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EFFECTS OF GROUP-SELECTION TIMBER HARVEST IN BOTTOMLAND HARDWOODS ON FALL MIGRANT BIRDS

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Abstract.—Due to projected demands for hardwood timber, development of silvicultural practices that provide for adequate regeneration in southeastern bottomland hardwoods without causing undue harm to wildlife resources is critical. Group-selection silviculture involves harvesting a small group of trees, which creates a canopy gap (usually <2 ha in size). Our objectives were to determine the extent of use of group-selection harvest gaps by fall migrant birds, to compare experimentally use of three sizes of gaps (10-m, 20-m, and 40-m radius), and to compare use of locations within gaps (center, edge, and adjacent forest). We captured 210 birds of 36 species in 1692 mist-net hours. Total captures were greater in 40-m radius gaps than in 20- and 10-m radius gaps and were greater in gap centers than at gap edges and adjacent forest. Forest interior/interior-edge Neotropical migrants and interior-edge short-distance migrants were captured most often in the centers of the largest gaps. We captured no interior-edge short-distance migrants or field-edge birds of any migratory group in the adjacent forest. A threshold gap size determining use by migrant birds may exist between 20 and 40 m in radius. Though reasons for greater capture success in gaps are unclear, forest interior Neotropical and short-distance migrants apparently shifted their habitat preferences during fall to include forest gap habitat.

EFECTO EN LAS AVES MIGRATORIAS DE LA TÉCNICA DE SELECCIÓN DE GRUPOS DE ÁRBOLES PARA EL COSECHO DE MADERA EN BOSQUES CON MADERAS DURAS EN TIERRAS BAJAS

Sinopsis.—Debido a la proyectada demanda de maderas duras en tierras bajas, es crítico el desarrollo de prácticas de silvicultura que provean de la regeneración adecuada de dichos bosques sin que se afecte la vida silvestre en dichas localidades. Las prácticas de silvicultura de selección de grupos, envuelven el cosecho de grupos pequeños de árboles, que crean aberturas en el docel (usualmente menos de 2 ha en tamaño) del bosque. Nuestro objectivo fue determinar el uso de dichas aberturas o claros por parte de aves migratorias y comparar, experimentalmente, el uso de claros de tres diferentes tamaños (radios de 10, 20 y 40 m) además del uso de localidades entre las aberturas (centro, borde y bosques adyacentes). Capturamos 210 pájaros pertenecientes a 36 especies en 1692 horas de captura con redes de niebla. Las capturas totales fueron mayor en los claros con radios de 40 m y en el centro de dichas aberturas comparado con los otros parámetros experimentales. Migratorios neotropicales del interior y el interior-y-borde de bosques y migratorios de cortas distancias del interior-y-borde de bosques, fueron capturados con mayor frecuencia en el centro de los claros de mayor tamaño. En bosques adyacentes no capturamos especies migratorias típicas de campos y bordes o migratorios de cortas distancias del interior-y-borde de bosques. Es posible exista un umbral en el tamaño de los claros que determine el uso por parte de los

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migrantes entre los radios de 20 a 40 m. Aunque no están claras las razones por las cuales se capturan mayor cantidad de aves en las aberturas, migrantes neotropicales del interior de bosques y migrantes a cortas distancias aparentemente cambian sus preferencias de habitats durante el otoño para incluir habitats formados por aberturas en el docel de los bosques.

Southeastern bottomland hardwood forests are an important source of hardwood timber, and demands on these forests are likely to increase. Hardwood timber removals by 2030 are projected to have increased by 64% over 1984 levels (USDA Forest Service 1988). Development of silvicultural practices that provide adequate hardwood regeneration on these sites is critical, and this field constitutes an arena of active research. Concurrent with such research, effects of various timber regeneration methods on wildlife habitat dynamics also should be evaluated.

Group-selection harvesting is a potential alternative to clear-cutting. Group selection is an uneven-aged system that involves the removal of groups of trees to create a canopy gap, usually <2 ha. These gaps allow sufficient light to reach the forest floor to encourage regeneration of desirable hardwood species. Ideally, these openings would mimic natural tree-fall gaps in their positive effect on establishment of regeneration.

