Ecological Applications, 11(6), 2001, pp. 1680–1691

EFFECTS OF GROUP-SELECTION OPENING SIZE ON BREEDING BIRD HABITAT USE IN A BOTTOMLAND FOREST

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Abstract. An increase in timber removals from southern bottomland forests of the United States has been predicted, warranting investigations of the effects of silvicultural alternatives on avian breeding habitat. We studied the effects of creating group-selection openings (man-made canopy gaps) of various sizes on breeding bird habitat use in a bottomland hardwood forest in the Upper Coastal Plain of South Carolina, USA. We used spot mapping and mist netting to estimate bird abundance at 0.06-, 0.13-, 0.26-, and 0.5-ha gaps and at uncut control areas during the 1996, 1997, and 1998 breeding seasons (1 May–1 August). There were significant increases in the number of species mapped ($P = 0.0001$) and netted ($P = 0.0001$) with successive increases in gap size. The greatest number of total spot-map detections ($P = 0.0002$) and mist net captures ($P = 0.0004$) also occurred in and around the large gaps. These patterns were the result of increased use of larger gaps by field-edge species, primarily Brown-headed Cowbird (*Molothrus ater*), Common Yellowthroat (*Geothlypis trichas*), and Indigo Bunting (*Passerina cyanea*), and some forest-edge species, such as White-eyed Vireo (*Vireo griseus*) and Northern Parula (*Parula americana*). Conversely, Acadian Flycatcher (*Empidonax virescens*) was less abundant in and adjacent to gaps. Because there were few differences in vegetation among gaps of different sizes, it is likely that birds that were detected more frequently in and adjacent to larger gaps selected those gaps based on other factors correlated with size. Creation of 0.5-ha group-selection openings in southern bottomland forests should provide breeding habitat for some field-edge species in gaps and habitat for forest-interior species and canopy-dwelling forest-edge species between gaps, provided that sufficient mature forest is maintained.

Key words: bottomland forest; breeding birds; gap size; gap vegetation; group selection; habitat use; neotropical migrant; silviculture; South Carolina; succession.

INTRODUCTION

Changes in microclimate (Minckler et al. 1973, Phillips and Shure 1990), plant species composition and structure (Runkle 1982, Brokaw 1985, Phillips and Shure 1990), and resource availability (Levey 1988) resulting from natural gap creation may alter patterns of avian habitat use. Studies in east-central Illinois (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986) and in the tropics (Schemske and Brokaw 1981, Wunderle et al. 1987, Levey 1988) have demonstrated differences between assemblages of birds captured in natural forest gaps and in the adjacent, intact forest. In temperate forests, many avian species (e.g., foliage-gleaning insectivores and frugivores) are more common in natural gaps than in the adjacent forest during spring and fall migration, possibly because of increased understory foliage density, greater insect abundance, or both (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986).

Although the importance of natural gaps to migrating birds in temperate areas has been investigated, little is known about avian use of man-made gaps during the breeding season, especially in bottomland forests. Between the years 2000 and 2030, acreage of bottomland forest in the southern United States is projected to decrease from $\sim 11.7 \times 10^6$ ha to 10.6×10^6 ha (USDA Forest Service 1988). Concurrently, annual hardwood timber removals from bottomland forests are projected to increase by ~18% (USDA Forest Service 1988). Bottomland hardwood forests in the southern United States consistently are identified as focal areas for avian conservation efforts because they provide optimal breeding and migration stopover habitats for many high-priority bird species (Hunter et al. 1993). These forests have been reported to contain more avian species and a greater density of breeding and wintering birds than surrounding upland forests (Dickson 1978). Large blocks of mature bottomland hardwood forest are more likely to contain habitat specialists, including forest-interior, neotropical migrants (Hodges and Krementz 1996, Kilgo et al. 1998). With increased timber removals predicted, further research is needed to assess the impacts of the various silvicultural practices on breeding birds in southeastern bottomland forests.

Clear-cutting, or removal of the entire stand in one cutting, is the most proven and popular method used to regenerate bottomland oaks in the South (Clatterbuck and Meadows 1993). However, complete removal

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Manuscript received 11 February 2000; revised 29 November 2000; accepted 1 January 2001.

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PLATE 1. The 70–100 yr-old bottomland forest surrounding the group-selection openings was characterized by a relatively sparse midstory, and an understory of dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*). The group-selection openings (like the 0.5-ha gap seen in the background behind the trees) provided patches of dense cover within the bottomland forest that generally lacked significant understory and midstory vegetation.

of the forest overstory renders the stand temporarily unsuitable for canopy-dependent bird species (Pashley and Barrow 1993, Kerpez 1994). Single-tree selection, in which single, mature trees are removed from throughout the stand at regular intervals, has been presented as an alternative to clear-cutting in southern bottomland forests. Single-tree selection leaves most of the forest canopy intact, and probably would result in relatively few changes in the breeding bird community (Medin and Booth 1989, Annand and Thompson 1997). Single-tree selection is an unfavorable silvicultural practice in southern bottomland forests, however, because it encourages economically undesirable, shade-intolerant tree species and often leads to high-grading of the forest (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997). Group selection, in which groups of trees covering no more than 0.5 ha are cleared, retains a portion of the forest canopy and allows sufficient sunlight for some growth of shade-intolerant, commercially valuable species (Clatterbuck and Meadows 1993, Kellison and Young 1997, Meadows and Stanturf 1997). The openings created during group selection may simulate naturally occurring, gap-phase disturbances (Pashley and Barrow 1993), which possibly provide increased concentrations of food resources or important refuge areas for birds.

Fifteen bird species that breed primarily in southeastern bottomland forests are of high concern and have been identified for management or monitoring attention (Hunter et al. 1993). Most are forest-interior species or canopy nesters, and would be absent from clear-cut stands for several years after harvest. However, several priority species, including Hooded Warbler (*Wilsonia citrina*) and Kentucky Warbler (*Oporornis formosus*), commonly forage or nest in natural treefall gaps and may be more abundant in selection harvest stands than in uncut stands during the breeding season (Hamel 1989, Annand and Thompson 1997, Robinson and Robinson 1999). Additionally, field-edge and forest-edge birds may colonize the areas in and around group-selection openings (Kerpez 1994, Germaine et al. 1997).

Area-related thresholds above which individual gap-phase disturbances positively affect early-successional and edge species and negatively affect forest-interior species need to be identified (Thompson et al. 1993). Identifying these thresholds would aid those developing the sustainable forest management strategies needed to simultaneously generate revenue by timber harvest and to maintain or improve the quality of avian habitat. Our objectives were to: (1) document and compare avian assemblages and habitat-use patterns among harvested gaps of increasing size and uncut forest (i.e., identify potential thresholds); (2) determine the effects of gap size on structure of vegetation; and (3) compare differences in gap vegetation with differences in breeding bird habitat use.

