SHORT-TERM BREEDING BIRD RESPONSE TO TWO HARVEST PRACTICES IN A BOTTOMLAND HARDWOOD FOREST

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ABSTRACT.—Clearcutting is the preferred timber harvest method in bottomland hardwood forests because it is most likely to result in regeneration of preferred species. However, clearcutting generally has negative impacts on forest birds. Patch-retention harvesting may provide similar silvicultural benefits, but its effects on birds are unknown. We surveyed breeding birds in uncut control, clearcut, and patch-retention treatment areas (11–13 ha) for one season prior to harvest and two seasons postharvest in a bottomland hardwood forest in the Lower Coastal Plain of southeastern South Carolina. Bird observations recorded along line transects were analyzed using the software EstimateS to estimate species richness and program Distance to estimate densities. We found greater species richness and bird densities in the patch-retention treatment than in the clearcut in both postharvest seasons. We detected no forest-interior birds in the clearcut after the harvest, but by the second postharvest season in the patch-retention treatment, the density of forest-interior birds had returned to approximately half of its preharvest level. Thus, based on density response, patch-retention harvesting appears to be less detrimental to forest birds than clearcutting. However, additional work is needed to determine whether retained patches influence avian survival and productivity. *Received 30 April 2004, accepted 30 October 2004*.

Bottomland hardwood forests in the southeastern United States serve as critical breeding habitat for numerous avian species, including many considered by Partners in Flight to be of high conservation concern (Hunter et al. 1993, Rich et al. 2004). Historical loss and fragmentation of these forests by conversion to agriculture, development, and other activities, concurrent with possible functional changes in the remaining forests, have likely contributed to the reduction in bird populations (Pashley and Barrow 1993). According to the National Resource Inventory of 1992 (Shepard et al. 1998), the area covered by wooded palustrine wetlands in the South declined by only about 1.5% from 1982 to 1992, a marked reduction in the rate of loss compared with that in preceding decades. Despite this apparent stabilization of forested wetland area, a much higher proportion of woodland Neotropical migrant species was in decline in the eastern United States over the period 1982-1991 than during 1966-1979 (Peterjohn and Sauer 1994). Thus, some aspect of the quality, not just quantity, of the existing bottomland hardwood forest may be a factor in

the decline of birds (Pashley and Barrow 1993). Indeed, much of the extant bottomland hardwood forest is now in streamside management zones and drainages <50 m wide (Kilgo et al. 1998).

Of the approximately 194 million ha of forested land in the United States during 1989, 85 million ha were in the southern U.S. (Wigley and Sweeney 1993). The forest products industry (18.8%) and individual landowners (71.1%) combined held title to nearly 90% of these forested lands (Wigley and Sweeney 1993). Ownership of bottomland hardwoods was apportioned in roughly the same manner, and nearly 20 million ha of non-federally owned, palustrine-forested wetlands were present in the South (Shepard et al. 1998). The primary use of these lands is for timber production (Wigley and Sweeney 1993). If existing bottomland hardwood forests are to remain a viable resource for Neotropical migratory birds, management options that minimize negative effects on breeding birds, but are acceptable to the forest products industry and private landowners, need to be identified and their use encouraged.

From a silvicultural perspective, clearcutting is the favored means of harvesting these forests (Clatterbuck and Meadows 1993, Meadows and Stanturf 1997). Among the reasons for its appeal is that it is the method that best promotes regeneration of shade-intolerant species such as oaks (*Quercus* spp.; Clatter-

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buck and Meadows 1993). The abundance of shrub-successional birds, several of which are of conservation concern (Rich et al. 2004), as well as total bird abundance, can be as great or greater in clearcuts (Hurst and Bourland 1996) and other early successional habitats (Buffington et al. 1997) as in mature bottomland hardwood forest. However, species richness and diversity are highest in mature bottomland hardwoods (Hurst and Bourland 1996, Buffington et al. 1997), and the impacts of clearcutting on most species that prefer mature forest-interior conditions are negative (Hurst and Bourland 1996, Baker and Lacki 1997). Thus, we need alternatives to clearcutting that retain the advantages for forest regeneration but that are less damaging to bird species that inhabit mature forest.