Effects of group-selection timber harvesting on wildlife in bottomland hardwoods largely are unknown. Timber harvest should influence bird use of these habitats because many bird species are closely associated with vegetation structure (James 1971, Wilson 1974). Forest openings may impact breeding forest birds negatively, leading to greater rates of nest predation or parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Wilcove 1985), though little evidence supports this possibility for southern bottomland hardwoods. Likewise, the effects of such gaps on migrating birds are unknown. Habitat change (e.g., timber harvest) along migration routes may have negative effects on Neotropical migrants (Moore and Simons 1992). Conversely, timber harvest may enhance habitat quality for some species during migration; increased light availability in harvest gaps may enhance soft mast productivity (Levey 1988) and may increase insect abundance by providing additional foraging substrates (Blake and Hoppes 1986). Thus, species of birds that breed in interior forest conditions may be attracted to canopy gaps during migration due to increased resource availability. Previous studies of migrant bird use of gaps surveyed birds in natural gaps (Willson et al. 1982, Blake and Hoppes 1986, Martin and Karr 1986) and, therefore, are correlative in nature. We used an experimental approach to determine the extent of use of gaps by fall migrant birds, to compare use of three sizes of gaps by fall migrants, and to compare use of various locations within gaps and adjacent forest. We focus on groupings defined by migratory status and breeding season habitat use.

STUDY AREA

This study was part of a multidisciplinary research project on gap dynamics in group-selection timber harvests that was conducted on the Sa-

vannah River Site, a 77,891-ha tract in Aiken, Barnwell, and Allendale counties, South Carolina (33°10′N, 81°40′W). The specific study sites were contiguous stands (total area = 120 ha) of second-growth bottomland hardwoods along the eastern edge of the Savannah River floodplain. The stands were logged ca. 1900 but have experienced little subsequent anthropogenic disturbance (Workman and McLeod 1990). The canopy ranged in height from 22–28 m and was composed primarily of bottomland oaks (overcup, *Quercus lyrata*; cherrybark, *Q. falcata* var. *paegodifolia*; willow, *Q. phellos*; laurel, *Q. laurifolia*; and swamp chestnut, *Q. michauxii*), sweetgum (*Liquidambar styraciflua*), loblolly pine (*Pinus taeda*), and red maple (*Acer rubrum*). The understory was composed primarily of dwarf palmetto (*Sabal minor*) and switchcane (*Arundinaria gigantea*) <2 m in height, and the midstory generally was open.

Thirty-six group-selection cuts, composing six replicates of six sizes (7–40 m in radius, 0.02–0.5 ha), were harvested during December 1994. These sizes fall within the range of commercial group-selection prescriptions and are comparable to naturally occurring windthrow gaps. Locations of gaps within the stand were selected such that mature oaks were present on the periphery of each to provide a seed source for regeneration. We sampled six of the gaps, two replicates each of three sizes (10, 20, and 40-m radius), to compare bird use among gap sizes. Mean distance between gaps was 64 m. Vegetation structure was similar among gaps during the study and averaged 0.9 m in height (C. E. Moorman, unpubl. data). Gaps were dominated by dwarf palmetto and herbaceous species, primarily *Eupatorium serotinum* and *E. capillifolium* (Castleberry et al. 1996).

METHODS

Fall migrant birds were sampled with mist nets from 3 Sep.–21 Oct. 1996. This interval covered the period of peak use of the site by Neotropical migrants in transit. We placed one net (2.6 × 12 m, 38-mm mesh) at the gap center, on the north edge, and 30 m into the forest north of the north edge in each of the six gaps. The north azimuth was used for this transect to minimize the potential bias of variation in vegetation structure caused by differential light availability within gaps. We used 38-mm-mesh nets to facilitate comparison of results with a concurrent study in which this size was used to sample breeding bird use of the study site (C. E. Moorman, unpubl.). Although 38-mm mesh may under-sample small passerines, treatment effects should not be confounded. All 18 nets were opened each day for 3 days per week. We began opening nets at first light and closing nets at approximately 1100 h. Captured birds were identified to species, age, and sex; weighed; banded with a metal leg band (Biological Resources Division, U.S. Geological Survey); and released. Due to small sample sizes, age, sex, and mass data were not analyzed. For analysis, we grouped species according to migratory status and breeding season habitat use as follows: forest interior and interior-edge Neotropical migrants; field-edge Neotropical migrants; interior-edge short-distance mi-

grants; field-edge short-distance migrants; and interior-edge residents (Whitcomb et al. 1981; Table 1). Because the number of net-hours was constant for all nets (i.e., each net was operated for 94 h) we used the total number of captured individuals (excluding recaptures) within a group for analysis. We compared numbers of individuals among gap sizes (including center, edge and forest nets for each gap) and net locations using a two-factor analysis of variance (ANOVA; SAS Inst. 1990), and we used Tukey's w procedure to separate means. We used Bonferroni-adjusted probabilities (Beal and Khamis 1991) to ensure an experiment-wide error rate of $\alpha = 0.05$. This procedure decreased the P value for significance from 0.05 to 0.01 because we analyzed five response groups.

