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Defining Forest Fragmentation by Corridor Width: The Influence of Narrow Forest-Dividing Corridors on Forest-Nesting Birds in Southern New Jersey

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Abstract: *In studies of forest fragmentation, a fundamental inconsistency exists in the distance criterion used to define the discreteness of forest fragments. We examined three types of ubiquitous, narrow, forest-dividing corridors for effects that influence the relative abundance and community composition of forest-nesting birds. Fixed-radius (100-meter) point counts were conducted on 54 transects established along three width classes of corridors: unpaved roads (8 meters wide), paved roads (16 meters wide), and powerlines (23 meters wide). Transect locations were distributed equally among corridor edge, forest margin 100 meters from corridor edge, and forest interior 300 meters from corridor edge. Forest-interior species of Neotropical migrants had significantly reduced relative abundances on edge transects along 16- and 23-meter corridors, compared with 8-meter corridors and with forest interior points along all three corridor-width classes. At a landscape scale, the consequences of*

Definiendo la fragmentación del bosque en base al ancho de los corredores: Influencia de los corredores divisores del bosque angostos sobre los pájaros nidificantes del bosque en el sudeste de Nueva Jersey

Resumen: *En los estudios de fragmentación del bosque existe una inconsistencia fundamental en el criterio de la distancia utilizada para definir la delimitación de los fragmentos del bosque. Examinamos tres tipos de corredores angostos muy comunes divisores del bosque, para investigar los efectos que influyen la abundancia relativa y la composición de la comunidad en los pájaros nidificantes del bosque. Conteos puntuales de radio fijo (100 m) fueron llevados a cabo en 54 transectos establecidas a lo largo de 3 clases de corredores de distinto ancho: carreteras sin pavimento (8 m de ancho), carreteras pavimentadas (16 m de ancho) y líneas de alto voltaje (23 m de ancho). La localización de los transectos fue distribuida en forma equitativa entre los bordes de los corredores; los márgenes del bosque, a 100 m del borde del corredor y el interior del bosque, a 300 m del borde del corredor. Las especies de migrantes neotropicales del interior del bosque, tuvieron una abundancia relativa significativamente menor en los bordes de los transectos, a lo largo de los corredores de 16 y 23 m, que en los corredores de 8 m y que en los puntos del interior del*

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apparently small reductions in forest area by the presence of narrow forest-dividing corridors may be cumulatively significant for abundances of forest-interior species. Brown-headed Cowbirds were more abundant than 20 of 21 forest-interior Neotropical migrants. We found surprisingly high abundances of cowbirds associated with narrow forest-dividing corridors, especially those with mowed grass. Corridor widths as narrow as 8 meters produce forest fragmentation effects in part by attracting cowbirds and nest predators to corridors and adjacent forest interiors. The most serious implication of this study is that narrow forest-dividing corridors may function as ecological traps for forest-interior Neotropical migrants. We suggest that these widespread corridors may be inconspicuous but important contributors to declines of forest-interior nesting species in eastern North America.

Introduction

Extensive fragmentation of formerly contiguous forest throughout much of eastern North America and the accelerating loss of tropical wintering habitats are viewed as the primary contributors to recent declines seen among many forest bird species (Hutto 1988; Terborgh 1989; Robbins et al. 1989a; 1992). Forest fragmentation creates conditions that increase the exposure of forest-nesting birds to nest predation and brood parasitism (Gates & Gysel 1978; Brittingham & Temple 1983; Wilcove 1985; Temple & Cary 1988; Yahner 1988; Yahner & Scott 1988; Böhning-Gaese et al. 1993) and produces widespread reproductive failure (Mayfield 1977; Askins et al. 1990; Robinson 1992). Forest-nesting Neotropical migrants seem especially vulnerable because many possess characteristics (open cup nests, placement of nests near or on the ground, lack of defense mechanisms against brood parasitism) that increase their susceptibility to nest predation and brood parasitism, and they compensate poorly for reproductive failure by generally producing only a single, relatively small, clutch per season (Greenberg 1980; Ehrlich et al. 1988).

Several regional studies of avian community composition in forest patches have provided enough consistent data to identify species that can be classified as forest-interior birds—those requiring large blocks of contiguous forest for successful breeding (Galli et al. 1976; Whitcomb et al. 1981; Lynch & Whigham 1984; Robbins

et al. 1989b). Despite the use of different procedures and analytical techniques, all these studies correlated declines in abundance and species richness of forest-interior bird species with declines in forest patch area (Askins et al. 1990). In studies of forest fragmentation, a fundamental inconsistency exists in the distance criterion used to define the discreteness of forest fragments. Some studies define a tract of forest as discrete if it is separated from other forests by at least 10 meters of open land (Lynch & Whigham 1984; Freemark & Merriam 1986; Askins et al. 1987). Most studies, however, do not define a tract as discrete unless it is separated from other forests by at least 100 meters of open land (Galli et al. 1976; Whitcomb et al. 1981; Ambuel & Temple 1983; Harris & Wallace 1984; Hayden et al. 1985; Robbins et al. 1989b; Gibbs & Faaborg 1990). The principal difference between these two definitions is that the latter usually does not include narrow rights-of-way such as roads and powerline corridors as sources of forest fragmentation. The primary objective of our study was to examine whether narrow forest-dividing corridors produce effects associated with forest fragmentation that influence the relative abundance and community composition of forest-nesting Neotropical migrants and edge-associated bird species. A secondary objective was to evaluate our results for their implications in on-road versus off-road forest surveys of avian relative abundance and species composition.

