The Condor 102:748–758

BREEDING BIRD ABUNDANCE IN BOTTOMLAND HARDWOOD FORESTS: HABITAT, EDGE, AND PATCH SIZE EFFECTS[1]

REX SALLABANKS,[2] JEFFREY R. WALTERS[3] AND JAIME A. COLLAZO
Department of Zoology, North Carolina State University, Box 7617, Raleigh, NC 27695

Abstract. We studied breeding bird communities in extensive bottomland hardwood forests along the lower Roanoke River in North Carolina during 1992 and 1993. We documented a rich avian community and recorded exceptionally high densities of two species (Prothonotary Warbler *Protonotaria citrea*, Acadian Flycatcher *Empidonax virescens*), as well as modest densities of three species rarely encountered elsewhere in the region (Cerulean Warbler *Dendroica cerulea*, Swainson's Warbler *Limnothlypis swainsonii*, American Redstart *Setophaga ruticilla*). The effects of patch size and edge on bird abundance were small in this forested landscape, but forest type had a large effect. We found half of the species analyzed to differ in abundance between the two primary habitat types, swamp forest and levee forest. In contrast, no species was consistently more abundant at patch interiors than near edges, and only two forest birds were more common in large compared with small patches. Species analyzed included permanent residents, short-distance migrants, Neotropical migrants, and those identified as forest-interior and area-sensitive species in other studies. Our results suggest that the Roanoke River bottomland forests may be functioning effectively as a reserve for a number of bird species.

Key words: *bottomland forests, edge, habitat, landscape, patch size, point counts.*

INTRODUCTION

Bottomland hardwood forests of the southeastern United States are critical breeding areas for many Neotropical migrants (Wharton et al. 1981, Hodges and Krementz 1996). Within the United States, bottomland hardwoods are being lost perhaps five times faster than any other major hardwood forest type (Abernathy and Turner 1987) and represent the wetland system with most rapidly diminishing acreage (Turner et al. 1981). Loss and alteration primarily takes the form of clearing and draining for crop production and, less frequently, conversion to forest plantations for timber production. These uses result in habitat fragmentation and degradation, as well as habitat loss, causing major impacts on breeding bird communities (Mitchell and Lancia 1990, Mitchell et al. 1991, Pashley and Barrow 1992). Changes in hydrology due to flood control are another common agent of habitat change in these systems.

Bottomland forests are particularly vulnerable to habitat fragmentation because they often occur as relatively narrow linear bands along rivers. The effects of habitat fragmentation and degradation on animal and plant populations have become an increasingly important concern in recent years (Schwartz 1997 and references therein). Of particular concern is the role of forest fragmentation in the decline of some migratory bird populations (Askins et al. 1990, Faaborg et al. 1995). As forests become more fragmented, the proportion of forest habitat near edges increases geometrically, creating edge effects (Harris 1988), ecological traps (Gates and Gysel 1978), and population sinks (Pulliam 1988, Donovan et al. 1995). In the eastern United States, birds near edges and in small fragments suffer from elevated rates of nest predation and of brood parasitism by the Brown-headed Cowbird, *Molothrus ater* (Brittingham and Temple 1983, Andrén and Angelstam 1988, Hoover et al. 1995). The magnitude of edge and patch size effects may depend on the extent of fragmentation in the regional landscape (Robinson et al. 1995, Faaborg et al. 1998, Hartley and Hunter 1998).

In this paper we report on breeding bird abundance in the most extensive bottomland hardwood forests remaining in the mid-Atlantic region, located on the lower Roanoke River in eastern North Carolina. The forested floodplain along the lower Roanoke ranges up to 8 km across and contains an estimated 60,000 ha of

[1] Received 14 July 1999. Accepted 12 July 2000.
[2] Current address: Sustainable Ecosystems Institute, 30 East Franklin Road, Suite 50, Meridian, ID 83642.
[3] Corresponding author and current address: Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061.

contiguous bottomland and swamp forest communities. Over 220 species of birds have been recorded in the floodplain, including at least 90 breeding residents and 40 breeding Neotropical migrants; this represents the highest breeding bird diversity known in the North Carolina Coastal Plain. Some Neotropical migrants breeding along the Roanoke (e.g., Cerulean Warbler *Dendroica cerulea* and Swainson's Warbler *Limnothlypis swainsonii*) are of special concern in North Carolina and elsewhere because of their declining numbers and restricted ranges (Lee and Parnell 1990). We studied the two primary natural communities in the Roanoke floodplain: cypress-gum swamp forest (brownwater subtype) and coastal plain levee forest (brownwater subtype) (Schafale and Weakley 1990).

Our primary objective was to determine the abundance and habitat relationships of breeding bird species, particularly Neotropical migrants, in order to assess the conservation value of the Roanoke bottomlands to birds. In 1989, the U.S. Fish and Wildlife Service acquired 13,000 ha of bottomland forest along the Roanoke to create the Roanoke River National Wildlife Refuge. An additional 5,500 ha are under state jurisdiction, and The Nature Conservancy, timber companies, and private individuals also retain significant holdings. Information about conservation values is needed to make informed decisions about management of current holdings and acquisition of additional land.