METHODS

Study area

We conducted field investigations within a 362-ha bottomland forest stand on the Savannah River Site (SRS), a 78 000-ha block of relatively contiguous forest, in Barnwell County, South Carolina, USA. The stand lies within the Upper Coastal Plain physiographic region and consists primarily of 70–100 yr-old bottomland hardwoods (see Plate 1). The canopy was dominated by laurel oak (*Quercus laurifolia*), cherrybark oak (*Q. falcata* var. *paegodifolia*), sweetgum (*Liquidambar styraciflua*), and loblolly pine (*Pinus taeda*). The midstory was sparse, and dense areas of dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*) were distributed patchily throughout the understory. Six replicates of four experimental gap (group-selection opening) sizes were harvested on ~65 ha of the stand in December 1994 (Fig. 1). The sizes

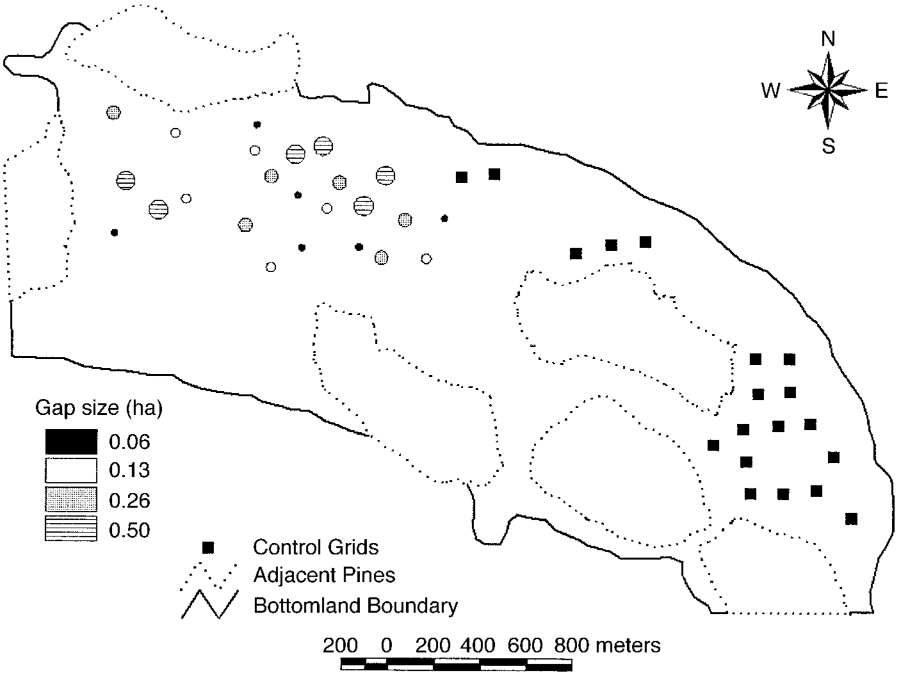

FIG. 1. Locations of group-selection openings, control grids, adjacent pine stands, and the bottomland hardwood forest stand boundary in Barnwell County, South Carolina, USA.

were 0.06, 0.13, 0.26, and 0.5 ha (14, 20, 29, and 40 m in radius, respectively); to create each size, we removed ~8, 16, 32, and 64 overstory stems, respectively. Minimum spacing between gap centers was 100 m, and the average distance between a gap's edge and the edge of its nearest neighbor was 102.7 m (range 44–230 m). The gaps were cleared to bare ground and were circular in shape. Some downed tree tops and small diameter stems were left as slash in and adjacent to harvested gaps, but most wood was removed during logging. We defined the gap to include all of the cleared area within the circumference delineated by the boles of trees left standing at the gap perimeter (i.e., extended gap). An adjacent uncut portion of the same stand was designated as a control site. We systematically established 19 points, >140 m apart, along north–south and east–west transects within the uncut area (Fig. 1). All control points were >200 m from harvested openings.

Bird sampling

We mapped singing males of bird species present from 7 May to 7 July in 1996, 1997, and 1998, using a modification of the spot-map technique (International Bird Census Committee 1970). A 130 × 130 m, or ~1.7-ha, grid was centered on each of the 24 gaps and on the 19 points (i.e., gap size = 0) in the control site. These grid dimensions provided maximum sampling effort without overlap in grid surveys. We conducted eight weekly censuses at each grid, and plotted the locations of male birds seen or heard. Neighboring grids were mapped simultaneously to minimize the possibility of counting the same individual in more than one grid during the same visitation round. We visited all spot-map grids before a new visitation round was begun. Because grids were too small to allow computation of territory density, we used the sum of all detections recorded during the eight visits as the response for each species in each grid. Some responses were greater than eight because of detection of multiple individuals of the same species at a replicate during a single visit (i.e., simultaneous singing).

Results obtained from mist netting may be biased (Remsen and Good 1996), but use of netting in combination with auditory–visual sampling may allow more accurate identification of bird-use patterns than the use of either method alone (Nur and Geupel 1993, Whitman et al. 1997). Therefore, we conducted mist netting at all gaps and at six control grids from 10 May to 25 July in 1996, 1997, and 1998. At each grid, five nets were located at ~32.5-m intervals on a north–south transect through the grid center, with two nets in the forest adjacent to gaps, two nets intersecting the gap edge, and one net in the gap interior. We performed netting at three sites each day, and each trio was netted for two consecutive days. Netting was conducted between sunrise and noon at two trios of sites each week, and each of the 30 sites was sampled twice during the breeding season, once before 15 June and once after. We visited all sites before a new round of sampling was begun, and captured birds were banded with a

USGS BRD (U.S. Geological Survey, Biological Resources Division) aluminum leg band. We also recorded the net location of each capture within the gap grid (i.e., gap edge, gap interior, or forest adjacent to gap).

Vegetation sampling

In July 1996, we measured the forest vegetation adjacent to gaps and at control sites, using a modification of the James and Shugart (1970) technique. We measured the vegetation at a single 0.04-ha circular plot (hereafter, forest plot) centered on a randomly chosen corner of each spot-map grid. Within each forest plot, we tallied all woody stems ≥3 cm in diameter at breast height (dbh) into three diameter classes (3–8 cm, 9–23 cm, >23 cm). Basal area of hardwood and pine stems, number of hardwood and pine stems, and number of snags (i.e., standing dead stems >3 cm dbh) also were calculated. We used a spherical densiometer (four samples per site) to estimate percent canopy cover and an ocular tube (20 samples per site) to determine percent ground cover (James and Shugart 1970). We determined heights of the three tallest canopy trees in each 0.04-ha forest plot using a clinometer, and their average was used as the forest plot canopy height.

We measured understory vegetation in gaps from mid-to-late July in 1996, 1997, and 1998, using the technique described by Wiens (1969), as modified by Rotenberry and Wiens (1980). We assumed that vegetative changes in the unharvested controls would be minimal, so understory vegetation at control grids was measured only once (July 1996) during the three years of the study. We measured vegetation at nine plots (hereafter, understory plots) in each 0.5-ha gap; seven plots in each 0.26-ha gap; and five plots in each of the 0.13-ha gaps, 0.06-ha gaps, and control grids. In gaps, we established understory plots 2 m from the north and south edges, at the center, and at one-half the radius in the east and west directions from the gap center. In 0.26-ha gaps, understory plots also were established at one-half the radius and 45° from two randomly chosen cardinal directions (e.g., northeast and southwest). In 0.5-ha gaps, understory plots also were created at one-half the radius and 45° from all cardinal directions. We established all five control grid plots within the 0.04-ha forest plots previously described. Control understory plots were located at the center of the 0.04-ha forest plot and 10 m from the forest plot center in each of the four cardinal directions. At gap and control grids, we measured the vertical distribution of understory vegetation at sampling points 2 m east and west of each understory plot center (e.g., 18 sampling points in 0.5-ha gaps). We estimated vertical structure by recording whether or not vegetation touched each 1-dm height interval of a 2-m rod passed vertically through the vegetation. Plants that hit the rod were recorded as woody, grass/sedge, forb, or slash. Where vegetation occurred in the sampling plane above 2 m in gaps, the maximum height of vegetation above 2 m was recorded.

From the rod data, we calculated percent horizontal cover for each of the four vegetative types (WOOD, FORB, GRASS, SLASH) in gap and control grids by dividing the number of sampling points where vegetation intersected the rods by the total number of sampling points measured. We indexed vertical structure by calculating the mean total number of decimeters with vegetative hits (TOTHIT) and the mean maximum decimeter height interval contacting vegetation in gaps (MAXHT). We calculated variation among sampling points in vertical structure within a gap as an index of horizontal heterogeneity. We used coefficients of variation (CV) of the two vertical structure variables (CVTOTHIT, CVMAXHT) to estimate such variation. To estimate heterogeneity at a smaller scale (within understory plot), we calculated a heterogeneity index based on within-plot differences in TOTHIT and MAXHT and averaged over an entire gap (Rotenberry and Wiens 1980). The total hits heterogeneity index (HIT-HI) and maximum height heterogeneity index (MAX-HI) were defined as: HIT-HI or MAX-HI = Σ (High $-$ Low)/$\Sigma\ \bar{x}$, where High is the high value for TOTHIT or MAX-HI within an understory plot, Low is the low value for TOTHIT or MAX-HI within an understory plot, and $\bar{x}$ is the mean value of TOTHIT or MAX-HI within an understory plot. Because MAXHT was calculated only for gaps, CVMAXHT and MAX-HI were not computed for control grids.