RESULTS

We captured 210 birds of 36 species in 1692 net hours. Thirty-eight individuals subsequently were recaptured for a total of 248 captures. The overall capture rate, including recaptures, was 15 birds/100 net hours. Total individuals, by migratory/habitat use group, were: 85 forest interior and interior-edge Neotropical migrants, 11 field-edge Neotropical migrants, 38 interior-edge short-distance migrants, 12 field-edge short-distance migrants, and 64 interior-edge residents (Table 2). Total individuals for all groups combined were affected by both gap size ($F_{2,9} = 9.73$, $P < 0.001$) and net location ($F_{2,9} = 11.19$, $P < 0.001$; Tables 3–4); captures were greater ($P < 0.01$, Tukey's test) in 40-m radius gaps than in 10- and 20-m radius gaps and greater in gap centers than edges and closed-canopy forest. Two of the migratory/habitat use groups exhibited differential use of gap sizes and net locations: forest interior/interior-edge Neotropical migrants (gap size: $F_{2,9} = 13.13$, $P = 0.002$; net location: $F_{2,9} = 10.43$, $P = 0.005$) and interior-edge short-distance migrants (gap size: $F_{2,9} = 154.75$, $P < 0.001$; net location: $F_{2,9} = 164.25$, $P < 0.001$). The interactions between gap size and net location were significant for both groups ($P < 0.001$); more birds were captured in the centers of the largest gaps. At the smaller gap sizes, number of individuals by net location did not differ. Although only 12 thrushes were captured during the study, the four species of thrushes were the only species within the forest interior/interior-edge Neotropical migrant group that were not captured in the centers of gaps. No interior-edge short-distance migrants and no field-edge birds of any migratory group were captured in the closed-canopy forest.

DISCUSSION

In our study, total number of individuals captured was greatest in the centers of the largest gaps. This pattern was especially pronounced for forest Neotropical and short-distance migrants. In contrast, Levey (1988) found no difference in the average number of mist net captures between large (approximately 0.5 ha, D. J. Levey, pers. comm.) and small gaps (approximately 0.02–0.06 ha or 1–4 treefalls) in tropical wet forest in Costa Rica, though he did find greater use of gap habitat than forested

TABLE 1. Mist-net captures by species during fall migration, 3 Sep.–21 Oct. 1996, within gaps in a group-selection-harvested bottomland hardwood forest in South Carolina.

Species	Total
Forest Interior/interior-edge Neotropical migrants	85
Eastern Wood-Pewee (*Contopus virens*)	2
Acadian Flycatcher (*Empidonax virescens*)	5
Veery (*Catharus fuscescens*)	4
Gray-cheeked Thrush (*Catharus minimus*)	1
Swainson's Thrush (*Catharus ustulatus*)	1
Wood Thrush (*Hylocichla mustelina*)	5
Tennessee Warbler (*Vermivora peregrina*)	1
Northern Parula (*Parula americana*)	6
Magnolia Warbler (*Dendroica magnolia*)	7
Black-throated Blue Warbler (*Dendroica caerulescens*)	6
Black-throated Green Warbler (*Dendroica virens*)	1
Black-and-white Warbler (*Mniotilta varia*)	1
American Redstart (*Setophaga ruticilla*)	13
Worm-eating Warbler (*Helmitheros vermivorus*)	1
Ovenbird (*Seiurus aurocapillus*)	5
Northern Waterthrush (*Seiurus noveboracensis*)	12
Hooded Warbler (*Wilsonia citrina*)	13
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	1
Field-edge Neotropical migrants	11
Chestnut-sided Warbler (*Dendroica pensylvanica*)	2
Yellow-breasted Chat (*Icteria virens*)	4
Indigo Bunting (*Passerina cyanea*)	5
Interior-edge short-distance migrants	38
Ruby-crowned Kinglet (*Regulus calendula*)	2
Hermit Thrush (*Catharus guttatus*)	1
Gray Catbird (*Dumetella carolinensis*)	5
White-eyed Vireo (*Vireo griseus*)	13
Common Yellowthroat (*Geothlypis trichas*)	13
Eastern towhee (*Pipilo erythrophthalmus*)	4
Field-edge short-distance migrants	12
Brown Thrasher (*Toxostoma rufum*)	3
Swamp Sparrow (*Melospiza georgiana*)	4
White-throated Sparrow (*Zonotrichia albicollis*)	5
Interior-edge residents	64
Red-bellied Woodpecker (*Melanerpes carolinus*)	3
Downy Woodpecker (*Picoides pubescens*)	1
Carolina Chickadee (*Poecile carolinensis*)	4
Tufted Titmouse (*Baeolophus bicolor*)	13
Carolina Wren (*Thryothorus ludovicianus*)	26
Northern Cardinal (*Cardinalis cardinalis*)	17
Total	210