Our secondary objective was to document effects of proximity to edge and patch size on bird abundance within the natural mosaic of habitat patches in the Roanoke system. This serves two purposes. First, it provides a baseline against which effects of human-induced fragmentation, both within the Roanoke system and in other, similar systems, can be measured. Second, it contributes to the accumulation of a data set on variation in effects of patchiness and landscape structure on bird abundance across systems, which is critical to understanding effects of fragmentation (Walters 1998). Most studies on the effects of habitat fragmentation have examined woodlots that have become isolated because of agricultural and/or urban encroachment (Walters 1998). Contrast between habitat types in these landscapes is great, and edges are external, non-natural, abrupt, and permanent (Saurez et al. 1997). In our study area, patches of one forest type are linked by relatively undisturbed forest of a second type, rather than by cleared agricultural or urban land. Using the terminology of Saurez et al. (1997), the edges we examined are external, natural ones that are either gradual with modest contrast between habitat types (swamp-levee boundaries) or abrupt with high contrast (river-levee edges).

METHODS

STUDY AREA

In 1992 and 1993, we studied breeding bird communities of swamp and levee forest along a 150-km portion of the lower Roanoke River in eastern North Carolina, from Halifax to near the river's mouth at Plymouth. The swamp forest occurs in backswamps, sloughs, and other areas that in most years are flooded much of the growing season. Dominant tree species are water tupelo (*Nyssa aquatica*) and bald-cypress (*Taxodium distichum*), with Carolina ash (*Fraxinus caroliniana*) as a common midstory tree species. The levee forest occurs at higher elevations than swamp forest, on natural levees adjacent to the river channel. The levee forest canopy is dominated by a mixture of bottomland hardwoods such as sycamore (*Platanus occidentalis*), American elm (*Ulmus americana*), green ash (*Fraxinus pennsylvanica*), sugarberry (*Celtis laevigata*), boxelder (*Acer negundo*), water hickory (*Carya aquatica*), and sweetgum (*Liquidambar styraciflua*). Midstory tree species include pawpaw (*Asimina triloba*) and ironwood (*Carpinus caroliniana*), and vines are an abundant and conspicuous component of the community.

There is little change in canopy height and overstory tree density in the transition from swamp to levee. Forests are mature second growth, with canopy height of about 30 m (mean = 32 m, range among study plots 26–41 m). In some swamp forest, mature bald-cypress have been removed by selective logging. There is sharp contrast in plant community composition between swamp and levee, and swamp forest contains much lower densities of understory plants and shrubs, and somewhat lower densities of midstory trees. The ecotone between levee and swamp is not as abrupt as between levee and river or swamp and agricultural field, but typically it extends only a few meters.

The Roanoke bottomlands contain 13 other plant community types besides swamp forest

FIGURE 1. Satellite photograph of Roanoke River, North Carolina floodplain showing five types of transects sampled for relative breeding abundance. Lighter patches adjacent to river are levee forest and dark patches are swamp forest. White patches are agricultural fields surrounding the bottomland forests. Transects indicated are (1) narrow levee interior, (2) wide levee interior, (3) small swamp interior, (4) large swamp interior, and (5) large swamp edge.

and levee forest, but these other communities are restricted in their distribution, for example to slopes, to areas near the mouth of the river, or to special locations such as beaver ponds. The upland habitat matrix surrounding the bottomland communities consists mostly of cropland and pastureland on higher terraces of the floodplain that flood rarely or not at all (Fig. 1). Fields tend to be large, although they are usually broken up by wind breaks, drainage ditches, and other shrubby cover.

ASSESSMENT OF BIRD COMMUNITIES

In order to determine the effects of habitat type, interior versus edge location, and patch size on bird communities, we established 35 permanent transects in levee and swamp forest tracts (primary transects). We placed 14 transects in the center of levee patches of varying width (150–1,500 m wide), and 14 in the center of swamp forest patches of varying size (12–2,500 ha). We placed the remaining seven transects within 50 m of the edge of the seven largest swamp patches (340–2,500 ha) (Fig. 1). Each habitat patch contained one transect, with the exception of large swamp patches which contained two transects (an interior transect and an edge transect). We assumed all transects to be independent samples because they were always at least 1 km apart.

We censused birds on four other levee transects that were not included in the above design. These transects were located in levee forest that contained substantial thickets of giant cane (*Arundinaria gigantea*) (cane transects). They were censused to determine associations between bird species and this unique habitat component, but were not included in statistical analyses.

We used the fixed-radius point count censusing technique (Hutto et al. 1986) to survey breeding bird communities in 1992 and 1993. Each transect was 300 m long, had three count stations at 0, 150, and 300 m, and was visited three times during the period 1 May–10 July in each year. We made counts at each count station for 10 min between sunrise (approximately 06:00) and 10:00. At each count, we identified all vocal and visual detections to species and recorded their distance as < 30 m or > 30 m.

We examined edge effects by comparing breeding bird abundances between locations relatively far from patch edges and locations relatively close to patch edges. For levee forest this was a comparison between wide (650–1,500 m) and narrow (150–300 m) levees; for swamp forest this was a comparison between large swamp interiors and large swamp edges. Narrow levees were impacted by two edges each (river-levee, swamp-levee) that were 75–150 m from the census point depending on the width of the levee (Fig. 1). Large swamp edges were impacted by one edge (swamp-levee) that was 50 m from the census point.