Statistical analysis

We grouped bird species into three habitat-use associations (field edge, forest edge, and forest interior) following Freemark and Collins (1992), Hamel (1992), and Kilgo et al. (1998). Two of these references were based on data collected from the southeastern United States, and should more closely describe the regional habitat associations of species detected during our study. Further, we grouped bird species as either residents or neotropical migrants (Hamel 1992). Nonbreeding migrant species (i.e., transients) were excluded from statistical analyses.

Using spot mapping data, we tested for differences in species richness, total detections, and numbers of detections by species, habitat association, and migratory strategy among treatments (i.e., four gap sizes and control grids) using a split-plot in time (3-yr) analysis of covariance (ANCOVA; SAS Institute 1996). Habitat variables measured in the forest plots were included as covariates in the ANCOVA. We examined correlations among forest plot habitat variables using Pearson product-moment correlation coefficients, and the most easily measured (i.e., most likely to be measured during timber inventories) variable of a correlated pair ($P \leq 0.05$) was retained as a covariate. Four of 11 variables measured in forest plots were retained for inclusion as covariates in analyses of mapping data (Table 1). When covariate effects were nonsignificant, they were eliminated. When the ANCOVA yielded a significant F sta-

TABLE 1. Vegetation in 0.04-ha circular plots in the forest bordering gap and control grids.

Variable	Mean (n = 43)	1 SE
No. hardwood stems ≥3 cm dbh (HWST)	59.95	2.92
Hardwood basal area (HWBA)	0.94	0.11
No. pine stems ≥3 cm dbh (PINEST)	1.60	0.45
Pine basal area (PINEBA)†	0.10	0.03
No. snags (SNAGS)	3.79	0.48
No. stems 3–8 cm dbh (CM38)	46.07	3.65
No. stems 8–23 cm dbh (CM823)	12.79	0.99
No. stems >23 cm dbh (CM23)†	6.49	0.77
Average tree height in m (HT)†	35.43	0.60
Percent ground cover (GCOV)	27	0.03
Percent canopy cover (CCOV)†	93	0.01

† Variable retained as a covariate in analyses of spot-map data.

tistic, we used the least square means procedure to separate covariate-adjusted means.

We investigated the spatial patterns of avian habitat use of the understory in and adjacent to gaps by testing for differences in the number of net captures in gap-interior, gap-edge, and forest nets. Because gap-interior nets were operated for one-half of the net-hours that gap-edge and forest nets were operated, we standardized all capture results as number of captures/100 net-hours. Recaptured individuals were included in all mist-netting analyses. We tested for differences in species richness from mist netting, total captures, and total captures by species, habitat association, migratory strategy, and net location among treatments, using a split-plot in time nested ANOVA with net location nested within the gap size treatment. When the ANOVA yielded a significant F statistic, we used the least square means procedure to separate means. For analyses of individual species' responses, we included only species with at least 40 spot-map detections or 20 mist-net captures during the three years of the study. These cutoffs were chosen based on breaks in the distribution of detections and captures.

For each variable sampled in the understory plots, we tested for significant differences among treatments using a split-plot in time ANOVA. Percentile variables were arcsine square-root transformed, but only untransformed means and standard errors are reported. We analyzed data from each year separately when year × treatment interactions were significant. Significance was accepted at $P \leq 0.05$ for statistical tests.

RESULTS

Gap vegetation

Values for eight of the 10 variables differed significantly among the three years of the study (Table 2). In 1996 and 1997, gap vegetation was predominately herbaceous (FORB), but hardwood stump sprouts and seedlings increased in number (WOOD) and height (MAXHT) in successive years of the study. Estimates of coverage (WOOD, GRASS, FORB) and vertical structure (TOTHIT) were higher in the gaps than in the control grids, but these values rarely differed significantly among the gap sizes (Table 2). In 1996, however, TOTHIT and FORB were greater in 0.5-ha gaps than in the 0.06-ha openings (Table 2).

All birds

We detected 49 bird species by mapping, and captured 40 bird species. More bird species were mapped as gap size increased, but the number of species recorded in the 0.06- and 0.13-ha gap grids was not different than that recorded in control grids (Table 3). The number of species captured also increased with successive increases in gap size, and species richness from netting was greater in the 0.5-ha gap grid than in any other treatment (Table 4).

Total detections for all species, neotropical migrant species, and resident species increased with gap size (Table 3). Total captures for all species, neotropical migrant species, and resident species also were greatest in and adjacent to the largest gaps (Table 4). Total captures differed among the gap-interior, gap-edge, and forest net placements ($P = 0.0154$). Numbers of gap-interior, gap-edge, and forest captures were similar in control, 0.06-ha, and 0.13-ha gaps, but more birds were captured at the edges of the 0.26- and 0.5-ha gaps and in the interiors of the 0.5-ha gaps (Fig. 2).

Field-edge species

As a group, field-edge species were mapped more often with each successive increase in gap size (Table 3). We captured more field-edge species in the 0.5-ha gaps than in any of the other treatments, and more in 0.26-ha gaps than in 0.06-ha gaps, 0.13-ha gaps, or control grids. No field-edge species were captured in control grids (Table 4). The number of captures of field-edge species differed among net placements ($P = 0.0001$), with more birds being captured in the interior nets at the three largest gap sizes and at the edges of the 0.5-ha gaps (Fig. 2). Few field-edge individuals were captured at edges of the two smallest gaps or in the forest understory adjacent to gaps (Fig. 2). Indigo Bunting (*Passerina cyanea*) detections increased with successive increase in gap size, and Common Yellowthroat (*Geothlypis trichas*) detections were greatest in the two largest gap sizes (Table 3). Indigo Bunting and Common Yellowthroat captures were highest in 0.5-ha gaps, and no individuals of either species were captured in controls (Table 4). Brown-headed Cowbird (*Molothrus ater*) detections were greatest in and adjacent to 0.5-ha gaps in 1997 (Table 3).

Forest-edge species

Generally, forest-edge species were mapped and captured more often in 0.5-ha gap grids than in any other treatment (Tables 3 and 4). Captures of forest-edge species differed among the three net placements ($P = 0.0140$), with nearly twice as many forest-edge birds

TABLE 2. Structure of vegetation in different-sized gaps in a South Carolina bottomland forest (1996–1998). Standard errors are in parentheses.

