to-year consistency.

Both the analysis of variance and the signed-ranks tests indicated that densities of 5 of the 14 bird species analyzed were significantly associated (P < 0.05) with distance from the corridor edge (Table 2). Species that were denser near the edge than in deeper forest were the cardinal (P < 0.01), Rufous-sided Towhee (P < 0.05), and Summer Tanager (P < 0.05) (Table 2). The Ovenbird (P < 0.01) and Acadian Flycatcher (P < 0.05) were denser in the forest interior.

The Blue Jay and Tufted Titmouse also indicated significant edge effects within the distance from the corridor edge to 268 m into the forest, which was the distance over which all species were analyzed. However, beyond...
TABLE 2
STATISTICS FOR SPECIES INDICATING A POTENTIAL EDGE EFFECT

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size (N)</th>
<th>Probability level of variance test</th>
<th>Signed-ranks test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Red-bellied Woodpecker (Melanerpes carolinus)</td>
<td>18, 8, 23</td>
<td>&gt;0.05</td>
<td>NS</td>
</tr>
<tr>
<td>Crested Flycatcher (Myiarchus crinitus)</td>
<td>4, 0, 4</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Acadian Flycatcher (Empidonax virescens)</td>
<td>11, 3, 14</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Blue Jay (Cyanocitta cristata)</td>
<td>10, 2, 12</td>
<td>*</td>
<td>*</td>
</tr>
<tr>
<td>Tufted Titmouse (Parus bicolor)</td>
<td>22, 6, 26</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>White-breasted Nuthatch (Sitta carolinensis)</td>
<td>18, 7, 22</td>
<td>&gt;0.25</td>
<td>NS</td>
</tr>
<tr>
<td>Carolina Wren (Thryothorus ludovicianus)</td>
<td>6, 0, 6</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Red-eyed Vireo (Vireo olivaceous)</td>
<td>68, 31, 93</td>
<td>&gt;0.10</td>
<td>NS</td>
</tr>
<tr>
<td>Black-and-white Warbler (Mniotilta varia)</td>
<td>4, 2, 5</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Ovenbird (Sieurus aurocapillus)</td>
<td>21, 5, 23</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Kentucky Warbler (Oporornis formosus)</td>
<td>6, 1, 6</td>
<td>&gt;0.25</td>
<td>NS</td>
</tr>
<tr>
<td>Summer Tanager (Piranga rubra)</td>
<td>11, 2, 13</td>
<td>**</td>
<td>*</td>
</tr>
<tr>
<td>Cardinal (Cardinalis cardinalis)</td>
<td>19, 4, 21</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Rufous-sided Towhee (Pipilo erythropthalmus)</td>
<td>8, 0, 8</td>
<td>*</td>
<td>*</td>
</tr>
</tbody>
</table>

* Same as in Table 1.
* The probability level represents all 4 years of censusing: *P < 0.05, **P < 0.01, NS = not significant.
* No significance level was estimated for species absent in one or more years.

268 m their densities increased to levels about equal to densities in the forest nearer the corridor (Fig. 2), and a regression of their densities from the edge to 488 m was not significant (P = 0.09 and 0.22, respectively). Therefore, there probably was not a significant edge effect. These two species had larger estimated territories than the other species. Therefore, analysis of their trends over the 488-m distance rather than the 268-m distance was probably more realistic. The significant results over the 268-
m distance may have resulted from shifts of the core areas of the near-edge territories toward the edge.

The Crested Flycatcher, Carolina Wren, Black-and-white Warbler, and Hooded Warbler were present in only 2 or 3 years and were not analyzed. In addition, many other species occurring less frequently in the forest plots (Kroodsma 1984) were not analyzed because of an insufficient quantity of data. Two pairs and several transient individuals of the Worm-eating Warbler (*Helmitheros vermivorus*), a species intolerant of forest fragmentation (Whitcomb et al. 1981, Tables 8–11), were observed only in deep forest more than 250 m from the corridor.

**DISCUSSION**

About 10 of the 13 or so bird species that have been shown to decline in forest fragments or show low tolerance to forest fragmentation (Bond 1957, Whitcomb et al. 1981) occurred in my study plots. Of these only the Ovenbird and Acadian Flycatcher appeared to be negatively affected by the presence of edge. The negative response of Ovenbirds to edge may help explain why this species is unable to persist even in forest islands that are much larger than its minimum territorial size (Galli et al. 1976, Forman et al. 1976, Whitcomb et al. 1981:166). Whitcomb et al. (1981: 166, 172) mention that the Worm-eating, Black-and-white, Kentucky, and Hooded warblers were also scarce in the vicinity of forest margins and may thus require forest islands considerably larger than their minimum territorial size. Of these species in my study, only the Kentucky (Fig. 2d) and Worm-eating warblers showed any indication of being less abundant near edge.

Other species that may be sensitive to forest fragmentation but which did not indicate a negative response to edges in my study include the Hairy Woodpecker, Blue-gray Gnatcatcher, Yellow-billed Cuckoo, Wood Thrush, and Scarlet Tanager (Whitcomb et al. 1981, Tables 8–11). These species' responses to forest fragmentation may therefore depend primarily on forest island size, island isolation, and other factors rather than on the effects of edge.

Cardinals, Summer Tanagers, and towhees were denser at the edges and apparently benefit from edges. However, making a conclusion on the value of edges to the cardinal and tanager is hampered by the additional occurrence of these species in the forest interior in this study as well as in other studies (e.g., Johnston and Odum 1956).

High levels of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Brittingham and Temple 1983) and predation (Gates and Gysel 1978) near edges are possible mechanisms for causing negative responses of bird density to edges. However, the relatively brief
existences, in the evolutionary time scale, of cowbird abundance in the eastern United States (Brittingham and Temple 1983) and of narrow man-made edges (Gates and Gysel 1978) suggest that other factors such as structural cues of vegetation were responsible for the observed negative responses of Acadian Flycatchers and Ovenbirds.

SUMMARY

Four breeding bird censuses were conducted with the territory-mapping method in two rectangular forested plots adjacent to power-line corridors in eastern Tennessee. The plots were subdivided into 20 or more strip transects parallel to the corridors. Density was estimated for each transect and plotted on distance from the corridor/forest edge. Plots for 22 bird species are presented. The plots were often characterized by distinct peaks and lows, indicating that territories tended to line up in rows parallel to the edge. The Acadian Flycatcher and Ovenbird were significantly denser (P < 0.05, 0.01, respectively) in forest interior. The Summer Tanager, cardinal, and towhee were denser (P < 0.05, 0.01, and 0.05, respectively) near the edge. Densities of the other species were not significantly associated with distance from the edge (P > 0.05).

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