We examined patch size effects by regressing breeding bird abundance against the size of habitat patches. Because levee forest occurs more as a linear habitat than as discrete patches, we regressed abundance against levee width to assess effects of levee patch size. For swamp forest, we used data from interiors of large (340–2,500 ha) and small (12–128 ha) patches (Fig. 1) to regress abundance against patch size.

STATISTICAL ANALYSIS

To avoid including birds that were outside the habitat/patch of interest, we only used detections within the 30-m radius in our analyses. We used ANOVA to examine relationships between the relative abundance of species and habitat type and transect location relative to edge. Model terms were year (1992 or 1993), habitat (levee or swamp forest), location [habitat] (swamp interior or edge, narrow or wide levee), year $\times$ habitat, and year $\times$ location [habitat]. The models' response variables were the mean number of detections of a particular species per transect per year. Mean number of detections was obtained by first averaging the three visits to a count station within a year, and then averaging the three count station means within a transect. Census data were power transformed to meet homogeneity of variance assumptions (Levene's test, $P > 0.05$) (Levene 1960). To assess the possibility that lack of independence of data collected from the same transect in consecutive years affected our results, we repeated the analyses using year as a repeated measure. Excluding year effects, results were identical using either approach, or analyzing only a single year's data.

For the regression analyses examining effects of patch size, we combined data from 1992 and 1993 except where *t*-tests (swamp forest) or ANOVA results (levee forest, see above) indicated a year effect. The response variable again was the mean number of detections per point count within a transect for each species. Data from levees were again power transformed, but this transformation was not necessary for data from swamp forest.

In addition to the above species-specific analyses, we also regressed average number of individuals and species against patch size for swamps and against forest width for levees. For these analyses we used the mean number of individuals and species detected per point count within a transect obtained by pooling all detections.

We used JMP software (JMP 1994) to perform statistical analyses.

RESULTS

We recorded 69 species of birds during morning censuses; 29 (42%) were Neotropical migrants (long-distance migrants), 4 (6%) were short-distance migrants, 5 (7%) were coastal migrants, and 31 (45%) were permanent residents. We recorded 24 of these 69 species 10 or more times within the 35 primary transects. We recorded four other species, White-eyed Vireo (*Vireo griseus*), Kentucky Warbler (*Oporornis formosus*), Swainson's Warbler, and Hooded Warbler (*Wilsonia citrina*), 10 or more times if the four additional cane transects are included. Each of these species was strongly associated with cane. The remaining 41 species included 10 waterbirds, 4 passage migrants, 3 species that soared above the forest, 7 species associated with agricultural lands, and 17 rare forest species. Notable among the latter were Cerulean Warbler, found only on upstream levee transects, Scarlet

TABLE 1. Results of ANOVA examining relationship of relative abundance of each individual species to habitat type (levee vs. swamp forest) [habitat], transect location (wide vs. narrow levee, swamp edge vs. interior) (location [habitat]), year (1992 vs. 1993) [year], habitat-year interaction (habitat × year), and location-year interaction (location × year) in bottomland forest along the Roanoke River, North Carolina. Entries are *P*-values for the indicated *F*-test, with significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) values in bold.

Species	Year $F_{1,48}$	Habitat $F_{1,24}$	Location $F_{2,48}$	Habitat × year $F_{1,48}$	Location × year $F_{2,48}$
Neotropical migrants					
Prothonotary Warbler	0.25	**0.002**	0.81	0.98	0.55
Acadian Flycatcher	0.22	0.30	0.20	0.74	0.86
Red-eyed Vireo	0.37	<**0.001**	**0.04**	0.42	0.16
Great-crested Flycatcher	0.19	**0.002**	0.81	0.72	0.23
Yellow-billed Cuckoo	0.38	0.59	0.55	0.87	0.70
Indigo Bunting	0.80	0.17	0.98	0.77	0.81
Eastern Wood-pewee	**0.004**	0.30	**0.02**	0.90	**0.08**
Yellow-throated Vireo	0.69	**0.002**	0.75	**0.03**	0.48
Summer Tanager	**0.08**	0.14	**0.06**	0.31	0.23
American Redstart	0.37	**0.002**	0.10	0.69	0.22
Wood Thrush	0.28	**0.002**	0.76	**0.09**	0.40
Northern Parula	0.38	<**0.001**	0.71	0.47	0.60
Short-distance migrants					
Blue-gray Gnatcatcher	<**0.001**	0.62	0.21	0.90	0.16
Common Yellowthroat	0.99	0.31	0.32	0.94	0.99
Permanent residents					
Carolina Chickadee	**0.005**	0.52	0.63	0.25	0.93
Carolina Wren	**0.001**	<**0.001**	0.37	0.15	0.72
Downy Woodpecker	0.70	**0.001**	0.56	**0.06**	0.56
Pileated Woodpecker	<**0.001**	0.70	0.44	0.32	0.31
White-breasted Nuthatch	0.18	**0.009**	0.41	0.70	0.74
Tufted Titmouse	0.78	0.49	0.11	0.83	0.51
Red-bellied Woodpecker	<**0.001**	0.43	<**0.005**	0.25	**0.008**
Northern Cardinal	0.38	**0.003**	0.14	0.52	0.82
Number significant[a]	6 + 1	11	3 + 1	1 + 2	1 + 1

[a] Total significant + marginally significant results for model term in column.