Variable, by year	Control	Treatment (gap size)				P‖
		0.06 ha	0.13 ha	0.26 ha	0.5 ha	
WOOD†‡						
1996	0.39^{b} (0.04)	0.63^{a} (0.08)	0.65^{a} (0.08)	0.51^{ab} (0.08)	0.58^{a} (0.08)	0.0145
1997	0.39^{b} (0.04)	0.82^{a} (0.08)	0.78^{a} (0.08)	0.63^{a} (0.08)	0.77^{a} (0.08)	0.0001
1998	0.39^{c} (0.04)	0.87^{ab} (0.07)	0.90^{a} (0.07)	0.76^{ab} (0.07)	0.78^{b} (0.07)	0.0001
FORB†‡						
1996	0.02^{c} (0.04)	0.35^{b} (0.07)	0.35^{b} (0.07)	0.45^{ab} (0.07)	0.56^{a} (0.07)	0.0001
1997	0.02^{b} (0.02)	0.32^{a} (0.04)	0.30^{a} (0.04)	0.41^{a} (0.04)	0.43^{a} (0.04)	0.0001
1998	0.02^{b} (0.02)	0.08^{a} (0.04)	0.17^{a} (0.04)	0.12^{a} (0.04)	0.17^{a} (0.04)	0.0002
GRASS†‡						
1996	0.23^{b} (0.05)	0.77^{a} (0.09)	0.85^{a} (0.09)	0.93^{a} (0.09)	0.77^{a} (0.09)	0.0001
1997	0.23^{b} (0.05)	0.85^{a} (0.08)	0.98^{a} (0.08)	0.91^{a} (0.08)	0.86^{a} (0.08)	0.0001
1998	0.23^{b} (0.05)	0.82^{a} (0.08)	0.85^{a} (0.08)	0.80^{a} (0.08)	0.76^{a} (0.08)	0.0001
SLASH†‡						
1996	0.16 (0.03)	0.27 (0.05)	0.13 (0.05)	0.05 (0.05)	0.24 (0.05)	0.0587
1997	0.16 (0.03)	0.05 (0.05)	0.05 (0.05)	0.12 (0.05)	0.14 (0.05)	0.0870
1998	0.16 (0.03)	0.10 (0.05)	0.07 (0.05)	0.07 (0.05)	0.13 (0.05)	0.3029
TOTHIT†‡						
1996	1.74^{c} (0.45)	4.87^{b} (0.80)	6.22^{ab} (0.80)	6.83^{ab} (0.80)	7.54^{a} (0.80)	0.0001
1997	1.74^{b} (0.31)	8.35^{a} (0.55)	9.89^{a} (0.55)	9.38^{a} (0.55)	9.64^{a} (0.55)	0.0001
1998	1.74^{b} (0.25)	7.78^{a} (0.44)	8.05^{a} (0.44)	8.18^{a} (0.44)	8.96^{a} (0.44)	0.0001
MAXHT‡§		1.30 (0.14)	1.47 (0.14)	1.34 (0.14)	1.61 (0.14)	0.4168
CVTOTHIT‡	1.26^{a} (0.10)	0.50^{b} (0.17)	0.50^{b} (0.17)	0.49^{b} (0.17)	0.46^{b} (0.17)	0.0001
CVMAXHT§		0.54 (0.04)	0.56 (0.04)	0.53 (0.04)	0.61 (0.04)	0.4771
HIT-HI‡	1.25^{a} (0.08)	0.62^{b} (0.14)	0.50^{b} (0.14)	0.45^{b} (0.14)	0.42^{b} (0.14)	0.0001
MAX-HI§		0.67 (0.06)	0.62 (0.06)	0.55 (0.06)	0.55 (0.06)	0.4558

Note: Means followed by the same letter were not significantly different. Prior to analysis, percentile data were arcsine square-root transformed, but only untransformed means and standard errors are reported. In addition to the four vegetative types, variables are abbreviated as follows: TOTHIT, total number of decimeters with vegetative hits; MAXHT, maximum decimeter height interval contacting vegetation in gaps; CVTOTHIT and CVMAXHT, coefficients of variation of these variables; HIT-HI, total hits heterogeneity index; MAX-HI, maximum height heterogeneity index. For definitions, see *Methods, Vegetation sampling.*

† Years were analyzed separately when there was a significant year × treatment interaction.

‡ Significant year effect ($P < 0.05$).

§ All variables associated with MAXHT were not measured in controls.

‖ P values are from the split-plot in time (3-yr) ANOVA.

captured in edge nets in 0.26- and 0.5-ha gap grids than at other net placements (Fig. 2). Blue-gray Gnatcatcher (*Polioptila caerulea*), Carolina Wren (*Thryothorus ludovicianus*), Downy Woodpecker (*Picoides pubescens*), and Northern Parula (*Parula americana*) detections were greater in the 0.26- and 0.5-ha gap grids than in the 0.06- and 0.13-ha gap grids (Table 3). In 1998, both Northern Cardinal (*Cardinalis cardinalis*) and White-eyed Vireo (*Vireo griseus*) were detected most frequently in and adjacent to the 0.5-ha gaps (Table 3). Only White-eyed Vireo captures in 1998 differed among treatments, with no captures in control or 0.06-ha gap grids and more captures in 0.5-ha gap grids than in other treatments (Table 4).

Forest-interior species

Spot-map detections for forest-interior species differed among treatments, and more birds were detected in control grids than in any of the four different-sized gaps (Table 3). When Acadian Flycatcher (*Empidonax virescens*) detections were excluded from the analysis, however, the difference was nonsignificant ($P = 0.4221$). Captures of the forest-interior group did not differ among treatments (Table 4). However, the number of captures differed among net locations ($P = 0.0046$), with the most captures at the edges of 0.26- and 0.5-ha gaps, and fewer captures in interiors of the 0.5-ha gaps (Fig. 2). Only three forest-interior species were captured ≥20 times, and captures of these species did not differ among treatments (Table 4).

DISCUSSION

The gap size (≥0.26 ha) at which numbers of individual birds and species richness began to differ from those in uncut forest was similar to that observed in other studies (Overcash and Roseberry 1987, Kerpez 1994). In Illinois, 0.1- to 0.2-ha wildlife openings in mature deciduous forest were not large enough to increase bird abundance, but changes began to occur in gaps of 0.3 ha (Overcash and Roseberry 1987). Patterns of response by birds in the different habitat-use groupings also were similar to those in other studies that

TABLE 3. Species richness and number of breeding season spot-map detections/grid/yr in different sized gaps in a South Carolina bottomland forest (1996–1998). Standard errors are in parentheses.