Several studies have been conducted to evaluate the impacts on birds of one such alternative, group-selection harvest. In this method, small groups of mature trees are cleared from a stand at regular spacing intervals (Meadows and Stanturf 1997). Moorman and Guynn (2001) concluded that when adequate mature forest was left unharvested, the abundance of most breeding forest-interior species was not impacted by group-selection harvest. Similarly, Moorman et al. (2002) determined that the productivity of a representative forest-interior species, the Hooded Warbler (Wilsonia citrina), was minimally affected. Kilgo et al. (1999) concluded that groupselection harvest gaps benefited many species of migrating forest-interior birds because they used the early successional patches during passage. However, when applied in the strictest sense (gap size no greater than 0.5 ha), this technique usually favors regeneration of stands that are dominated by low-value, shade-tolerant trees because of limitations on light availability (Meadows and Stanturf 1997).

Two-age harvest prescriptions, in which a predetermined quantity of basal area is retained in an even distribution across the site (a modification of the shelterwood method), have also been evaluated (Baker and Lacki 1997, Norton and Hannon 1997, Duguay et al. 2001). In Kentucky, such prescriptions did not alleviate negative effects of clearcutting on the abundance of certain forest-interior birds, but some indices of bird community structure

were higher in harvested areas (Baker and Lacki 1997). In Canadian boreal forest, seven of eight bird species lost from clearcuts were retained at low abundance levels in partial cuts (Norton and Hannon 1997). In hardwood forests of West Virginia, avian abundance and nesting success were comparable for most bird species tested among control areas, twoage harvest, and clearcut treatments 15 years after harvest (Duguay et al. 2001). Both Norton and Hannon (1997) and Duguay et al. (2001) concluded that the two-age method was a viable conservation alternative. However, from a timber management perspective, shelterwood methods can be difficult to implement because of the critical importance of choosing the appropriate establishment cutting intensity (Meadows and Stanturf 1997).

A third alternative, representing a hybrid of group selection and clearcutting methods, is patch-retention harvest, in which residual trees and snags are retained in small patches that mimic or actually represent remnants of the original forest. Patch-retention harvesting is appealing to forest managers, because leaving patches of uncut forest is operationally easier (for equipment such as feller-bunchers) than attempting to retain a high basal area of more evenly distributed trees (Tittler et al. 2001; J. P. Martin, MeadWestvaco Corporation, pers. comm.). Additionally, the incidence of windthrow may be lower for trees in patches compared with isolated residual trees. Reported impacts to forest bird communities have been less severe in patch-retention harvests than in clearcuts within boreal forests of Canada (Schieck et al. 2000, Tittler et al. 2001) and aspen forests in Minnesota (Merrill et al. 1998). However, this method has not been widely tested.

Our objective was to compare the effects on bird species composition of retaining patches of bottomland hardwood forest within a clearcut with performing a traditional clearcut or leaving the forest intact (unharvested control). In particular, we addressed whether the responses of individual species and/or avian habitat-use groups differed between a patch-retention cut and a clearcut area, and whether bird species composition changed in these areas from preharvest to 2 years post-harvest. In effect, we sought to determine whether bird species composition of the

patch-retention area more closely resembled that of the unharvested control, particularly with respect to birds that depend on mature forest-interior habitat.