Tanager (*Piranga olivacea*), Wild Turkey (*Meleagris gallopavo*), Barred Owl (*Strix varia*), and Red-shouldered Hawk (*Buteo lineatus*).

We omitted species with fewer than 10 total detections within the 30-m radius on the 35 primary transects in both years from species-specific analyses, as well as species flying above the canopy. We excluded 1 of the remaining 24 species, Common Grackle (*Quiscalus quiscula*), because it tended to occur in large flocks, complicating statistical analyses. We excluded another species, the Brown-headed Cowbird, because most detections of this species were flyovers. The distributions of the remaining 22 species were subjected to statistical analysis (see Appendix 1 for common and scientific names).

Habitat type was much more important than patch size or proximity to edge in explaining species abundance. Half of the 22 species analyzed were significantly more common in one of the two primary habitat types than in the other (Table 1). Six species were more common in swamp forest (Prothonotary Warbler, Great Crested Flycatcher, Yellow-throated Vireo, Northern Parula, Downy Woodpecker, White-breasted Nuthatch) and five were more common in levee forest (Red-eyed Vireo, American Redstart, Wood Thrush, Carolina Wren, Northern Cardinal). We will refer to those more common in swamp forest as swamp specialists, those more common in levee forest as levee specialists, and those equally common in the two habitats as generalists.

Six species exhibited differences in abundance between years, five of which were habitat generalists (Table 1). Generally, species exhibited the same habitat associations in both years with only three species showing significant or marginally significant ($P < 0.10$) habitat × year interactions (Table 1). In all three cases, differences between years can be related to extensive flooding in 1993. Records for the first six months of 1993 indicated Roanoke River flows to be greatly above normal. Flows between 1 January 1993 and 30 June 1993 rank as the fourth highest in 83 years; flows between 1 April 1993 and 30 April 1993 were the second highest on record (Rulifson and Manooch 1993). As a result, flooding was much more extensive in 1993 than in 1992, extending even into levee forest for several weeks.

The Wood Thrush, a ground forager that was found primarily in levee forest in 1992, was rarer and less habitat specific in 1993. The Yellow-throated Vireo and Downy Woodpecker, associated with swamp forest in 1992, exhibited increased use of narrow levees in 1993 when they were extensively flooded. Two of the other four swamp specialists exhibited a similar pattern (Prothonotary Warbler, Great Crested Flycatcher), although the habitat × year interaction was not statistically significant in these cases.

In contrast to strong effects of habitat type on many species, proximity to edge had only weak effects on a few species. Four species exhibited location effects: all were habitat generalists except the Red-eyed Vireo, a levee specialist. In two of these species, the inconsistency of the location effect was manifested in a significant location × year interaction (Table 1). The Eastern Wood-pewee was more common in narrow levees and at swamp edges in 1992, but not in 1993 when the swamp-levee edge was obscured by flooding. The Red-bellied Woodpecker was more common on wide levees and in swamp interiors in 1992, but was less common in those locations in 1993. The Red-eyed Vireo was similar to the Eastern Wood-pewee in that the location effect detected was observed only in 1992, although the location × year interaction was not significant ($P = 0.16$, Table 1) in this case. Furthermore, opposite effects were observed in the two habitat types: in swamp forest, Red-eyed Vireos were more common at the locations nearest edge (swamp edges), whereas in levee forest they were more common at the locations farthest from edges (wide levees). The fourth species, the Summer Tanager, exhibited a marginally significant location effect ($P = 0.06$, Table 1) that can be described as a weak and somewhat inconsistent tendency to be detected at locations farthest from edges (wide levees, large swamp interiors).

Similarly, for only 2 of the 22 species was a relationship between forest patch size and abundance detected in regression analyses. Both cases involved specialists whose abundance within their preferred habitat was positively related to patch size. Abundance of the Prothonotary Warbler, a swamp specialist, was positively correlated with swamp forest patch size, whereas abundance of the other five swamp specialists was unrelated to swamp forest patch size (Table 2). Abundance of swamp specialists in levee forest was either too low to permit analysis (i.e., species not detected in half or more of the transects) (Northern Parula, White-breasted Nuthatch), unrelated to levee width (Prothonotary Warbler), negatively related to levee width (Downy Woodpecker), or tending toward a negative relationship with levee width (Great Crested Flycatcher, Yellow-throated Vireo) (Table 2). Among the five levee specialists, abundance of only the American Redstart was positively correlated with levee width (Table 2). In swamp forest, abundance of levee specialists was either too low to permit analysis (American Redstart, Wood Thrush), unrelated to swamp forest patch size (Carolina Wren, Northern Cardinal), or tending toward a negative relationship with swamp forest patch size (Red-eyed Vireo) (Table 2). The only relationships with patch size found among habitat generalists were negative. Abundance of Acadian Flycatchers was negatively related to size of swamp forest patches (Table 2). There was a tendency toward a similar relationship for Eastern Wood-pewees, and toward a negative relationship between levee width and abundance of Tufted Titmice (Table 2).