Measures pooled overall and by species groups and species	Control	Treatment (gap size)				*P*‖
		0.06 ha	0.13 ha	0.26 ha	0.5 ha	
Species richness	17.14^{cd} (0.39)	15.67^{d} (0.70)	18.28^{bc} (0.70)	19.22^{ab} (0.70)	21.06^{a} (0.70)	0.0001
Total detections†	52.32^{b} (2.39)	48.11^{b} (4.26)	51.22^{b} (4.26)	66.56^{a} (4.26)	73.28^{a} (4.26)	0.0002
Neotropical migrant†	31.82^{c} (1.89)	29.94^{c} (3.37)	35.17^{bc} (3.37)	43.67^{ab} (3.37)	45.06^{a} (3.37)	0.0021
Resident species†	20.49^{b} (1.12)	15.83^{c} (1.99)	18.39^{bc} (1.99)	22.89^{ab} (1.99)	28.22^{a} (1.99)	0.0011
Field-edge species†	0.82^{d} (0.39)	1.78^{d} (0.69)	4.50^{c} (0.69)	10.89^{b} (0.69)	15.33^{a} (0.69)	0.0001
Common Yellowthroat†‡	0.60^{c} (0.25)	0.85^{c} (0.42)	2.37^{b} (0.42)	5.10^{a} (0.42)	5.22^{a} (0.42)	0.0001
Brown-headed Cowbird†§						
1996	0.00 (0.07)	0.17 (0.12)	0.00 (012)	0.33 (0.12)	0.33 (0.12)	0.0591
1997	0.05^{b} (0.08)	0.00^{b} (0.15)	0.00^{b} (0.15)	0.33^{b} (0.15)	2.17^{a} (0.15)	0.0001
1998	0.37 (0.18)	0.17 (0.32)	0.33 (0.32)	0.67 (0.32)	1.17 (0.32)	0.1781
Indigo Bunting	0.00^{d} (0.17)	0.56^{d} (0.31)	1.67^{c} (0.31)	4.39^{b} (0.31)	6.39^{a} (0.31)	0.0001
Forest-edge species†	38.12^{c} (1.91)	34.83^{c} (3.40)	41.06^{bc} (3.40)	47.72^{ab} (3.40)	51.67^{a} (3.40)	0.0031
Yellow-billed Cuckoo†	0.74 (0.12)	0.78 (0.21)	0.83 (0.21)	0.89 (0.21)	1.33 (0.21)	0.1895
Ruby-thr. Hummingbird†	1.68 (0.17)	1.61 (0.31)	1.17 (0.31)	2.17 (0.31)	1.61 (0.31)	0.2818
Red-headed Woodpecker†	0.39 (0.24)	0.00 (0.43)	0.28 (0.43)	0.50 (0.43)	1.33 (0.43)	0.2559
Red-bellied Woodpecker†	1.84 (0.18)	1.61 (0.32)	2.06 (0.32)	1.89 (0.32)	2.72 (0.32)	0.1455
Downy Woodpecker	1.75^{a} (0.17)	0.94^{b} (0.29)	1.78^{ab} (0.29)	2.33^{a} (0.29)	2.33^{a} (0.29)	0.0111
Great-crested Flycatcher†§						
1996	0.68 (0.21)	0.67 (0.37)	1.17 (0.37)	1.50 (0.37)	1.33 (0.37)	0.2315
1997	2.95^{a} (0.34)	0.50^{b} (0.60)	1.00^{b} (0.60)	0.83^{b} (0.60)	1.83^{ab} (0.60)	0.0021
1998§	0.93 (0.23)	0.32 (0.41)	0.24 (0.41)	0.79 (0.41)	1.2 (0.41)	0.3599
Carolina Chickadee†	1.47 (0.19)	0.78 (0.33)	0.89 (0.33)	1.50 (0.33)	1.39 (0.33)	0.2858
Eastern Tufted Titmouse†	3.19 (0.26)	2.11 (0.46)	2.67 (0.46)	2.94 (0.46)	2.94 (0.46)	0.3489
Carolina Wren†	5.60^{b} (0.41)	5.44^{b} (0.73)	5.17^{b} (0.73)	6.56^{ab} (0.73)	8.00^{a} (0.73)	0.0432
Blue-gray Gnatcatcher	5.07^{a} (0.26)	2.67^{b} (0.46)	3.39^{b} (0.46)	5.17^{a} (0.46)	4.94^{a} (0.46)	0.0002
White-eyed Vireo†§						
1996	0.32 (0.12)	0.00 (0.21)	0.17 (0.21)	0.00 (0.21)	0.67 (0.21)	0.1550
1997	0.26 (0.11)	0.00 (0.19)	0.17 (0.19)	0.00 (0.19)	0.50 (0.19)	0.2867
1998	0.00^{c} (0.23)	0.17^{bc} (0.41)	0.33^{bc} (0.41)	0.83^{b} (0.41)	2.50^{a} (0.41)	0.0002
Yellow-throated Vireo	1.18 (0.16)	0.83 (0.28)	1.39 (0.28)	1.78 (0.28)	1.67 (0.28)	0.1135
Red-eyed Vireo†‡	5.18 (0.65)	6.24 (1.16)	7.67 (1.16)	8.15 (1.16)	7.04 (1.15)	0.1422
Northern Parula†	3.65^{b} (0.81)	7.06^{a} (1.44)	7.78^{a} (1.44)	8.22^{a} (1.44)	8.00^{a} (1.44)	0.0119
Summer Tanager†‡	1.74 (0.25)	1.50 (0.44)	2.22 (0.45)	1.72 (0.44)	2.59 (0.45)	0.4208
Northern Cardinal†§						
1996	2.79 (0.46)	2.33 (0.81)	2.33 (0.81)	2.33 (0.81)	3.67 (0.81)	0.3549
1997	2.74 (0.37)	4.17 (0.65)	4.00 (0.65)	2.67 (0.65)	4.17 (0.65)	0.1137
1998	1.79^{b} (0.33)	1.33^{b} (0.58)	1.33^{b} (0.58)	2.83^{ab} (0.58)	3.67^{a} (0.58)	0.0214
Forest-interior species	13.37^{a} (0.79)	9.17^{b} (1.41)	8.00^{b} (1.41)	7.94^{b} (1.41)	6.28^{b} (1.41)	0.0002
Hairy Woodpecker	0.26 (0.10)	0.39 (0.17)	0.44 (0.17)	0.56 (0.17)	0.78 (0.17)	0.1360
Pileated Woodpecker	0.89 (0.13)	0.56 (0.23)	0.61 (0.23)	0.72 (0.23)	0.83 (0.23)	0.6504
Acadian Flycatcher†	5.81^{a} (0.33)	3.89^{b} (0.58)	2.44^{bc} (0.58)	1.06^{cd} (0.58)	0.50^{d} (0.58)	0.0001
White-breasted Nuthatch†	0.30 (0.10)	0.44 (0.18)	0.44 (0.18)	0.83 (0.18)	0.67 (0.18)	0.1228
Pine Warbler†‡	1.47 (0.27)	0.69 (0.48)	1.19 (0.48)	1.23 (0.48)	1.57 (0.48)	0.6600
Kentucky Warbler	0.47 (0.14)	0.17 (0.25)	0.39 (0.25)	0.39 (0.25)	0.56 (0.25)	0.8350
Hooded Warbler	2.82 (0.48)	2.44 (0.86)	2.22 (0.86)	2.78 (0.86)	1.22 (0.86)	0.5874

Notes: Only species with ≥ 40 detections between 1996 and 1998 were included in the table. Scientific names of species not mentioned in text are: Ruby-throated Hummingbird (*Archilochus colubris*), Red-headed Woodpecker (*Melanerpes erythrocephalus*), Red-bellied Woodpecker (*Melanerpes carolinus*), Great-crested Flycatcher (*Myiarchus crinitus*), Carolina Chickadee (*Poecile carolinensis*), Eastern Tufted Titmouse (*Baeolophus bicolor*), Red-eyed Vireo (*Vireo olivaceus*), Summer Tanager (*Piranga rubra*), Hairy Woodpecker (*Picoides villosus*), Pileated Woodpecker (*Dryocopus pileatus*), White-breasted Nuthatch (*Sitta carolinensis*), and Pine Warbler (*Dendroica pinus*). Means followed by the same letter were not significantly different.

† Significant year effect ($P < 0.05$).

‡ The number of detections was significantly ($P < 0.05$) correlated with a covariate: Common Yellowthroat with HT; Great-crested Flycatcher with CM23; Red-eyed Vireo with CM23; Summer Tanager with PINEBA; Pine Warbler with PINEBA.

§ Significant year × treatment interaction ($P < 0.05$); data were analyzed separately for each year.

‖ *P* values are from the split-plot in time (3-yr) ANCOVA.

investigated relationships between avian habitat use and group-selection openings (Kerpez 1994, Annand and Thompson 1997, Germaine et al. 1997). Although Acadian Flycatcher abundance declined in the larger gap grids, abundance of forest-edge and field-edge species increased.

Observed differences between the structure of understory vegetation in the forest and gaps were typical of an area recently disturbed by timber harvesting (Oliver 1981). However, growth of vegetation normally is more prolific in larger openings (Runkle 1982, Phillips and Shure 1990), and plant species composition typi-

TABLE 4. Species richness and number of breeding-season mist-net captures/100 net-hours in different-sized gaps in a South Carolina bottomland forest (1996–1998). Standard errors are in parentheses.