TABLE 2. Mist-net captures during fall migration, 3 Sep.–21 Oct. 1996, by gap size and net location within gaps in a group-selection-harvested bottomland hardwood forest in South Carolina.

Group	Gap size (radius)									Total
	10 m			20 m			40 m			
	Center	Edge	Forest[a]	Center	Edge	Forest	Center	Edge	Forest	
Forest interior/interior-edge Neotropical migrants	3	3	2	8	8	2	43	11	5	85
Field-edge Neotropical migrants	0	0	0	2	0	0	9	0	0	11
Interior-edge short-distance migrants	1	1	0	5	2	0	23	6	0	38
Field-edge short-distance migrants	1	2	0	1	0	0	7	1	0	12
Interior-edge residents	13	7	2	7	3	7	8	14	3	64
Total	18	13	4	23	13	9	90	32	8	210

[a] Forest nets were 30 m from gap edges.

TABLE 3. Comparison of mist-net captures (mean (SE) per net) during fall migration, 3 Sep.–21 Oct. 1996, among three sizes of group-selection harvest gaps in a bottomland hardwood forest in South Carolina. Means followed by the same letter do not differ ($P > 0.01$).

Group	10-m radius	20-m radius	40-m radius	P
Forest interior/interior-edge Neotropical migrants	1.3 (0.4) B	3.0 (1.0) B	9.7 (4.0)A	0.002
Field-edge Neotropical migrants	0.0 (0.0) A	0.3 (0.1) A	1.5 (1.1) A	0.155
Interior-edge short-distance migrants	0.3 (0.2) B	1.2 (0.5) B	4.8 (2.2) A	0.001
Field-edge short-distance migrants	0.5 (0.3) A	0.2 (0.2) A	1.3 (1.1) A	0.523
Interior-edge residents	3.7 (1.3) A	2.8 (0.9) A	4.2 (1.2) A	0.611
Total	5.8 (1.9) B	7.5 (4.9) B	21.7 (8.3) A	0.006

habitat. Number of birds in our study increased consistently with increasing gap size, but birds did not differentiate among closed-canopy forest understory ($\bar{x} = 3.5$ individuals/net, $n = 6$ nets) and 10-m radius gaps ($\bar{x} = 5.8$). Overall, however, birds were more abundant in gaps ($\bar{x} = 21.8$) than in closed-canopy forest ($\bar{x} = 3.5$; Table 4). Moreover, 40-m radius gaps averaged almost three times as many individuals ($\bar{x} = 21.7$) as 20-m radius gaps ($\bar{x} = 7.5$; Table 3). These results suggest that a threshold in gap size may exist for southern bottomland hardwood forests, above which use of gaps by migrating birds increases disproportionately. Our data indicate that this threshold is a forest opening with a radius between 20 and 40 m.

The greater capture success in gaps often is related to greater availability of soft mast (Levey 1988, Martin and Karr 1986, Thompson and Willson 1978). Avian use of Costa Rican gaps was associated with high

TABLE 4. Comparison of mist-net captures (mean (SE) per net) during fall migration, 3 Sep.–21 Oct. 1996, among three net locations within group-selection harvest gaps in a bottomland hardwood forest in South Carolina. Means followed by the same letter do not differ ($P > 0.01$).