COMMUNITY INDICES

Insensitivity to location and patch size also was apparent when number of individuals and number of species were considered. For swamp forests in both years, there was no relationship between the number of individuals and patch size or between number of species and patch size ($r^2 < 0.12$, $P > 0.28$ in all four cases). There was no relationship between the number of individuals and levee forest width in either year (Fig. 2A), or between number of species and levee forest width in 1992 (Fig. 2B) ($r^2 < 0.20$, $P > 0.15$ in all three cases). However, there was a significant negative relationship between num-

TABLE 2. Results (r^2 values) of regression analyses of relationships of abundance of bird species with swamp forest patch size and levee forest width along the Roanoke River, North Carolina. Species more common in swamp forest are classified as swamp specialists, those more common in levee forest as levee specialists, and those equally common in the two habitats as generalists. For years with significant differences in abundance, values for 1992 (upper) and 1993 (lower) are reported separately. Species not detected indicated by (—); (+ or −) indicate direction of relationships. For all regressions, df = 1, 12. Significant relationships are indicated by * ($P < 0.05$) or ** ($P < 0.01$).

Species	Swamps	Levees
Swamp specialists		
Prothonotary Warbler	0.28 (+)*	0.06 (−)
Great-crested Flycatcher	0.12 (−)	0.18 (−)
Yellow-throated Vireo	0.16 (−)	0.15 (−)
Northern Parula	0.02 (+)	0.09 (−)
Downy Woodpecker	0.01 (+)	0.29 (−)
White-breasted Nuthatch	0.03 (+)	0.03 (−)
Levee specialists		
Red-eyed Vireo	0.14 (−)	0.07 (+)
American Redstart	—	0.16 (+)*
Wood Thrush	0.00 (−)	0.00 (+)
Carolina Wren	0.01 (−)	0.15 (−)
	0.01 (+)	0.00 (+)
Northern Cardinal	0.00 (+)	0.09 (−)
Generalists		
Acadian Flycatcher	0.40 (−)*	0.11 (+)
Yellow-billed Cuckoo	0.10 (+)	0.01 (−)
Indigo Bunting	0.12 (−)	0.01 (−)
Eastern Wood-pewee	0.19 (−)	0.07 (−)
	0.17 (−)	0.03 (−)
Summer Tanager	0.01 (−)	0.01 (+)
Blue-gray Gnatcatcher	0.05 (−)	0.09 (+)
	0.01 (−)	0.06 (+)
Common Yellowthroat	0.19 (+)	0.03 (−)
Carolina Chickadee	0.15 (−)	0.00 (+)
	0.02 (−)	0.00 (+)
Pileated Woodpecker	0.04 (−)	0.02 (−)
	0.06 (+)	0.00 (+)
Tufted Titmouse	0.07 (+)	0.27 (+)*
Red-bellied Woodpecker	0.02 (−)	0.04 (+)
	0.16 (+)	0.05 (−)

ber of species and levee forest width in 1993 ($r^2 = 0.43$, $F_{1,12} = 9.00$, $P = 0.01$) (Fig. 2B), when narrow levees were flooded.

DISCUSSION

The lower Roanoke River floodplain is clearly an important breeding area for many birds, including Neotropical migratory species. The two most common birds breeding on the floodplain are Neotropical migrants (Prothonotary Warbler and Acadian Flycatcher). The abundances re-

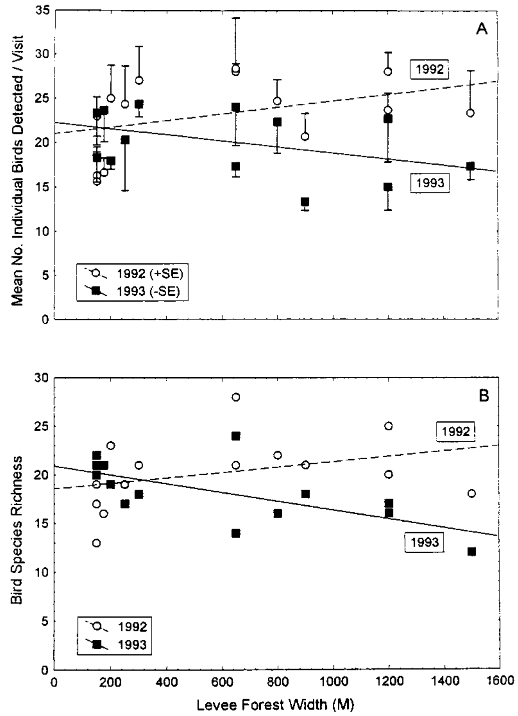

FIGURE 2. Number of individuals (A) and species (B) as a function of levee forest width.

corded for these species, and several others such as Pileated Woodpecker, are remarkable. At the community level, avian abundance and species richness are similar to, if not higher than, those reported for other bottomland hardwood forests (Mitchell and Lancia 1990, Smith et al. 1995). The Roanoke bottomland forests contain a large population of a migratory species that is otherwise uncommon in the North Carolina Coastal Plain (American Redstart), and small but significant populations of two migrants of regional concern (Swainson's Warbler, Cerulean Warbler, the latter of which also is otherwise absent from the North Carolina Coastal Plain).

The value of the primary habitat types found along the Roanoke varies among species. Some birds prefer swamps (Northern Parula and White-breasted Nuthatch) and some favor levees (Red-eyed Vireo and Northern Cardinal), whereas others use swamps and levees equally (Acadian Flycatcher and Pileated Woodpecker) (Table 1). Bird-habitat associations were strong and consistent between years. Where differences occurred between 1992 and 1993, they were most likely related to the extensive flooding that occurred in 1993, which probably promoted intrusion of swamp specialists into at least narrow levees and reduced habitat available to ground-dwelling levee specialists. A notable habitat association was that between giant cane and several uncommon species, including Swainson's Warbler. One management activity that would increase the conservation value of the Roanoke forests would be to increase the abundance of cane.