Measures pooled overall and by species groups and species†	Control	Treatment (gap size)				*P*‖
		0.06 ha	0.13 ha	0.26 ha	0.5 ha	
Species richness	4.86^{bc} (0.57)	4.79^{c} (0.57)	5.49^{bc} (0.57)	6.46^{b} (0.57)	8.89^{a} (0.57)	0.0001
Total no. captures	10.56^{b} (1.58)	12.15^{b} (1.58)	12.01^{b} (1.58)	14.72^{b} (1.58)	21.53^{a} (1.58)	0.0004
Neotropical migrant	3.26^{b} (1.06)	3.61^{b} (1.06)	3.96^{b} (1.06)	6.04^{b} (1.06)	9.38^{a} (1.06)	0.0020
Resident species	7.29^{b} (1.02)	8.54^{b} (1.02)	8.06^{b} (1.02)	8.68^{b} (1.02)	12.15^{a} (1.02)	0.0246
Field-edge species	0.00^{c} (0.32)	0.49^{c} (0.32)	0.69^{c} (0.32)	1.94^{b} (0.32)	3.89^{a} (0.32)	0.0001
Common Yellowthroat	0.00^{c} (0.23)	0.21^{bc} (0.23)	0.07^{c} (0.23)	0.76^{ab} (0.23)	1.39^{a} (0.23)	0.0011
Indigo Bunting	0.00^{c} (0.27)	0.28^{bc} (0.27)	0.63^{bc} (0.27)	1.04^{b} (0.27)	2.15^{a} (0.27)	0.0001
Forest-edge species	8.19^{b} (1.11)	9.17^{b} (1.11)	9.17^{b} (1.11)	9.79^{b} (1.11)	14.86^{a} (1.11)	0.0021
Eastern Tufted Titmouse	0.69 (0.31)	0.42 (0.31)	0.63 (0.31)	1.04 (0.31)	0.63 (0.31)	0.7105
Carolina Wren	5.49 (0.89)	6.74 (0.89)	5.69 (0.89)	5.90 (0.89)	8.33 (0.89)	0.1806
White-eyed Vireo‡§						
1996	0.21 (0.15)	0.00 (0.15)	0.00 (0.15)	0.00 (0.15)	0.42 (0.15)	0.2216
1997	0.21 (0.26)	0.00 (0.26)	0.42 (0.26)	0.21 (0.26)	0.42 (0.26)	0.7639
1998	0.00^{b} (0.29)	0.00^{b} (0.29)	0.21^{b} (0.29)	0.42^{b} (0.29)	2.50^{a} (0.29)	0.0001
Red-eyed Vireo	0.35 (0.21)	0.28 (0.21)	0.35 (0.21)	0.21 (0.21)	0.49 (0.21)	0.9171
Summer Tanager	0.28 (0.23)	0.21 (0.23)	0.14 (0.23)	0.76 (0.23)	0.35 (0.23)	0.3403
Northern Cardinal‡	0.97 (0.38)	1.25 (0.38)	1.53 (0.38)	1.18 (0.38)	2.29 (0.38)	0.1503
Forest-interior species	2.36 (0.75)	2.50 (0.75)	2.15 (0.75)	2.99 (0.75)	2.78 (0.75)	0.9398
Acadian Flycatcher	0.35 (0.17)	0.35 (0.17)	0.21 (0.17)	0.21 (0.17)	0.28 (0.17)	0.9564
Kentucky Warbler	0.07 (0.24)	0.49 (0.24)	0.35 (0.24)	0.35 (0.24)	0.63 (0.24)	0.5855
Hooded Warbler	1.18 (0.58)	1.53 (0.58)	1.46 (0.58)	2.01 (0.58)	1.74 (0.58)	0.8824

Note: Means followed by the same letter were not significantly different ($P > 0.05$).

† Only species with ≥20 captures during the three years of the study were included in the table.

‡ Significant year effect ($P < 0.05$).

§ Significant year × treatment interaction ($P < 0.05$); data were analyzed separately for each year.

‖ *P* values are from the split-plot in time (3-yr) nested ANOVA.

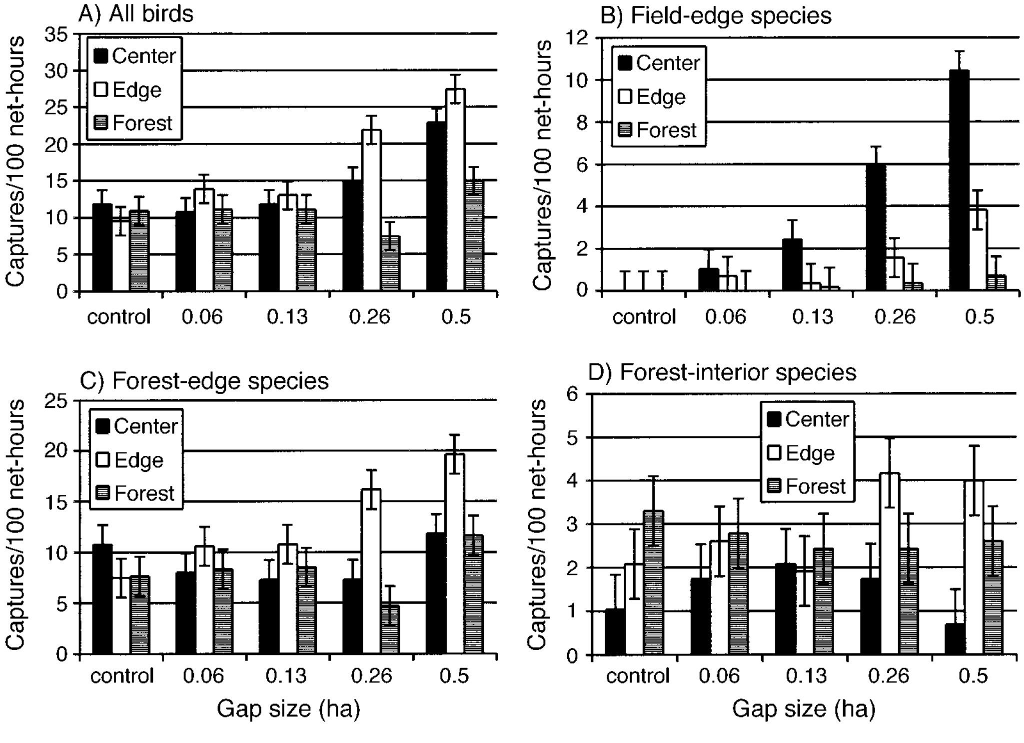

FIG. 2. Mean (± 1 SE) number of net captures/100 net-hours at the three net placements (center, edge, and forest) for: (A) all birds; (B) field-edge species; (C) forest-edge species; and (D) forest-interior species in a South Carolina bottomland (1996–1998).

cally differs between small and large (>150 m^2) gaps (Brokaw 1985). Phillips and Shure (1990) documented increased net primary productivity and plant species richness with successive increases in gap size across a range of sizes similar to those in our study. Therefore, the paucity of vegetative differences among the four gap sizes in our study was unexpected. Although vegetative structure generally increased with gap size, the differences were not consistently significant. The absence of consistent differences in vegetation among gaps may be a product of variation among replicates within a single treatment, which may have resulted from excessive disturbance of the gaps located along more frequently traveled portions of the logging roads.

The absence of distinct vegetative differences among gap sizes and the positive relationship between bird response and gap size suggest that birds more frequently detected in and adjacent to larger gaps selected those gaps based on other factors correlated with size. Changes in micro-environmental factors (e.g., solar radiation, soil moisture, and temperature) and amount of food resources that would elicit detectable changes in bird responses may occur at significant levels only in gaps ≥0.26 ha. Field-edge species, such as Indigo Bunting and Common Yellowthroat, may require ≥0.26 ha of open habitat, regardless of the density of vegetation in the gaps. Low capture rates of field-edge species in forest nets indicated that these species were largely restricted to gap habitat.

Many researchers have documented positive relationships between numbers of forest-interior birds and forest patch size (e.g., Blake and Karr 1987), but field-edge species also are sensitive to the size of disturbed patches (Rudnicky and Hunter 1993). Indigo Buntings, which typically are more abundant in selection harvests than in uncut stands (Annand and Thompson 1997, Rodewald and Smith 1998, Robinson and Robinson 1999), were reported absent from a 0.12-ha opening, but occurred in all but one of the 19 larger openings in Virginia (Kerpez 1994). In our study, the minimum threshold size appeared to be ∼0.26 ha for Indigo Bunting and Common Yellowthroat. We located three Common Yellowthroat nests and seven Indigo Bunting nests in the harvested area, all in or adjacent to 0.26- or 0.5-ha gaps (C. E. Moorman, *unpublished data*). Because of the rarity of Blue Grosbeaks (*Guiraca caerulea*) and the absence of Yellow-breasted Chats (*Icteria virens*), gaps ≤0.5 ha probably fall below their minimum threshold size for territory establishment. In Illinois, group-selection openings as large as 0.4 ha also were not of sufficient size to attract many open-country bird species (Robinson and Robinson 1999).