METHODS

The study was conducted on a 350-ha area located in the Lower Coastal Plain of southeastern South Carolina on the floodplain of the fourth-order, blackwater Coosawhatchie River (Burke et al. 2003), a relatively small, anastomosing stream that drains an area of approximately 1,000 km². Topography in the low-relief (≤2 m) floodplain is characterized by a network of slightly elevated hummocks and scour channels (Burke et al. 2003). Water tupelo (Nyssa aquatica), swamp tupelo (N. sylvatica var. biflora), sweetgum (Liquidambar styraciflua), bald cypress (Taxodium distichum), laurel oak (Quercus laurifolia), and red maple (Acer rubrum) dominate the plant communities of the floodplain (Burke et al. 2000). Where present, the understory (in undisturbed forest) consists of widely scattered patches of Vaccinium spp., Sabal minor, and Arundinaria gigantea; very little under- or midstory structure exists.

Three 11- to 13-ha treatment areas were established in the fall of 1999: an uncut control, a patch-retention area, and a clearcut. This size range approximated an operational harvest. The three treatment areas were arranged linearly, parallel to the direction of water flow. They were approximately equidistant (300– 400 m) from the main body of the Coosawhatchie River and were similar with respect to soils, hydrology, and preharvest plant communities (Burke et al. 2000, Eisenbies and Hughes 2000, Murray et al. 2000). A 100-m forested buffer separated the patch-retention from the clearcut area, with a somewhat narrower and more irregular buffer between the uncut control and patch-retention areas. In the patch-retention treatment, three "patches" of two sizes (two 0.20 ha and one 0.61 ha) were left uncut, one each in an area representative of a convex, concave, or flat landform. Thus, 1.01 ha of forest was retained within the 13.1ha patch-retention treatment area. Using the average basal area for the study site (46 m²/ ha; Burke et al. 2003), the residual basal area of the patch-retention treatment was 3.6 m²/ ha.

We surveyed breeding birds along line transects (Bibby et al. 2000) for 1 year preharvest (1999) and 2 years postharvest (2000-2001). We arranged transects such that each treatment area was completely covered without duplication of coverage, assuming a 50-m detection zone on each side of the line. We conducted three to four counts each year between 15 May and 11 June. Single-observer surveys began around 06:00 EST and continued until all treatments had been surveyed, usually around 11:00. During each survey, the observer proceeded along the transect, stopping only to record detections. The observer mapped locations of all birds encountered by sight and/or sound and estimated the perpendicular distance (0–50 m, to the nearest 10 m) from the transect line to detected individuals. To account for the potentially confounding effect of time of day, we varied the order in which the treatments were surveyed.

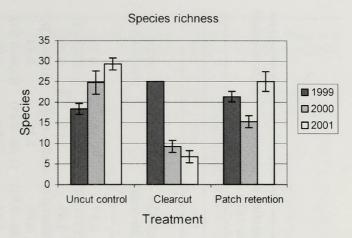
We estimated species richness using the software EstimateS, ver. 6.0b1 (Colwell 1997). Based on detection data, this program provides values for several species-richness estimators. We present the first-order jackknife estimates because they are robust and have performed well in other studies (as cited in Nichols et al. 1998, Hellmann and Fowler 1999). We obtained density estimates using program Distance, ver. 3.5 (Thomas et al. 1998). We used grouped data (10-m intervals) stratified by treatment and year. Although they were not independent, we treated each visit to a given treatment within a season as a "replicate." Upon determination of the most appropriate model for the detection function (uniform, half-normal, or hazard rate) using likelihood ratio tests, Distance provides an estimate of density and error (Buckland et al. 1993). Because Distance bases each density estimate on a unique detection function, the estimates can be compared among sites with differences in detectability. We tested for annual differences in estimated density within each treatment area by determining whether the 95% confidence intervals overlapped; we accepted as different those confidence intervals that did not overlap (Hodges and Krementz 1996). We compared density estimates for all birds combined, for individual species with at least 25 observations, and for four avian habitat-use groups: forest interior (I), interior-edge (I-E), field-edge (F-E), and edge-shrub (E-S) (Whitcomb et al. 1981).