PATCH SIZE AND EDGE EFFECTS

Although we readily detected habitat preferences, we detected few effects of patch size or proximity to edge among the 35 primary transects. Proximity to edge, in fact, more frequently had positive effects on abundance of individual species than negative effects. The only consistent pattern we detected is that species characteristic of one habitat type tended to be more abundant within the second habitat type near edges. This presumably reflects proximity to the preferred habitat. In addition, one species, the Eastern Wood-pewee, appeared to be more abundant along edges between levee and swamp than within either habitat.

Of the four species (Acadian Flycatcher, Northern Parula, American Redstart, and Pileated Woodpecker) included in our analyses classified as ''forest interior species'' by Whitcomb et al. (1981) and Freemark and Merriam (1986), only the American Redstart was more common in larger patches along the Roanoke. Within swamp forest, the Acadian Flycatcher actually was less abundant in larger patches. Our results differ from those of other studies that indicate bird density and species richness to be proportional to patch size (Freemark and Merriam 1986, Blake and Karr 1987, Loyn 1987), and to riparian forest width (Stauffer and Best 1980, Keller et al. 1993). Among bottomland hardwood forest corridors of different widths studied in Georgia, wider corridors had richer avian communities (Hodges and Krementz 1996). Species-specific analyses indicated positive relationships with corridor width for several species, including three (Northern Parula, Red-eyed Vireo, Blue-gray Gnatcatcher) for which we found no such relationships. We did, however, find a positive relationship for Prothonotary Warblers, as did Hodges and Krementz (1996), and we found evidence of higher abundance in smaller swamp forest patches for the one species, the Acadian Flycatcher, for which Hodges and Krementz (1996) found a negative relationship between abundance and corridor width.

An obvious difference between our study and those cited above is that the forest patches we studied were bordered by other types of forest or river rather than by agricultural or suburban lands, or in the case of Hodges and Krementz (1996), pine plantations. The narrow levees we sampled were as narrow as the forest corridors in which Hodges and Krementz (1996) found abundances to be reduced, but the entire forest matrix in which they were embedded was much wider. These results suggest that effects of patchiness, including fragmentation, are dependent on the nature of edges (Schieck et al. 1995, Saurez et al. 1997) and intervening habitats. For some species, such as American Redstarts and Prothonotary Warblers, effects of patch size may hold across a variety of landscapes, reflecting perhaps basic features of population dynamics. For other species, effects of patch size and edge may be landscape-specific, reflecting a particular interaction between that landscape and population dynamics. This thesis is consistent with studies that report numerous patch size effects in naturally patchy systems where edge and habitat contrasts are high (Helle 1985, Dobkin and Wilcox 1986), and with studies that have shown fragmentation by silviculture to have fewer effects than fragmentation by agriculture (Haila et al. 1989, Lemkuhl et al. 1991, Schieck et al. 1995). Silviculture creates forest edges that are transient in nature and less abrupt (DeGraaf 1992, McGarigal and McComb 1995), perhaps thereby reducing edge-related phenomena such as nest predation and brood parasitism (Rudnicky and Hunter 1993, Hanski et al. 1996, King et al. 1996). In our study area, predation on artificial nests is higher along edges between forest and agricultural areas than along edges between forest types or between forest and the river (Saracco and Collazo 1999).

Effects of fragmentation are not always manifested in changes in abundance. For example, in the Midwest, regional movements maintain abundance of many species in small forest patch and edge sinks, despite extremely high levels of nest predation and parasitism (Robinson et al. 1995, Faaborg et al. 1998). This is likely only in systems in which fragmentation (or patchiness) does not disrupt dispersal. Perhaps small swamp forest patches along the Roanoke are sinks as well, but this is not reflected in differences in abundance because the landscape is conducive to the movement of birds from productive large patches to unproductive small ones. We think this possibility unlikely, but cannot rule it out until sufficient data on productivity and mortality are available. Studies of reproduction and mortality are necessary to determine whether population dynamics, like abundance, are little affected by patch size and edges.

Factors other than a species–area relationship may account for much of the variation in bird-habitat associations such as those studied here. A lack of sensitivity to area may in fact be related to factors not measured or incorporated in analyses (e.g., degree of isolation, floristics, forest physiognomy, food resources, or nest sites). Such factors have been found to be as important, or more important, than area per se in explaining species abundance patterns in patches of varying sizes and isolation (Rafe et al. 1985, Boecklen 1986).

This initial study indicates the value of the Roanoke bottomland forests as a reserve for birds to be extremely high potentially. Many species are abundant, including several Neotropical migratory species that are rare in the region. It remains to be determined whether these species are able to maintain their populations in this area. If, but only if, productivity and survival are high, the Roanoke forests may house not only locally sustainable populations, but also regionally important source populations.