Forest-edge species were detected in highest numbers in and around the largest gaps, especially at gap edges. Increased food resource availability, increased vegetative structure, and the possibility of simultaneous access to two habitat types may explain the greater use of large gaps by forest-edge species (Strelke and Dickson 1980). Many arthropods favor plants growing in sunlight over those growing in shade (White 1984), and higher densities of invertebrates have been reported at edges between forest and disturbed areas (Helle and Muona 1985). Several of the forest-edge species recorded more often in the larger gap grids, including Carolina Wren, Northern Cardinal, and White-eyed Vireo, are understory species and probably benefited from the dense vegetation characteristic of the gaps.

The Acadian Flycatcher repeatedly has been documented as a species that is negatively affected by low-intensity disturbance (Kerpez 1984, Annand and Thompson 1997, Rodewald and Smith 1998), and was the only species that declined in abundance with increasing gap size. Despite its suggested avoidance of the large group-selection openings on our study site, the Acadian Flycatcher was the forest-interior species most commonly detected during spot mapping. Based on spot-map locations, it appeared that singing males remained >30 m from the gap edges, regardless of gap size. Acadian Flycatchers established territories in mature forest between gaps, provided that there was sufficient area ≥30 m from gap edges. Therefore, implementation of group-selection cuts at a low density should allow maintenance of a breeding population of Acadian Flycatchers within the disturbed stand. Further research is needed to investigate relationships between breeding birds and opening density, spacing, and juxtaposition within a stand.

Most forest-interior species were not less abundant in and adjacent to gaps, and may not be edge sensitive. Hooded Warblers have nested in group-selection openings (Annand and Thompson 1997), although no nests were located in openings during our study (Moorman 1999). Canopy-dwelling species, such as Northern Parula and Blue-gray Gnatcatcher, commonly were observed foraging with family groups in the gaps (C. E. Moorman, *personal observation*). Early- and midsuccessional habitats characterized by a dense understory and thick ground cover provide important postfledging habitat for juveniles of species that breed in nearby mature forest (Anders et al. 1998, Vega Rivera et al. 1998). As growth of vegetation continues to reduce the abruptness between openings and the adjacent forest, gap specialists and some canopy species may increase their use of gaps as nesting, foraging, or brood-rearing habitat.

Abundance, in the absence of productivity measurements, can be a misleading indicator of habitat quality (Van Horne 1983). Hooded Warblers nesting close to gaps and other abrupt edges on our study site did not experience reduced reproductive success, despite evidence of Cowbird parasitism within close proximity to gaps and stand edges (Moorman 1999). Numbers of avian nest predators such as Blue Jays (*Cyanocitta cristata*) and American Crows (*Corvus brachyrhynchos*) were low (Moorman 1999) and apparently unaffected by treatments, but Brown-headed Cowbirds were most abundant at the edge of 0.5-ha gaps in one year. In Illinois, Brown-headed Cowbirds did not appear in wildlife openings <0.3 ha, and were most abundant in larger (0.7–1.0 ha) openings (Overcash and Roseberry 1987). Parasitism by Brown-headed Cowbirds is a major threat to the reproductive success of neotropical migrants (Mayfield 1977), and areas with high Cowbird densities may experience high parasitism rates (Hoover and Brittingham 1993). Further investigation of the effects of group selection on reproductive success of species breeding in southeastern bottomland forests is warranted.

Individual birds were recorded at more than one gap within and among years, so bird use of a single gap could have been partially altered by the presence and proximity of adjacent gaps (e.g., bird use of a small gap may have been higher because it was adjacent to a large gap). However, during each round of spot mapping and during each of the two rounds of mist netting, adjacent grids (gap and control) were sampled simultaneously to reduce the chance that the same bird would be counted in two different treatment replicates within a single visitation round. Each round of sampling was considered a snapshot of avian habitat use in the bottomland stand. Further, opening sizes were allocated randomly within the bottomland stand (i.e., big gaps were not always near small gaps), so effects of adjacent gaps should have roughly averaged out. Although creation of single replicates of each opening size in separate stands (blocks) may represent a better experimental design, such an approach was neither logistically feasible nor representative of actual group selection. In commercial harvests, the placement of group-selection openings typically is guided by the location of existing roads, the volume of timber to be removed, and the distribution of tree sizes and species, rather than by the distance to the nearest adjacent gap. However, research to determine whether stand-level opening density and spacing affect avian use of individual group-selection cuts is needed.

IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

When contemplating group selection as a viable forest management option for concurrent economic gain and wildlife conservation, one must consider several constraints. First, in order to provide adequate sunlight to regenerate preferred bottomland hardwood species, such as the moderately shade-intolerant and intolerant oaks, silvicultural openings must be $\geq$0.5 ha (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997). Second, landscape context must be considered when predicting the effects of selection harvests on songbird populations (Harris 1989). Group-selection openings created in a heavily fragmented landscape are likely to have greater negative effects (e.g., increased Cowbird parasitism) than openings in a heavily forested area like the Savannah River Site (Robinson et al. 1995). In fragmented landscapes, group-selection cuts may have all the negative features of clearcuts (e.g., increased brood parasitism and nest depredation rates) with the added impacts of increased edge and more roads (Pashley and Barrow 1993, King et al. 1998). Although Hooded Warbler productivity was minimally affected by group-selection openings on our study site (Moorman 1999), additional investigation of the effects of group selection on the reproductive success of other species in more heavily fragmented landscapes is needed.

Intermediate-scale disturbance, such as group selection, should increase local bird diversity by providing microhabitats not otherwise available within undisturbed forest (i.e., regenerating areas for field-edge bird species) while allowing most forest-interior species to remain at the same or slightly lower densities (Denslow 1985, Thompson et al. 1993, Lent and Capen 1995). Breeding Bird Survey data for the Upper Coastal Plain of the southeastern United States indicate that from 1966 to 1998, Indigo Bunting populations declined, yet populations of Acadian Flycatcher and other forest-interior species present on our site remained stable or increased (Sauer et al. 2000). Large (0.25–0.50 ha) openings would provide breeding habitat for species that prefer small, early-successional patches, such as Indigo Bunting and Common Yellowthroat, whereas small openings (<0.26 ha) would result in little change in the avian community. When timber harvesting and subsequent regeneration of commercially valuable species are management objectives, openings <0.5 ha most likely are inappropriate. Therefore, we believe that harvesting of 0.5-ha group-selection openings in bottomland forests embedded in relatively unfragmented landscapes represents a viable option from both silvicultural and avian conservation perspectives.

ACKNOWLEDGMENTS

Funding for the project was provided by the Department of Energy and the USDA Forest Service–Savannah River through the USDA Forest Service Southern Hardwoods Lab, under Cooperative Agreement SRS 30-CA-96-018. Experimental manipulations used in our study were conducted with support from USDA CSREES (Cooperative State, Research, Education and Extension Service) National Research Initiative Competitive Grant 93-37101-8662. W. M. Ford, W. P. Smith, and J. I. Blake were helpful during the genesis of the project. S. A. Gauthreaux, P. B. Hamel, J. C. Kilgo, J. D. Lanham, and L. E. Nix offered constructive comments on earlier versions of the manuscript, and N. V. L. Brokaw, J. D. Brawn, and one anonymous reviewer helped with further improvements. Clemson University provided travel support, and the personnel at the USDA Forest Service–Savannah River offered spontaneous on-site assistance. R. Katz, D. Moss, S. Welch, C. Collins, M. MacKinnon, J. Sircely, and J. Kilgo provided invaluable assistance in the field.

LITERATURE CITED

Anders, A. D., J. Faaborg, and F. R. Thompson III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. Auk **115**:349–358.

Annand, E. M., and F. R. Thompson. 1997. Forest bird response to regeneration practices in central hardwood forests. Journal of Wildlife Management **61**:159–171.