Logistical constraints prevented us from replicating our treatment units in an experimental manner; harvesting multiple units on the study area was not feasible or desirable for the landowner. We used a before-after, control impact (BACI) design (Johnson 2002), in which we sampled both before and after the harvest treatments on both control and treatment areas. This design was used in an attempt to minimize the effect of variables unrelated to the treatments. Nevertheless, our results must be viewed with caution, since—lacking replication—we do not know whether they would be applicable on other sites.

RESULTS

Prior to the harvest (1999), the estimated species richness of breeding birds was lower in the control area than in the patch-retention area (Fig. 1). However, we could not make statistical comparisons between the estimate from the clearcut area in 1999 with the others, because it had a variance of 0 (the first-order jackknife estimator uses the number of unique species recorded on multiple visits; since we detected two unique species on each visit, the variance of these identical values was 0). Estimated total density did not differ among the three treatment areas prior to harvest (Fig. 1).

Following harvest, total density was similar and species richness actually increased in the uncut control area. However, both measures declined immediately after harvest (2000) in both the clearcut and patch-retention areas (Fig. 1). The decrease was especially large in the clearcut, where estimated species richness declined from 25.0 to 9.3, and estimated density fell from 33.0 to 2.8 pairs/10 ha. In the second postharvest year (2001), density increased in both the clearcut (Fig. 1) and patchretention (nonsignificantly) areas. Species richness rebounded in the patch-retention area, rising from 15.3 to 25.0, but not in the clearcut. From preharvest to 2 years postharvest in the clearcut, 15 species of the forestinterior or interior-edge groups disappeared, whereas 5 species of these groups disappeared in the patch-retention area (Tables 1 and 2). During the postharvest period, species composition also changed in both treatments. In the clearcut, only 2 of 11 (18%) species de-



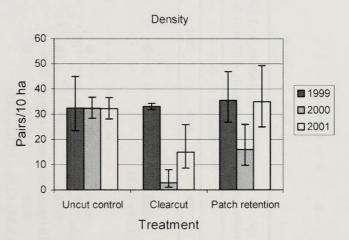


FIG. 1. Species richness and density (mean ± 95% confidence intervals) for breeding birds in three harvest treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. No confidence interval is given for species richness in the clearcut area in 1999 because the variance was 0 (see text for explanation).

tected postharvest were recorded in both postharvest seasons (Tables 1 and 2), whereas in the patch-retention area, 11 of the 21 (52%) species detected postharvest were recorded in both seasons.

In the patch-retention area, 35 of 43 (81%) birds observed in 2000 were recorded within retained forest patches, but in 2001, only 37 of 89 (42%) observations occurred in retained forest patches. Although the total number of birds observed in the patch-retention area essentially doubled, the number of birds observed within the retained patches remained about the same.

We estimated densities for 11 species (Table 1). Individual species appeared to respond to the clearcut treatment in different ways. Three of the 11 species had disappeared after