Methods

Study Area and Field Methods

Field work was conducted in southern New Jersey from early April through mid-July 1991 in Cumberland and Cape May Counties (Fig. 1). Eighteen roadside transects, each 1.6 km in length, were established along narrow forest-dividing corridors that bisected mature, contiguous forest. Contiguous forest was defined as forested area greater than 1000 ha and unbroken by any other rights-of-way or development. Plots for transect locations were selected randomly from candidate sites determined from 7.5-minute photoquads taken in 1986.

Six roadside transects were established along each of the following three types of forest-dividing corridors representing three different classes of corridor widths: (1) unpaved roads, (2) paved secondary roads, and (3) powerline rights-of-way having unpaved vehicular access roads. Four observers were alternated among roadside transects, and all three types of corridors were surveyed within the same week to the extent allowed by observer availability. For each roadside transect, six edge points were established at 322-meter intervals. At each edge point, corridor width was measured from treeline to treeline with a spooled meter tape. Treeline was defined as the line of tree trunks along the forest edge. Corridor vegetation was classified as grass or as

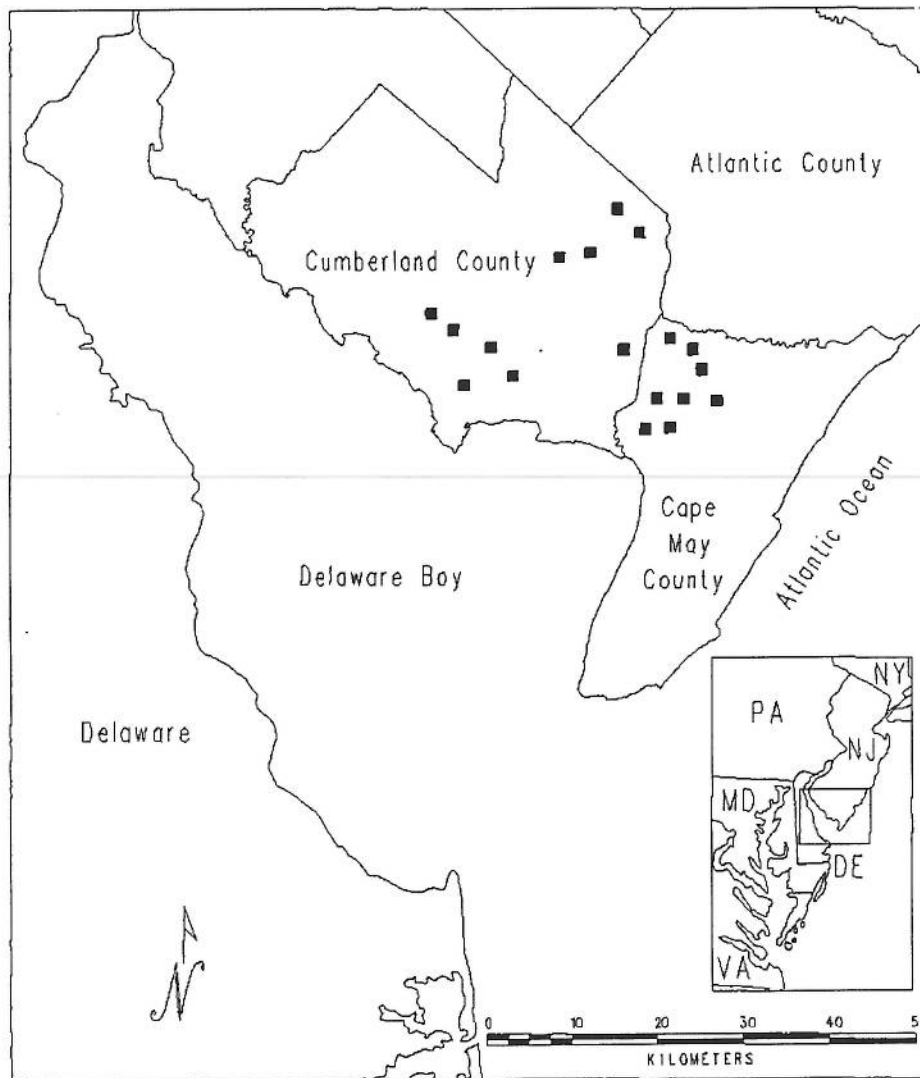


Figure 1. Regional map of Middle Atlantic States and southern New Jersey showing locations of 18 avian survey transects within contiguous forest tracts of Cumberland and Cape May counties.

shrub/sapling if either dominated a total area of coverage at least 4 meters in width.

Parallel to each roadside transect, two forest transects were established by measuring a fixed distance from each corridor-edge point perpendicularly into the forest (Fig. 2). Three "forest margin" points were established 100 meters from the edge, and three "forest interior" points were established 300 meters from the edge. Margin and interior points were established alternately along points of each roadside transect toward the larger contiguous forest. Forest transects were surveyed within three days of the corresponding roadside transect survey, weather permitting. Surveys of forest