Blake, J. G., and W. G. Hoppes. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodlot. Auk **103**:328–340.

Blake, J. G., and J. R. Karr. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology **68**:1724–1734.

Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology **66**:682–687.

Clatterbuck, W. K., and J. S. Meadows. 1993. Regenerating oaks in the bottomlands. Pages 184–195 *in* D. L. Loftis and C. E. McGee, editors. Oak regeneration: serious problems, practical recommendations. USDA Forest Service Southeastern Forest Experiment Station General Technical Report SE-84, Asheville, North Carolina, USA.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. Pages 363–373 *in* S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Dickson, J. G. 1978. Forest bird communities of the bottomland hardwoods. Pages 66–75 *in* D. M. DeGraaf, editor. Proceedings of the workshop on management of southern forests for nongame birds. USDA Forest Service Southeastern Forest Experiment Station General Technical Report **SE-14**, Asheville, North Carolina, USA.

Freemark, K. E., and B. Collins. 1992. Landscape ecology of birds breeding in temperate forest fragments. Pages 443–454 *in* J. M. Hagan and D. W. Johnston, editors. Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, D.C., USA.

Germaine, S. S., S. H. Vessey, and D. E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. Condor **99**:708–718.

Hamel, P. B. 1989. Breeding bird populations on the Congaree Swamp National Monument, South Carolina. Pages 617–628 *in* R. R. Sharitz and J. W. Gibbons, editors. Freshwater wetlands and wildlife. Department of Energy (DOE) Symposium Series Number 61.

Hamel, P. B. 1992. The land manager's guide to the birds of the South. The Nature Conservancy, Southeastern Region, Chapel Hill, North Carolina, USA.

Harris, L. D. 1989. The faunal significance of fragmentation of southeastern bottomland forests. Pages 126–134 *in* D. D. Hook and R. Lea, editors. Proceedings of the Symposium on the Forested Wetlands of the Southeastern United States. USDA Forest Service Southeastern Forest Experiment Station General Technical Report **SE-50**, Asheville, North Carolina, USA.

Helle, P., and J. Muona. 1985. Invertebrate numbers in edges between clear-fellings and mature forests in northern Finland. Silva Fennica **19**:281–294.

Hodges, M. F., and D. G. Krementz. 1996. Neotropical migratory breeding bird communities in riparian forests of different widths along the Altamaha River, Georgia. Wilson Bulletin **108**:496–506.

Hoover, J. P., and M. C. Brittingham. 1993. Regional variation in Cowbird parasitism of Wood Thrushes. Wilson Bulletin **105**:228–238.

Hunter, W. C., D. N. Pashley, and R. E. F. Escano. 1993. Neotropical migratory landbird species and their habitats of special concern within the southeast region. Pages 159–171 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report **RM-229**, Fort Collins, Colorado, USA.

International Bird Census Committee. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Notes **24**:722–726.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes **24**: 727–736.

Kellison, R. C., and M. J. Young. 1997. The bottomland hardwood forest of the southern United States. Forest Ecology and Management **90**:101–115.

Kerpez, T. A. 1994. Effects of group-selection and clearcut openings on wildlife in Appalachian hardwood forests. Dissertation. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Kilgo, J. C., R. A. Sargent, B. R. Chapman, and K. V. Miller. 1998. Effect of stand width and adjacent habitat on breeding bird communities in bottomland hardwoods. Journal of Wildlife Management **62**:72–83.

King, D. I., R. M. DeGraaf, and C. R. Griffin. 1998. Edge-related nest predation in clearcut and groupcut stands. Conservation Biology **12**:1412–1415.

Lent, R. A., and D. E. Capen. 1995. Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest. Ecography **18**:97–108.

Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. Ecology **69**:1076–1089.

Martin, T. E., and J. R. Karr. 1986. Patch utilization by migrating birds: resource oriented? Ornis Scandinavia **17**: 165–174.

Mayfield, H. F. 1977. Brown-headed Cowbird: agent of extermination? American Birds **31**:107–113.

Meadows, J. S., and J. A. Stanturf. 1997. Silvicultural systems for southern bottomland hardwood forests. Forest Ecology and Management **90**:127–140.

Medin, D. E., and G. D. Booth. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. USDA Forest Service Intermountain Research Station Research Paper **INT-408**, Ogden, Utah, USA.

Minckler, L. S., J. D. Woerheide, and R. C. Schlesinger. 1973. Light, soil moisture, and tree reproduction in hardwood forest openings. USDA Forest Service North Central Forest Experiment Station Research Paper **NC-89**, St. Paul, Minnesota, USA.

Moorman, C. E. 1999. Relationships between artificially created gaps and breeding birds in a southeastern bottomland forest. Dissertation. Clemson University, Clemson, South Carolina, USA.

Nur, N., and G. R. Geupel. 1993. Evaluation of mist-netting, nest-searching and other methods for monitoring demographic processes in landbird populations. Pages 237–244 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report **RM-229**, Fort Collins, Colorado, USA.

Oliver, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management **3**:153–168.

Overcash, J. L., and J. L. Roseberry. 1987. Evaluation of Shawnee National Forest wildlife openings. Cooperative Wildlife Research Laboratory, SIU-C. Southern Illinois University, Carbondale.

Pashley, D. N. and W. C. Barrow. 1993. Effects of land use practices on neotropical migratory birds in bottomland hardwood forests. Pages 315–320 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report **RM-229**, Fort Collins, Colorado, USA.

Phillips, D. L., and D. J. Shure. 1990. Patch-size effects on early succession in southern Appalachian forests. Ecology **71**:204–212.

Remsen, J. V., and D. A. Good. 1996. Misuse of data from mist-net captures to assess relative abundance in bird populations. Auk **113**:381–398.

Robinson, S. K., F. R. Thompson III, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science **267**:1987–1990.

Robinson, W. D., and S. K. Robinson. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. Conservation Biology **13**:58–66.

Rodewald, P. G., and K. G. Smith. 1998. Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. Journal of Wildlife Management **62**:1411–1417.

Rotenberry, J. T., and J. A. Wiens. 1980. Habitat structure, patchiness, and avian communities in North American steppe vegetation: a multivariate analysis. Ecology **61**: 1228–1250.

Rudnicky, T. C., and M. L. Hunter, Jr. 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. Ecological Applications **3**:357–366.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology **63**:1533–1546.

SAS Institute. 1996. SAS user's guide: statistics. SAS Institute, Cary, North Carolina, USA.

Sauer, J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 2000. The North American Breeding Bird Survey, Results and Analysis 1966–1999. Version 98.1, USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA.

Schemske, D. W., and N. Brokaw. 1981. Treefalls and the distribution of understory birds in a tropical forest. Ecology **62**:938–945.

Strelke, W. K., and J. G. Dickson. 1980. Effect of forest clearcut edge on breeding birds in east Texas. Journal of Wildlife Management **44**:559–567.

Thompson, F. R., III, J. R. Probst, and M. G. Raphael. 1993. Silvicultural options for neotropical migratory birds. Pages 353–362 *in* D. M. Finch and P. W. Stangel, editors. Status and management of neotropical migratory birds. USDA Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report **RM-229**, Fort Collins, Colorado, USA.

USDA Forest Service. 1988. The South's fourth forest: alternatives for the future. USDA Forest Service Forest Resources Report Number 24, Washington, D.C., USA.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893–901.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush post-fledgling movements and habitat use in northern Virginia. Condor **100**:69–78.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**:90–105.

Whitman, A. A., J. M. Hagan III, and N. V. L. Brokaw. 1997. A comparison of two bird survey techniques used in a subtropical forest. Condor **99**:955–965.

Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland birds. Ornithological Monographs **8**:1–93.

Willson, M. F., E. A. Perter, and R. S. Condit. 1982. Avian frugivore activity in relation to forest light gaps. Caribbean Journal of Science **18**:1–6.

Wunderle, J. M., Jr., A. Diaz, I. Velazquez, and R. Schorron. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. Wilson Bulletin **99**:22–37.