ACKNOWLEDGMENTS

This study was funded by The Nature Conservancy, the National Fish and Wildlife Foundation, and the U.S. Fish and Wildlife Service. We especially thank J. M. Lynch of The Nature Conservancy for his many contributions to all aspects of the project, including the selection of sites for transect location. J. Holloman, Manager of the Roanoke River National Wildlife Refuge, provided generous support and technical assistance throughout the study. S. R. Sallabanks, M. Wilson, S. B. Anderson, and M. Anjaneyulu assisted with data collection. W. P. Smith, J. Hagar, W. D. Koenig, and three anonymous reviewers provided constructive, critical reviews of earlier versions of this paper. M. Gumpertz offered statistical advice. Finally, we thank the following land-owners along the Roanoke for allowing us access to their property: The Nature Conservancy, the U.S. Fish and Wildlife Service, the North Carolina Wildlife Resources Commission, Georgia Pacific, Timberlands Unlimited, Inc., Union Camp, North Carolina Department of Corrections, A. McLennon, J. G. Burgwyn, S. Graves, M. Ranson, B. Johnston, and B. Johnson.

LITERATURE CITED

ABERNATHY, Y., AND R. TURNER. 1987. U.S. forested wetlands: status and changes 1940–1980. BioScience 37:721–727.

ANDRÉN, H., AND P. ANGELSTAM. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. Ecology 69:544–547.

ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. Current Ornithol. 7:1–57.

BLAKE, J. G., AND J. R. KARR. 1987. Breeding birds of isolated woodlots: area and habitat relationships. Ecology 68:1724–1734.

BOECKLEN, W. J. 1986. Effects of habitat heterogeneity on the species–area relationships of forest birds. J. Biogeogr. 13:59–68.

BRITTINGHAM, M. C., AND S. A. TEMPLE. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31–35.

DEGRAAF, R. M. 1992. Effects of even-aged management on forest birds at northern hardwood stand interfaces. For. Ecol. Manage. 46:95–110.

DOBKIN, D. S., AND B. A. WILCOX. 1986. Analysis of natural forest fragments: riparian birds in the Toiyabe mountains, Nevada, p. 293–299. *In* J. Verner, M. L. Morrison, and C. J. Ralph [EDS.], Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Univ. Wisconsin Press, Madison, WI.

DONOVAN, T. M., F. R. THOMPSON III, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conserv. Biol. 9:1380–1395.

FAABORG, J., M. BRITTINGHAM, T. DONOVAN, AND J. BLAKE. 1995. Habitat fragmentation in the Temperate Zone, p. 357–380. *In* T. E. Martin and D. M. Finch [EDS.], Ecology and management of Neotropical migratory birds. Oxford Univ. Press, Oxford.

FAABORG, J., F. R. THOMPSON III, S. K. ROBINSON, T. M. DONOVAN, D. R. WHITEHEAD, AND J. BRAWN. 1998. Understanding fragmented Midwestern landscapes: the future, p. 193–207. *In* J. M. Marzluff and R. Sallabanks [EDS.], Avian conservation: research and management. Island Press, Washington, DC.

FREEMARK, K. E., AND H. G. MERRIAM. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biol. Conserv. 36:115–141.

GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. Ecology 59:871–883.

HAILA, Y., I. K. HANSKI, AND S. RAIVIO. 1989. Methodology for studying the minimum habitat requirements of forest birds. Annales Zoologici Fennici 26:173–180.

HANSKI, I. K., T. J. FENSKE, AND G. J. NIEMI. 1996. Lack of edge effect in nesting success of breeding birds in managed forest landscapes. Auk 113:578–585.

HARRIS, L. D. 1988. Edge effects and conservation of biotic diversity. Conserv. Biol. 2:330–332.