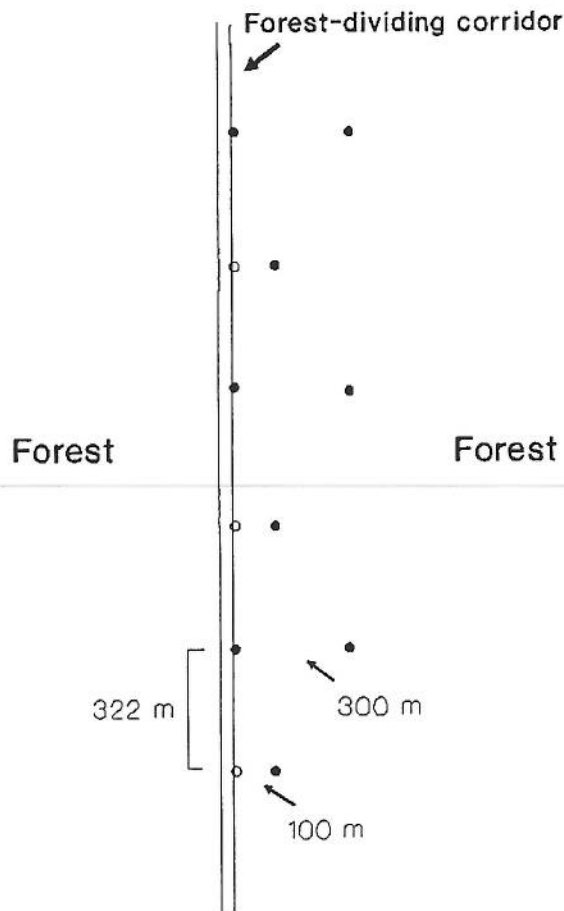


Figure 2. Sampling design of 1.6-km transects for point-count surveys conducted in forest interior (300 meters from corridor edge), forest margin (100 meters from corridor edge), and on forest edge along a narrow forest-dividing corridor. Forest-margin points are independent of corridor-edge points designated by shaded circles but overlap with edge points designated by unshaded circles (see text).

transects always followed roadside transects to minimize disturbance to the birds.

Habitat was classified as oak-pine forest or hardwood swamp forest at roadside points and at forest points. In the oak-pine forest, dominant tree species were white oak (*Quercus alba*), black oak (*Q. velutina*), pitch pine (*Pinus rigida*), Virginia pine (*P. virginiana*), and American holly (*Ilex opaca*). Dominant shrubs were lowbush blueberry (*Vaccinium vacillans*) and mountain laurel (*Kalmia latifolia*). In the hardwood swamp forest, dominant tree species were red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), sweetgum (*Liquidambar styraciflua*), and American holly. Dominant shrubs were highbush blueberry (*V. corymbosum*) and sweet pepperbush (*Clethra alnifolia*). The herbaceous layer was largely absent from both forest types.

Twenty-minute, fixed-radius (100-meter) point counts, modified from Blondel et al. (1981) were conducted three times at each point approximately three weeks apart, for a total of 648 point-count surveys. Each survey point covered an area of 3.14 ha; the total area of independent points surveyed was approximately 509 ha. All forest-margin points were independent of forest-interior points, all corridor-edge points were independent of forest-interior points, and all forest-margin points were independent of their alternating corridor-edge points (Fig. 2). Forest-margin points overlapped in area with their closest corridor edge points (unshaded circles in Fig. 2) and were not independent; these edge points were used only in comparisons among edge transects. Thus sampling effort was equal for all statistical comparisons among different types of transects (three independent points per transect for edge, margin, and interior).

Surveys at each point were alternated between early morning (sunrise to 3 hours after sunrise) and late morning (3 hours after sunrise to 6 hours after sunrise) periods. Surveys were not conducted on days with precipitation or strong winds. One minute of silence preceded the beginning of each 20-minute point count to reduce the effects of observer disturbance on survey results. Each 20-minute point count was divided into 5-minute intervals; every 5 minutes the locations of all individuals detected within 100 meters of the point were mapped following international standard mapping methods (International Bird Census Committee 1970). In addition, the number of passing vehicles per 5-minute interval at each roadside transect was recorded.

To minimize double counting of territorial birds, individuals of the same species mapped within 50 meters of each other were counted as one individual unless recorded as counter-singing or aggressively-interacting males. The highest value across visits was used as the estimate of relative abundance of a species at a point (Robbins et al. 1989b). Only breeding species were included in analyses, as determined by presence, behavior

(aggressive interactions, countersinging, etc.), and past breeding records (Leck 1984). Black-billed Cuckoo (*Coccyzus erythrophthalmus*) and Yellow-billed Cuckoo (*C. americanus*) were combined as cuckoo species (*Coccyzus* spp.) because similar vocalizations did not allow reliable differentiation. Breeding species were classified as forest-interior Neotropical migrants (based on previous studies indicating sensitivity to reduced forest area or to increased forest isolation), other forest-nesters, nest predators, or brood parasites. Other forest-nesters with few detections were excluded from analyses because of Poisson-like distributions. All April data were excluded from statistical analyses to minimize the potential for confounding migrants with territorial birds.

Data Analysis

Independence of forest type from corridor type and distance from corridor edge were tested with chi-square analyses. A significant chi-square value would infer non-independence and necessitate stratification by habitat in comparisons among corridor types or distances from corridor edge. Differences in relative frequencies of each species between the two forest types were tested among independent survey points with chi-square goodness-of-fit tests, or with binomial tests if expected frequencies were small (Zar 1984).

To determine whether the number of birds detected by sound was significantly affected by vehicular disturbance, we examined Pearson correlations between the number of birds detected by sound and the number of passing vehicles recorded during 5-minute intervals on the transect with the highest traffic volume.

Differences among corridor types were tested with Hierarchic ANOVA to determine if differences in relative abundance by corridor type (treatment groups) were significant over and above differences among transects (subgroups). Only corridor edge transects were included in the hierarchic design because differences in relative abundance by distance from corridor edge could not be accommodated in the hierarchic model (subgroups in hierarchic designs must be random [Sokal & Rohlf 1981] but distances from corridor edge were chosen deliberately). Assumptions of normality and homogeneous variances were tested by examination of normal probability plots and by F_{max} -tests ($p < 0.05$). Species that had nonnormal distributions or heterogeneous variances after transformation attempts ($\log_{10} [Y + 1]$ and $\sqrt{Y + 3/8}$) were analyzed nonparametrically with Kruskal-Wallis ANOVA. The estimated number of territories for each species was totaled for each roadside transect, and the transects were compared by corridor type to reduce the number of ties (Sokal & Rohlf 1981).