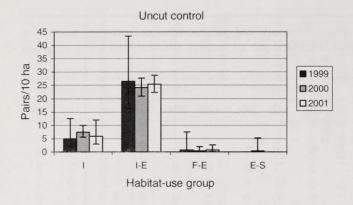
		Uncut control			Clearcut			Patch retention	
Species (no. of observations)	1999	2000	2001	1999	2000	2001	1999	2000	2001
Forest-interior species									
Acadian Flycatcher (93)	4.47	5.03	2.80	4.88	0	0	3.63	0	0.18
(Empidonax virescens)	(1.97-10.2)	(1.97–10.2) (3.54–7.16)	(1.65–4.75)	(1.24–19.3)			(1.36–9.68)		(0.01–2.57)
Interior-edge species									
Red-bellied Woodpecker (35)	1.99	1.12	1.68	1.44	•	0	0.97	0.18	0.36
(Melanerpes carolinus)	(1.16-3.40)	(0.40 - 3.14)	(0.86 - 3.28)	(0.27-7.53)			(0.13-7.39)	(0.01-2.57)	(0.03-5.14)
Great Crested Flycatcher (37)	1.24	0.74	1.86	98.0	0.65	0	1.45	1.26	0.36
(Myiarchus crinitus)	(0.15-10.5)	(0.21-2.60)	(0.99-3.50)	(0.09-8.66)	(0.23-1.81)		(0.19-11.1)	(0.26-6.05)	(0.07-2.00)
Red-eyed Vireo (127)	7.24	4.66	4.47	8.26	0.22	0	6.05	2.38	0.54
(Vireo olivaceus)	(4.72-11.1)	(3.19-6.82)	(3.60-5.55)	(5.34-12.8)	(0.02 - 3.05)		(3.84 - 9.53)	(1.48-3.83)	(0.08 - 3.50)
Carolina Chickadee (43)	2.34	1.49	1.68	98.0	0.43	0	4.44	0.54	1.93
(Poecile carolinensis)	(0.48-11.5)	(0.30 - 7.46)	(0.52-5.39)	(0.02-31.0)	(0.08-2.37)		(1.47 - 13.4)	(0.08 - 3.50)	(1.07 - 3.49)
Tufted Titmouse (50)	1.74	2.42	1.49	2.87	0.22	0	1.45	0.36	0.54
(Baeolophus bicolor)	(0.36 - 8.38)	(1.17-5.00)	(0.78-2.84)	(0.64-12.9)	(0.02 - 3.05)		(0.43 - 4.91)	(0.07-2.00)	(0.19-1.53)
Carolina Wren (47)	1.24	1.12	1.31	1.15	0	0.65	2.42	0.73	3.33
(Thryothorus ludovicianus)	(0.53-2.91)	(0.30 - 4.15)	(0.56 - 3.07)	(0.40 - 3.31)		(0.10 - 4.15)	(1.58-3.72)	(0.73-0.73)	(0.95-11.7)
Blue-gray Gnatcatcher (131)	7.18	8.01	60.6	4.71	0.65	1.29	8.95	1.27	2.36
(Polioptila caerulea)	(3.45-15.0)	(6.29-10.2)	(7.30-11.3)	(0.82-26.9)	(0.23-1.81)	(0.23-7.12)	(6.60-12.1)	(0.81-2.00)	(1.28 - 4.35)
Northern Parula (72)	2.24	3.17	2.98	4.31	0	0	2.66	0.18	2.02
(Parula americana)	(0.45-11.1)	(2.22-4.53)	(2.16-4.12)	(2.62–7.07)			(0.51-13.8)	(0.01-2.57)	(0.31-13.0)
Common Yellowthroat (42)	0	0	0	0	0	7.25	0	0	7.02
(Geothlypis trichas)						(4.81-11.0)			(4.36–11.3)
Edge-shrub species									
Indigo Bunting (27)	0	0	0	0.29	0	2.37	0	0	5.25
(rasserma cyanea)				(0.01-10.3)		(1.37-4.10)			(2.21–12.2)

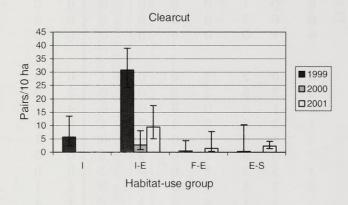
TABLE 2. Number of bird observations in uncut control, clearcut, and patch-retention treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. Included are all species not analyzed using program Distance (Thomas et al. 1998).