Group	Center	Edge	Forest	P
Forest interior/interior-edge Neotropical migrants	9.0 (4.2) A	3.7 (1.1) AB	1.3 (0.3) B	0.005
Field-edge Neotropical migrants	1.8 (1.1) B	0.0 (0.0) B	0.0 (0.0) B	0.052
Interior-edge short-distance migrants	4.8 (2.2) A	1.5 (0.5) B	0.0 (0.0) C	0.001
Field-edge short-distance migrants	1.5 (1.1) A	0.5 (0.3) A	0.0 (0.0) A	0.366
Interior-edge residents	4.7 (1.1) A	4.0 (1.2) A	2.0 (0.7) A	0.165
Total	21.8 (8.1) A	9.7 (2.4) B	3.5 (0.7) B	0.004

concentrations of fruiting plants (Levey 1988). Likewise, Martin and Karr (1986) and Willson et al. (1982) reported greater use of gaps by fall migrants in an Illinois woodlot, which they associated with greater foliage cover of fruiting plants. However, the most abundant fruiting species within our gaps were dwarf palmetto and American beautyberry (*Callicarpa americana*). Because we sampled birds after the second growing season post-harvest, many fruiting plants more highly preferred by birds (e.g., *Vitis, Smilax, Parthenocissus, Toxicodendron,* etc.), though present, did not fruit (JCK, pers. observ.). These plants require woody substrates to fruit and these substrates had not yet regenerated sufficiently to support vines. Thus, soft mast availability apparently was a minor factor affecting bird use of our gaps.

Greater capture success in gaps than in closed-canopy forest also has been related to increased structural diversity of gap understory habitat, which provides increased foraging opportunities for foliage gleaning insectivores (Blake and Hoppes 1986, Levey 1988, Martin and Karr 1986). Capture rates of foliage insectivores correlated positively with insect abundance during fall migration in gaps in an Illinois woodlot (Blake and Hoppes 1986). Additionally, because understory density often is associated with greater soft mast availability, the structure of the gaps may attract frugivorous birds, regardless of actual fruit availability. Most migrants are insectivorous during spring and summer but shift their diet preferences to fruit during fall (Levey and Stiles 1992). Thus, greater understory density alone may be sufficient to explain the higher capture rates. Whatever the proximal cause of the observed pattern, our results corroborate the findings of other studies (Blake and Hoppes 1986, Hutto 1985, Levey 1988, Martin and Karr 1986, Willson et al. 1982, Winker et al. 1992) that many forest-dwelling migratory birds exhibit a seasonal shift in understory habitat use away from forested habitat towards shrub/scrub habitat.

The apparent shift in habitat use away from forested habitat may result from a bias in sampling methodology. For example, midstory and canopy birds generally are not sampled adequately with standard mist nets and may therefore have been under-represented in our closed-canopy forest captures. Also, variation in flight patterns among habitats due to differences in vegetation height (Remsen and Good 1996) could have influenced capture rates because mist nets sample only the bottom 2.6 m of the forest. However, two lines of evidence suggest that the observed pattern was not entirely a result of mist-netting bias. First, midstory and canopy species that are common on the study site during the breeding season (e.g., Acadian Flycatcher, Eastern Wood-Pewee, Northern Parula; see Table 1 for scientific names) were not captured in gaps at that time (C. E. Moorman, unpubl. data), but were captured there during fall, indicating a seasonal movement into gaps. Second, many species that exhibited the apparent habitat shift were understory species (e.g., Black-throated Blue Warbler, Hooded Warbler, Northern Waterthrush) that are susceptible to mist-net sampling in forested habitat. For example, Hooded Warblers

were captured primarily in forested habitat on the study site during the breeding season (C. E. Moorman, unpubl. data), yet only 1 of the 13 we captured during fall was in the forest. Though a vertical shift in habitat use is possible (i.e., continued use of forests but above mist net level), these data reflect a lateral shift into gap understory habitat. Additionally, the magnitude of the difference between gap and forested habitat for groups with higher capture rates in gaps (edge nets excluded) was 12-fold. Thus, we believe that the results at least partially reflect habitat preference. Nevertheless, inferences related to differences in abundance between gap and closed-canopy forest should be viewed with caution. Comparisons of capture rates among gap sizes should not be subject to the same bias because vegetation height was similar among gap sizes.

We conclude that group-selection harvest gaps apparently increased the utility of the bottomland hardwood forest to many species of migrating birds during the fall. Despite the uncertainty surrounding potential sampling biases, we documented use of the gaps by many species of fall migrants, several of which did not use gaps during the breeding season. Future work should address resource availability and foraging ecology within gaps. If migrants are attracted to gaps based on their gross understory structure, but are unable to forage efficiently then gaps may serve only to drain limited energy reserves. Also, until information on the effects of gaps on the breeding productivity of migrants is available, the net overall value of this habitat to Neotropical and short-distance migrants remains unclear.

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