Differences in relative abundance between grass and

shrub/sapling edge points were tested for avian nest predators and cowbirds by two-tailed t -tests using separate variance estimates (Zar 1984; SPSS, Inc., 1988).

Differences in relative abundance between forest edge and interior points were tested for species groups by paired t -tests matching forest interior points with their corresponding perpendicular roadside points for each corridor type. We used Mann-Whitney U -tests to examine forest-edge avoidance or attraction by comparing the relative abundances of species groups between forest margin points (encompassing 0–200 meters from edge) and forest interior points (encompassing 200–400 meters from edge) for each corridor type. Kruskal-Wallis ANOVA was used to test for differences among forest-margin and forest-interior points across corridor types.

Results

Forest type was independent of corridor type ($X^2 = 3.24$, $df = 2$, $p = 0.20$) and of distance from corridor edge ($X^2 = 3.85$, $df = 2$, $p = 0.15$). Thus, for further analyses, we concluded that the proportion of forest types among corridor types and among distances from corridor edge was not significantly different.

There was no significant correlation between the number of birds detected by sound and the number of passing vehicles per 5-minute interval ($n = 48$, $r = -0.02$, $p = 0.46$). Thus, vehicular disturbance among types of corridors was not a confounding factor in this study.

Forest-dividing corridor widths averaged approximately 8 meters for unpaved roads, 16 meters for paved secondary roads, and 23 meters for powerline corridors (Table 1), and differed significantly among corridor types (one-way ANOVA, $df = 17$, $p < 0.001$; Duncan Multiple Range Test, $p < 0.05$ for all pairwise comparisons).

Of the 42 species included in our analyses, Brown-headed Cowbirds were more than twice as abundant as all avian nest predators combined, and were more abundant than 20 of the 21 forest-interior Neotropical migrants (Table 2).

Based on 162 independent survey points, 10 species of forest-interior Neotropical migrants were present on

Table 1. Comparative widths (m) of three types of narrow forest-dividing corridors in forests of southern New Jersey.^a

Corridor Type	$\bar{x} \pm SE^b$	Minimum	Maximum
Unpaved road	8.3 \pm 0.2	6.2	11.2
Paved road	16.3 \pm 0.5	10.9	21.8
Powerline	22.5 \pm 1.2	13.3	41.0

^a $n = 36$ points for each corridor type.

^b All means differ significantly from each other (Duncan Multiple Range Test, $p < 0.05$).

Table 2. Relative abundances of species at independent survey points and proportion of points in each habitat type at which each species was detected.^a

Species	Abundance (n = 162)	Forest Type ^b	
		Oak-Pine Forest (n = 123)	Hardwood Swamp (n = 39)
Ovenbird (<i>Seiurus aurocapillus</i>)	565	1.00	0.97
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	316	0.98	0.67
Pine Warbler (<i>Dendroica pinus</i>)	281	0.98	0.77
Brown-headed Cowbird (<i>Molothrus ater</i>)	233	0.81	0.82
Carolina Chickadee (<i>Parus carolinensis</i>)	162	0.75	0.51
Common Yellowthroat (<i>Geothlypis trichas</i>)	137	0.47	0.64
Wood Thrush (<i>Hylocichla mustelina</i>)	122	0.39	0.72**
Tufted Titmouse (<i>Parus bicolor</i>)	118	0.57	0.64
Black-and-white Warbler (<i>Mniotilta varia</i>)	115	0.47	0.69
Eastern Wood-Pewee (<i>Contopus virens</i>)	106	0.61	0.28*
Great Crested Flycatcher (<i>Myiarchus crinitus</i>)	102	0.52	0.39
Gray Catbird (<i>Dumetella carolinensis</i>)	96	0.49	0.39
Cuckoo species (<i>Coccyzus</i> spp.)	93	0.46	0.49
Red-eyed Vireo (<i>Vireo olivaceus</i>)	76	0.24	0.54**
White-eyed Vireo (<i>Vireo griseus</i>)	69	0.21	0.56***
Prairie Warbler (<i>Dendroica discolor</i>)	67	0.30	0.23
Blue Jay (<i>Cyanocitta cristata</i>)	66	0.39	0.36
Blue-gray Gnatcatcher (<i>Poliophtila caerulea</i>)	65	0.31	0.41
Scarlet Tanager (<i>Piranga olivacea</i>)	58	0.32	0.21
Blue-winged Warbler (<i>Vermivora pinus</i>)	54	0.31	0.21
Mourning Dove (<i>Zenaidura macroura</i>)	50	0.30	0.13
Northern Flicker (<i>Colaptes auratus</i>)	46	0.30	0.13
Red-bellied Woodpecker (<i>Melanerpes carolinus</i>)	44	0.28	0.21
American Robin (<i>Turdus migratorius</i>)	42	0.19	0.21
Acadian Flycatcher (<i>Empidonax virens</i>)	35	0.10	0.39***
Downy Woodpecker (<i>Picoides pubescens</i>)	29	0.19	0.13
American Crow (<i>Corvus brachyrhynchos</i>)	28	0.16	0.15
Brown Thrasher (<i>Toxostoma rufum</i>)	27	0.17	0.13
Hooded Warbler (<i>Wilsonia citrina</i>)	26	0.07	0.26**
White-breasted Nuthatch (<i>Sitta carolinensis</i>)	25	0.16	0.05
Prothonotary Warbler (<i>Protonotaria citrea</i>)	21	0.02	0.26***
Northern Parula (<i>Parula americana</i>)	18	0.06	0.15
Yellow-throated Warbler (<i>Dendroica dominica</i>)	17	0.01	0.18***
Common Grackle (<i>Quiscalus quiscula</i>)	16	0.07	0.10
American Redstart (<i>Setophaga ruticilla</i>)	14	0.05	0.13
Summer Tanager (<i>Piranga rubra</i>)	14	0.09	0.03
Worm-eating Warbler (<i>Helminthos vermivorus</i>)	10	0.03	0.10
Fish Crow (<i>Corvus ossifragus</i>)	5	0.03	0.03
Kentucky Warbler (<i>Oporornis formosus</i>)	4	0.00	0.08*
Yellow-throated Vireo (<i>Vireo flavifrons</i>)	3	0.02	0.00
Northern Waterthrush (<i>Seiurus noveboracensis</i>)	1	0.00	0.03