	Uncut control			Clearcut			Patch retention		
Species	1999	2000	2001	1999	2000	2001	1999	2000	2001
Forest-interior species									
Barred Owl (Strix varia)	0	0	1	0	0	0	0	0	0
Pileated Woodpecker (Dryocopos pileatus)	2	1	5	0	0	0	0	0	1
White-breasted Nuthatch (Sitta carolinensis)	0	11	6	1	0	0	2	0	2
Pine Warbler (Dendroica pinus)	0	0	0	2	0	0	1	0	0
American Redstart (Setophaga ruticilla)	0	0	1	0	0	0	0	0	0
Ovenbird (Seiurus aurocapilla)	0	0	1	0	0	0	0	0	0
Kentucky Warbler (Oporornis formosus)	0	0	3	0	0	0	0	0	0
Hooded Warbler (Wilsonia citrina)	0	1	0	0	0	0	0	0	0
Interior-edge species									
Yellow-billed Cuckoo (Coccyzus americanus)	4	0	2	3	0	0	3	0	0
Downy Woodpecker (Picoides pubescens)	3	7	8	2	0	0	0	3	0
Eastern Wood-Pewee (Contopus virens)	0	1	0	0	0	0	0	4	1
White-eyed Vireo (Vireo griseus)	1	2	0	0	1	0	1	0	0
Yellow-throated Vireo (Vireo flavifrons)	3	4	4	4	0	0	0	0	1
Blue Jay (Cyanocitta cristata)	0	0	0	2	0	0	1	0	0
Prothonotary Warbler (Protonotaria citrea)	1	5	2	5	0	0	2	0	0
Summer Tanager (Piranga rubra)	0	2	5	1	0	0	0	2	1
Northern Cardinal (Cardinalis cardinalis)	5	1	1	4	2	3	1	1	4
Edge-shrub species									
Red-headed Woodpecker (Melanerpes erythrocephalus)	0	2	0	0	0	0	1	0	0
Field-edge species									
Killdeer (Charadrius vociferus)	0	0	0	0	0	0	0	2	0
American Crow (Corvus brachyrhynchos)	3	2	2	2	0	0	3	0	1
Yellow-breasted Chat (Icteria virens)	0	0	1	0	0	0	0	0	0
Eastern Towhee (Pipilo erythrophthalmus)	0	0	1	0	0	0	0	0	0
Field Sparrow (Spizella pusilla)	0	0	0	0	0	0	0	0	1
Blue Grosbeak (Passerina caerulea)	0	0	0	0	0	2	0	0	0
Wetland species									
Wood Duck (Aix sponsa)	0	0	0	1	0	0	0	0	0

the first postharvest year, and seven (e.g., Acadian Flycatcher, Empidonax virescens; Redeyed Vireo, Vireo olivaceus; and Northern Parula, Parula americana; all Neotropical migrants) had disappeared by the second postharvest year. Only two species detected more than once before the harvest, Carolina Wren (Thryothorus ludovicianus) and Blue-gray Gnatcatcher (Polioptila caerulea), used the clearcut in the second postharvest year. Finally, Common Yellowthroat (Geothlypis trichas) and Indigo Bunting (Passerina cyanea), which were essentially absent preharvest (only one observation of Indigo Bunting in 1999) and in the first postharvest season, colonized the clearcut in the second postharvest year and accounted for 70% of the total observations.

In the patch-retention treatment, as in the clearcut, the abundance of most species we analyzed appeared to decline in the first post-harvest year, but only Acadian Flycatcher was not observed at all. During the second post-harvest season, however, abundance of most species stabilized or rebounded slightly; for 9 of 11 species, densities in 2001 were not significantly less than those in 1999. Common Yellowthroat and Indigo Bunting, absent during the preharvest and the first postharvest seasons, accounted for 40% of the total observations in this treatment during the second postharvest year.





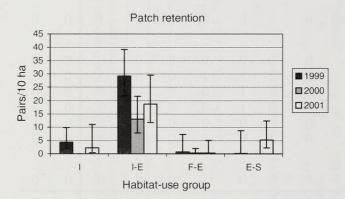


FIG. 2. Densities of avian habitat-use groups (mean \pm 95% confidence intervals) in three harvest treatment areas in a bottomland hardwood forest in South Carolina, 1999–2001. I = Forest Interior, I-E = Interior-Edge, F-E = Field-Edge, and E-S = Edge-Shrub.