^a n = number of independent survey points.^b Significantly disproportionate occurrence between habitats (Chi-square test or binomial test; *p < 0.05, **p < 0.01, ***p < 0.001).

fewer than 30 territories each. In contrast, the Ovenbird was the most abundant species and was detected at virtually every point in both forest types. Of the remaining forest-interior Neotropical migrants, seven (plus the White-eyed Vireo, a scrub-dwelling Neotropical migrant) were detected at a significantly greater proportion of points in hardwood swamp forest than in oak-pine forest (Table 2). Among Neotropical migrants, only Eastern Wood-Pewee occurred significantly more frequently in oak-pine forest (Table 2). Mourning Dove, Northern Flicker, and White-breasted Nuthatch showed marginally greater occurrences than expected ($p <$

0.10) in oak-pine forest (Table 2). In contrast to forest-interior species, no species of other forest-nester occurred significantly more frequently in hardwood swamp forest.

Forest-interior Neotropical migrants as a group, and four of the nine forest-interior species that could be tested parametrically, had significantly greater relative abundances on edge transects along unpaved corridors than along paved road or powerline corridors (Table 3). Among forest-interior Neotropical migrants tested non-parametrically, none differed significantly among corridor types, even when grouped and tested parametrically

Table 3. Differences in relative abundances of birds on forest-edge transects along three types of forest-dividing corridors: unpaved roads, paved roads, and powerline corridors.^a

Species	p	Differences among Corridors ^b
Forest-Interior Neotropical Migrants ^c	0.000 ^d	unpaved > paved or powerline
Cuckoo spp.	0.560 ^d	
Eastern Wood-Pewee	0.022 ^d	unpaved > powerline
Acadian Flycatcher	0.396 ^e	
Great Crested Flycatcher	0.419 ^d	
Blue-gray Gnatcatcher	0.211 ^d	
Wood Thrush	0.030 ^d	unpaved > paved or powerline
Red-eyed Vireo	0.813 ^d	
Yellow-throated Warbler	0.873 ^e	
Worm-eating Warbler	0.368 ^e	
Black-and-white Warbler	0.000 ^d	unpaved > paved or powerline
Northern Parula	0.283 ^e	
Prothonotary Warbler	0.765 ^e	
Ovenbird	0.025 ^d	unpaved > powerline
American Redstart	0.363 ^e	
Hooded Warbler	0.301 ^e	
Scarlet Tanager	0.095 ^d	
Summer Tanager	0.630 ^e	
Other Forest Nesters	0.741 ^d	
Mourning Dove	0.204 ^d	
Northern Flicker	0.154 ^d	
Red-bellied Woodpecker	0.654 ^d	
Downy Woodpecker	0.114 ^d	
Tufted Titmouse	0.607 ^d	
Carolina Chickadee	0.691 ^d	
White-breasted Nuthatch	0.810 ^d	
American Robin	0.376 ^d	
Gray Catbird	0.818 ^d	
Brown Thrasher	0.857 ^d	
White-eyed Vireo	0.492 ^d	
Prairie Warbler	0.072 ^d	
Pine Warbler	0.581 ^d	
Common Yellowthroat	0.667 ^d	
Blue-winged Warbler	0.453 ^d	
Rufous-sided Towhee	0.141 ^d	
Avian Nest Predators	0.118 ^d	
Blue Jay	0.344 ^d	
American Crow	0.461 ^d	
Fish Crow	0.111 ^e	
Common Grackle	0.239 ^d	
Brood Parasite		
Brown-headed Cowbird	0.025 ^d	paved > unpaved or powerline

^a n = 108 point-count locations.

^b Duncan Multiple Range Test, $p < 0.05$.

^c Yellow-throated Vireo, Kentucky Warbler, and Northern Waterthrush were not detected at forest edge points.

^d Hierarchic ANOVA, $df = 2$.

^e Kruskal-Wallis test, $n = 18$.

(Hierarchic ANOVA, $F = 0.11$, $df = 2$, $p = 0.90$). Yellow-throated Vireo, Kentucky Warbler, and Northern Waterthrush were not detected on edge transects.

Brown-headed Cowbirds were significantly more abundant on forest-edge transects along paved secondary roads than along unpaved roads or powerline corridors (Table 3). None of the other forest-nester species or nest predators differed significantly ($p > 0.05$) in relative abundance on forest-edge transects among corridor types (Table 3).

Unpaved roads had only trace amounts of vegetation within their corridors, and all of the points along paved secondary roads consisted of maintained shoulders of mowed grass. Among corridor types, only powerline corridors contained both shrub/sapling and mowed grass vegetation. On edge transects of powerline corridors, Brown-headed Cowbirds had greater relative abundance ($p < 0.05$) at points with mowed grass, and avian nest predators had greater relative abundance ($p < 0.01$) at points with shrub/sapling vegetation (Fig. 3).