Density estimates within each of the four habitat-use groups did not differ over the 3 years in the uncut control area (Fig. 2). However, in both the clearcut and patch-retention areas, the density of the forest-interior group declined in the first postharvest year. In the second postharvest year, density of forest-interior birds rebounded in the patch-retention area, but not in the clearcut. Density of the forest-interior group was also greater in the patch-retention area than in the clearcut in the

second postharvest season. The density of the edge-shrub group increased in both of these treatment areas in the second postharvest year, due primarily to the abundance of Indigo Buntings (Table 1).

DISCUSSION

Retention of patches of forest within an otherwise clearcut area appears to enhance postharvest forest bird diversity compared to that in clearcuts without such patches (Merrill et al. 1998, Schieck et al. 2000). We observed greater species richness and overall bird densities in the patch-retention treatment area than in the clearcut in both 2000 and 2001. A high percentage of the total bird detections in the patch-retention area were recorded inside retained patches. By the second postharvest year, the estimated density of the forest-interior group in the patch-retention area had recovered to approximately half that in the uncut control, whereas in the clearcut, no individuals of this group were detected. These findings corroborate the results of studies from other regions. For example, in aspen forests of northern Minnesota, Merrill et al. (1998) found high bird diversity in 0.54-ha patches within clearcuts that averaged 14.6 ha. Similarly, the overwhelming majority of birds detected in our postharvest patch-retention area (excluding Common Yellowthroat and Indigo Bunting) occurred inside the patches. Merrill et al. (1998) noted that birds using retained patches did not necessarily nest there but used them for foraging, singing, or other activities. In boreal forest of Alberta, Canada, avian community composition in harvested sites was most similar to that of unharvested, old growth sites when retained trees and snags included large trees and were clumped together (Schieck et al. 2000). Such clumps may have resembled the original forest by preserving some of its structure and microclimates (Schieck et al. 2000).

The harvested portions of both the clearcut and patch-retention areas had been colonized by early successional species (e.g., Common Yellowthroat, Indigo Bunting) by the second postharvest year. Their appearance in the second year after harvest was not unexpected, as at least one growing season is required for establishment of early successional grasses and forbs. Moorman and Guynn (2001) also re-

ported these species in small group-selection cuts in bottomland hardwoods during the second postharvest year. Migratory songbirds may discover potential future breeding habitat during the season-ending dispersal phase and return there the following year (Brewer and Harrison 1975, Morton 1992).

We suggest that patch-retention timber harvest may be more desirable than clearcutting when landowners are interested in maintaining songbird habitat, and that its impacts on bird populations warrant further investigation. Patch-retention harvesting offers some of the silvicultural advantages of clearcutting, but maintains elements of the preharvest stand that are apparently attractive to songbirds. Our findings indicate that, to some degree, the residual patches of forest continue to be used by forest birds, while the surrounding clearcut portion provides suitable habitat for edgeshrub and other early successional species.

That the densities of many birds did not differ in the patch-retention area before and after harvest does not necessarily indicate that the habitat quality was similar (Van Horne 1983). Site fidelity among individual birds may explain some use of the patches after harvest (though not the increased use in the second postharvest year), even if the quality of the patches was poor. Whether retained forest patches have negative impacts on avian population dynamics is unclear, as our study did not address this question. Field-forest edges may be ecological traps for birds by concentrating nesting activity but also attracting nest predators (Gates and Gysel 1978). Similarly, the patches may provide perches for Brownheaded Cowbirds (Molothrus ater), facilitating parasitism of nearby nests. Thus our retention patches, with their high edge:area ratios, could possibly have functioned as population sinks. However, studies in which the effect of variable tree retention (two-age type harvests) on nesting success has been examined have generally found little or no evidence for such a phenomenon (Tittler and Hannon 2000, Duguay et al. 2001, Stuart-Smith and Hayes 2003), and cowbird parasitism rates in southeastern forests are low (Kilgo and Moorman 2003). Nevertheless, avian productivity in residual forest patches such as those in our patch-retention treatment has yet to be determined, and this issue should be the focus of future research.

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