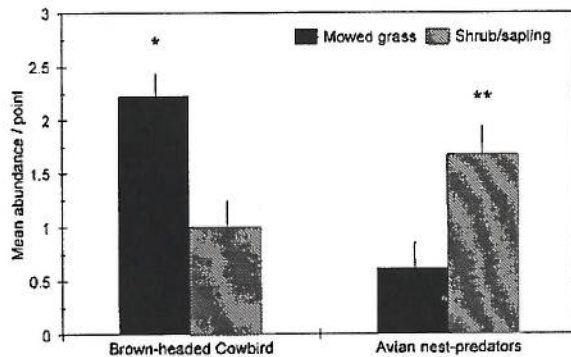


Figure 3. Comparison of mean abundances (\pm SE) per point for Brown-headed Cowbirds and avian nest predators at mowed grass ($n = 22$) and shrub/sapling ($n = 14$) points within powerline corridors (two-tailed t -test, (* $p < 0.05$, ** $p < 0.01$).

due to higher abundances of crows ($p = 0.05$) and grackles ($p = 0.03$, Mann-Whitney U -tests).

The overall relative abundance of forest-interior Neotropical migrants did not differ significantly between forest-edge and interior points along unpaved roads (Table 4), but was significantly greater in the forest interior than at edge points along paved secondary roads ($p < 0.01$) and along powerline corridors ($p = 0.05$; Table 4). Among these species, Acadian Flycatcher, Wood Thrush, Yellow-throated Vireo, Yellow-throated Warbler, Worm-eating Warbler, Black-and-white Warbler, Kentucky Warbler, Prothonotary Warbler, Ovenbird, American Redstart, and Hooded Warbler exhibited a consistent pattern of greater relative abundance on interior-forest points than on edge points along the two wider types of corridors, but the relative rarity of most of these species resulted in too few paired differences to test statistically (Zar 1984).

Other forest nesters as a group showed no significant differences ($p > 0.05$) in relative abundance between forest-edge and forest-interior points along any of the three corridor types (Table 4). Avian nest predators were significantly more abundant ($p < 0.05$) at forest-edge points than at forest-interior points along powerline corridors, and cowbirds were significantly more abundant ($p < 0.01$) at edge points along paved roads

(Table 4). Relative abundances of cowbirds and avian nest predators were equivalent at powerline edge points, but cowbird abundance was roughly double that of avian nest predators on forest-edge points along the two narrower width classes of corridors (Table 4).

Comparison of group relative abundances at forest-margin and interior points within corridor types revealed no statistically significant differences ($p > 0.05$) for forest-interior Neotropical migrants, other forest-nesting birds, avian nest predators, or cowbirds (Fig. 4). Relative abundances among forest-interior and forest-margin points across corridor types likewise indicated no significant differences (Kruskal-Wallis ANOVA, $p > 0.10$) for any group, although avian nest predators appeared to be distinctly more variable than other groups (Fig. 4).

Discussion

Narrow Corridors as Sources of Fragmentation

Although not viewed generally as sources of forest fragmentation, narrow forest-dividing corridors do affect the distribution and abundance of birds in ways that are associated typically with the effects of forest fragmentation. Relative abundances of forest-interior Neotropical migrants were reduced significantly on edge transects of corridors 16–23 meters in width but not along corridors only 8 meters wide. The relative abundance of these species as a group did not differ between forest-edge and interior points along 8-meter corridors, but it was significantly lower at forest-edge compared with interior points along 16- and 23-meter corridors.

Do these differences result from edge avoidance by forest interior species? We addressed this question directly by comparing forest-margin and forest-interior points and found that, as a group, forest-interior species did not avoid forested areas between corridor edges and 200 meters into the forest along any of the three types of corridors that we examined. We therefore infer that most of these species do not perceive narrow forest-dividing corridors as sources of forest fragmentation. Instead, their decreased abundances are a consequence of the absence of forest habitat within corridors, reflected by reduced forest area within survey point radii on corridor-edge transects. Forest-edge survey points

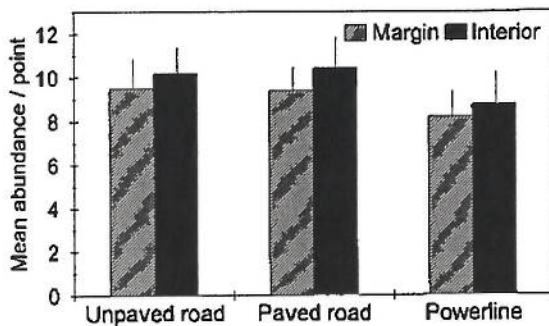
Table 4. Mean relative abundances (\pm SE) of species groups on forest-edge and forest-interior points.^a

Species	Unpaved Roads		Paved Roads		Powerlines	
	Edge	Interior	Edge	Interior	Edge	Interior
Forest-Interior Neotropical Migrants	10.3 \pm 0.7	10.2 \pm 1.1	8.0 \pm 1.0	10.4 \pm 1.4**	6.8 \pm 0.8	8.7 \pm 1.3*
Other Forest Nesters	10.2 \pm 0.8	8.2 \pm 0.8	10.7 \pm 1.2	9.8 \pm 1.1	9.9 \pm 0.6	9.3 \pm 0.7
Avian Nest Predators	1.1 \pm 0.2	0.8 \pm 0.2	1.1 \pm 0.4	1.2 \pm 0.3	1.5 \pm 0.2	0.5 \pm 0.2*
Brown-headed Cowbird	2.0 \pm 0.4	1.2 \pm 0.2	2.1 \pm 0.3	0.9 \pm 0.1**	1.5 \pm 0.3	1.3 \pm 0.3

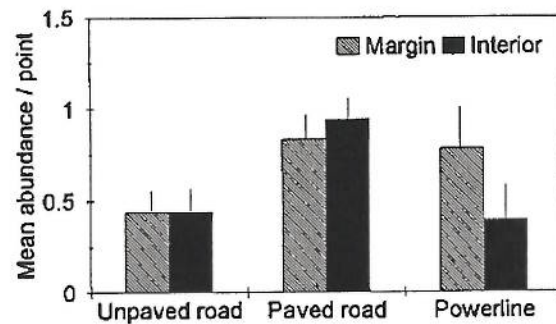
^a $n = 18$ paired points; paired t -test.

* $p \leq 0.05$, ** $p < 0.01$.

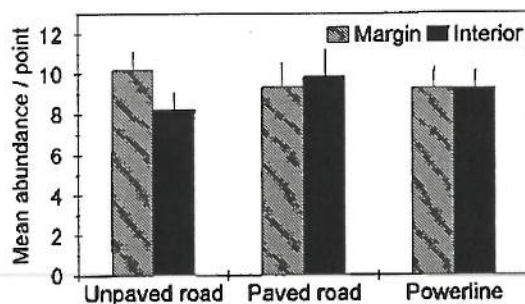
Forest-interior Neotropical migrants



Avian nest-predators



Other forest-nesters



Brown-headed Cowbird

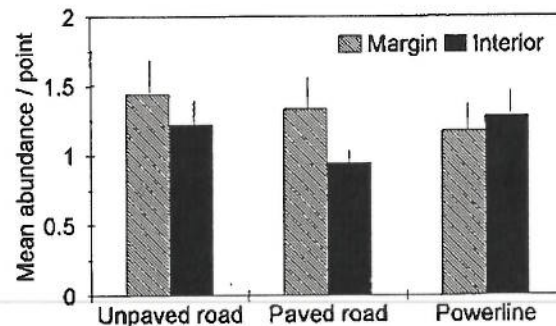


Figure 4. Comparison of species abundances ($\bar{X} \pm SE$) between points encompassing distances of 0–200 meters from corridor edge (forest-margin points) and points encompassing 200–400 meters from corridor edge (forest-interior points) for each corridor type (Mann-Whitney U-test; $n_1, n_2 = 18$; no significant differences, $p > 0.05$).

located along corridors of 8, 16, and 23 meters in width have approximately 5, 10, and 15% less forested area respectively than comparable survey points located in the forest interior. Our results indicate that a 5% reduction in total forest area is below the threshold of forest loss necessary to produce a reduction in the relative abundance of forest-interior nesting species when considered as a group. At a landscape scale, the ubiquitous distribution of narrow, paved, secondary roads and powerline or railroad rights-of-way through forested areas raises the prospect of significant cumulative reduction in the potential abundance of forest-interior species.

In contrast, the relative abundances of other forest-nesting species not associated exclusively with forest interiors were unaffected by the presence of narrow corridors. None of these species differed in relative abundance on edge transects among the three width classes of corridors, and their relative abundance as a

group did not differ between edge and forest-interior points.

The relative abundances of avian nest predators also did not differ significantly at forest-edge points among the three width classes of narrow corridors, although some species were more abundant where shrub/sapling vegetation was present within corridors. Cowbirds, which were more than twice as abundant as all avian nest predators combined, had greater relative abundances than nest predators at forest-edge points along 8-meter and 16-meter corridors, and they exhibited significantly elevated abundances associated with the presence of mowed grass in the corridors.

Our results suggest that small-width, forest-dividing corridors may create "ecological traps" (Gates & Gysel 1978) for forest-interior Neotropical migrants. These species did not avoid the forest margins along corridors 8–23 meters wide, but these corridors differentially at-

tracted avian nest predators and cowbirds. Hence, forest-interior songbirds near these corridor edges are likely subjected to increased levels of predation and brood parasitism (Mayfield 1965; Gates & Gysel 1978; Chasko & Gates 1982; Brittingham & Temple 1983). The ecological-trap hypothesis first proposed by Gates and Gysel (1978) suggested that passerines are attracted to the vegetative diversity of edge habitats but experience greater predator activity at the edge. Their hypothesis, however, pertained primarily to predation and cowbird parasitism on edge species nesting in or near relatively wide (more than 45 meters), nonforested zones. Our results strongly suggest that along forest-dividing corridors of small width, forest-interior Neotropical migrants may be the primary victims in an ecological trap scenario, pertaining especially to brood parasitism if areas of mowed grass are present at the forest edge. Gates and Giffen (1991) described a potentially analogous scenario for forest-interior species along forest-stream ecotones.

We found that cowbirds (in contrast to avian nest predators) were distressingly common even in forest interiors. Although cowbirds had significantly greater relative abundance at edge points along paved roads than at corresponding forest points, their relative abundance at forest-margin and forest-interior points varied little among corridor width classes. Cowbirds preferentially selected corridors with areas of mowed grass, where both sexes often foraged, and powerline poles on which males displayed. The best strategy for a female cowbird would be to search for nests as close as possible to feeding and breeding areas, thus expending the least amount of time and energy for acquiring food and mates and allowing more time for locating host nests and laying eggs (Brittingham & Temple 1983). With an apparently abundant supply of potential host nests near the forest edge, grassy, forest-dividing corridors appear to provide optimal habitat for cowbirds. Considering that the cowbird was the fourth most abundant species in our study, was present at more than 80% of all survey points, and was more abundant than 20 of the 21 forest-interior Neotropical migrants, the potential impact of the Brown-headed Cowbird in southern New Jersey may be extraordinary. Thus, forest-dividing corridors of small width, especially when maintained with areas of short grass, may be important indirect factors contributing to the population declines of forest-interior Neotropical migrant birds in eastern North America.

What constitutes a sufficient break in continuous habitat to define a discrete forest fragment? Askins et al. (1987) viewed a 10-meter criterion as essential for delineating forest tracts because of the complex mosaic of closely adjacent forests that characterizes much of southeastern Connecticut. With similar reasoning, the 10-meter criterion is also most appropriate for delineating forest tracts in southern New Jersey. Such a conser-

vative definition of isolation, however, could have the effect of underestimating the functional area of forest tracts as perceived by birds. Lynch and Whigham (1984) explained that while they would have treated a 100-ha tract bisected by a roadway as two 50-ha fragments, some birds may respond to such a tract as continuous forest.

The results from our study indicate that forest-interior Neotropical migrants do not avoid forest margins along corridors that are 8–23 meters in width. Other studies (Ferris 1979; Chasko & Gates 1982; Kroodsma 1984) indicate that edge avoidance by forest-interior species does occur along wider (more than 50 meters) forest-dividing corridors.

There is no compelling reason to assume that all species of forest birds necessarily perceive fragments on the basis of the same defining criterion. Likewise, the converse may also hold: not all edge species may perceive edge habitat as such. The complete absence of European Starlings from our study area could be interpreted as indicative of the intact-forest character of the study area, because starlings typically avoid forest interiors (Ehrlich et al. 1988). The abundance of cowbirds, however, implies that these two edge species view fragmentation (and what constitutes suitable edge) differently. Our data on cowbird abundance suggest that corridor widths as narrow as 8 meters lie above the threshold width perceived by cowbirds as the criterion for edge—and, therefore, fragmented rather than intact—habitat. It seems likely to us that a cowbird's perception of edge is based on a variety of cues. For example, would corridors less than 8 meters wide with significant amounts of grass be attractive to cowbirds? Would cessation of mowing along maintained corridors reduce the local abundance of cowbirds and increase host productivity in forests along narrow forest-dividing corridors? Such questions present fertile areas for further research, with important management implications for cowbirds and for forest-interior Neotropical migrant landbirds.

On-Road Versus Off-Road Point Counts

For monitoring breeding populations of migratory birds, Askins et al. (1990) noted that only a broad regional approach such as the annual Breeding Bird Survey (Reid & Droege 1988; Robbins et al. 1989a; Droege 1990; Dobkin 1994) can overcome the problem of site-specific perturbations often present in long-term local studies (Hall 1984; Holmes & Sherry 1988; Leck et al. 1988; Wilcove 1988). This approach necessitates the use of time-efficient roadside surveys, which has generated much interest in their use for population monitoring and management (Ralph et al. 1994).

Our results lead us to caution that estimates of avian relative abundances derived from roadside surveys

along forest-dividing corridors as narrow as 16 meters are not directly comparable to off-road surveys. The precise threshold width for comparability between on- and off-road surveys likely will vary regionally with avian species and vegetation composition.

In contrast, the species composition of forest-interior avifaunas derived from roadside surveys along narrow forest-dividing corridors should be nearly comparable to forest-interior surveys. Differences in species composition will be relatively small and will arise largely from sampling error. The absence of some rare forest-interior species from roadside surveys (such as Yellow-throated Vireo, Kentucky Warbler, and Northern Waterthrush in our study) inevitably will occur due to chance alone.

Further Implications for Conservation and Management

The mixed oak-pine forest of southern New Jersey is the largest remaining expanse of forest on the Atlantic coastal plain between Virginia and Maine (Forman 1979; Collins et al. 1988), yet breeding populations of many forest-interior Neotropical migrants appear to be very small. At least 10 of the 21 species in this group occurred so infrequently as to be considered rare in the areas we studied.

In contrast, forest-nesting species that breed in canopy gaps or along forest margins (Kroodsma 1982; Ehrlich et al. 1988) were numerous and included four of the five most abundant species. Such species are not so adversely affected by forest fragmentation and the resulting loss of contiguous forest; most are short-distance migrants not subject to tropical deforestation pressures, and many of these species are uncommonly or rarely parasitized by cowbirds (Friedmann & Kiff 1985; Ehrlich et al. 1988).

The mature oak-pine forests of southern New Jersey are characterized by relatively low productivity (Forman 1979), with trees that do not attain the large stature and complete canopy closure of typical upland and floodplain eastern deciduous forests (Collins et al. 1988). It is perhaps not surprising that forest-interior Neotropical migrants disproportionately selected hardwood swamp forest over oak-pine forest. Approximately 75% of these species had greater relative frequencies in hardwood swamp forest, and some, such as Acadian Flycatcher, Hooded Warbler, Northern Parula, Yellow-throated Warbler, Prothonotary Warbler, Northern Waterthrush, and Kentucky Warbler, appeared to depend heavily on hardwood swamp forest for breeding territories. Our data demonstrate that hardwood swamp forest has greater conservation value than oak-pine forest for forest-interior Neotropical migrants in southern New Jersey, in addition to its importance for threatened raptors (Laidig & Dobkin unpublished data). Destruction of hardwood swamp forest permitted under current wetland mitigation regulations (New Jersey Administra-

tive Code 7:7A 1.0 et seq.) could adversely affect these populations, as the development of forested wetlands in exchange for the restoration of coastal wetlands results in net loss of critical breeding-season habitat for forest-interior Neotropical migrants.

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