HARTLEY, M. J., AND M. L. HUNTER JR. 1998. A meta-

analysis of forest cover, edge effects and artificial nest predation rates. Conserv. Biol. 12:465–469.
HELLE, P. 1985. Effects of forest fragmentation on bird densities in northern boreal forests. Ornis Fennica 62:35–41.
HODGES, M. F., JR., AND D. G. KREMENTZ. 1996. Neotropical migratory breeding bird communities in riparian forests of different widths along the Altamaha River, Georgia. Wilson Bull. 108:496–506.
HOOVER, J. P., M. C. BRITTINGHAM, AND L. J. GOODRICH. 1995. Effects of forest patch size on nesting success of Wood Thrushes. Auk 112:146–155.
HUTTO, R. L., S. M. PLETSCHET, AND P. HENDRICKS. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593–602.
JMP. 1994. Software for statistical visualization for Windows. Version 3.2.2. JMP, Cary, NC.
KELLER, C. M. E., C. S. ROBBINS, AND J. S. HATFIELD. 1993. Avian communities in riparian forests of different widths in Maryland and Delaware. Wetlands 13:137–144.
KING, D. I., C. R. GRIFFIN, AND R. M. DEGRAAF. 1996. Effects of clearcutting on habitat use and reproductive success of the Ovenbird in forested landscapes. Conserv. Biol. 10:1380–1386.
LEE, D. S., AND J. F. PARNELL. [EDS.]. 1990. Endangered, threatened, and rare fauna of North Carolina. Part III. A re-evaluation of the birds. North Carolina Biol. Survey and North Carolina State Mus. Nat. Sci., Raleigh, NC.
LEMKUHL, J. F., L. E. RUGGIERO, AND P. A. HALL. 1991. Landscape patterns of forest fragmentation and wildlife richness and abundance in the southern Washington Cascade range, p. 425–442. *In* L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Hutt [TECH. COORDS.], Wildlife and vegetation in unmanaged Douglas-fir forests. USDA Forest Service, Pacific Northwest Res. Sta., Gen. Tech. Rep. PNW-GTR-285, Portland, OR.
LEVENE, H. 1960. Robust tests for equality of variances, p. 278–292. *In* I. Olkin, S. G. Ghurye, W. Hoeffding, W. G. Mado, and H. B. Mann [EDS.], Contributions to probability and statistics. Stanford Univ. Press, Stanford, CA.
LOYN, R. H. 1987. Effects of patch area and habitat on bird abundances, species number and tree health in fragmented Victorian forests, p. 65–77. *In* D. A. Saunders, G. W. Arnold, A. A. Burbridge, and A. J. M. Hopkins [EDS.], Nature conservation: the role of remnants of native vegetation. Surrey Beatty and Sons, Chipping Norton, UK.
MCGARIGAL, K., AND W. C. MCCOMB. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65:235–260.
MITCHELL, L. J., AND R. A. LANCIA. 1990. Breeding bird community changes in bald-cypress-tupelo wetland following timber harvesting. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 44: 189–201.
MITCHELL, L. J., R. A. LANCIA, R. LEA, AND S. A. GAUTHREAUX JR. 1991. Effects of clearcutting and natural regeneration on breeding bird communities of bald-cypress-tupelo wetlands, p. 155–161. *In* J. Kusler and S. Daly [EDS.], Proceedings of symposium on wetlands and river corridor management. Assoc. Wetland Managers, Berne, NY.
PASHLEY, D. N., AND W. C. BARROW. 1992. Effects of land use practices on Neotropical migratory birds in bottomland hardwood forests, p. 315–320. *In* D. M. Finch and P. W. Stangel [EDS.], Status and management of Neotropical migratory birds. USDA Forest Service, Rocky Mountain Forest and Range Experimental Station, Gen. Tech. Rep. Rm-229, Fort Collins, CO.
PULLIAM, H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132:652–661.
RAFE, R. W., M. B. USHER, AND R. G. JEFFERSON. 1985. Birds on reserves: the influence of area and habitat on species richness. J. Appl. Ecol. 22:327–335.
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.
RUDNICKY, T. C., AND M. L. HUNTER. 1993. Avian nest predation in clearcuts, forests, and edges in a forest-dominated landscape. J. Wildl. Manage. 57: 358–364.
RULIFSON, R. A., AND C. S. MANOOCH III [EDS.]. 1993. Roanoke River water flow committee report for 1991–1993. Albemarle-Pamlico estuarine study, Project No. Apes 93–18, North Carolina Department of Environment, Health and Natural Resources, Raleigh, NC.
SARACCO, J. F., AND J. A. COLLAZO. 1999. Predation on artificial nests along three edge types in a North Carolina bottomland hardwood forest. Wilson Bull. 111:541–549.
SAUREZ, A. V., K. S. PFENNIG, AND S. K. ROBINSON. 1997. Edges are not all equal: nesting success of a disturbance-dependent songbird. Conserv. Biol. 11:928–935.
SCHAFALE, M. P., AND A. S. WEAKLEY. 1990. Classification of the natural communities of North Carolina: third approximation. North Carolina Natural Heritage Program, Raleigh, NC.
SCHIECK, J., K. LERTZMAN, B. NYBERG, AND R. PAGE. 1995. Effects of patch size on birds in old-growth montane forests. Conserv. Biol. 9:1072–1084.
SCHWARTZ, M. W. [ED.]. 1997. Conservation in highly fragmented landscapes. Chapman and Hall, New York.
SMITH, W. P., D. J. TWEDT, R. J. COOPER, D. A. WIEDENFELD, P. B. HAMEL, AND R. P. FORD. 1995. Sample size and allocation of effort in point count sampling of birds in bottomland hardwood forests, p. 7–18. *In* C. J. Ralph, J. R. Sauer, and S. Droege [EDS.], Monitoring bird populations by point counts. USDA Forest Service, Pacific Southwest Research Station, Gen. Tech. Rep. PSW-GTR-149, Albany, CA.
STAUFFER, D. F., AND L. B. BEST. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. J. Wildl. Manage. 44: 1–15.
TURNER, R. E., S. FORSYTHE, AND N. CRAIG. 1981. Bot-

tomland hardwood forest land resources of the southeastern U.S., p. 13–18. *In* J. R. Clark and J. Benforado [EDS.], Wetlands of bottomland hardwood forest. Elsevier, New York.

WALTERS, J. R. 1998. The ecological basis of avian sensitivity to habitat fragmentation, p. 181–192. *In* J. M. Marzluff and R. Sallabanks [EDS.], Avian conservation: research and management. Island Press, Washington, DC.

WHARTON, C. H., V. W. LAMBOUR, J. NEWSON, P. V. WINGER, L. L. GADDY, AND R. MANCKE. 1981. The fauna of bottomland hardwoods in the southeastern United States, p. 87–160. *In* J. R. Clark and J. Benforado [EDS.], Wetlands of bottomland hardwood forest. Elsevier, New York.

WHITCOMB, R. F., C. S. ROBBINS, J. F. LYNCH, B. L. WHITCOMB, M. K. KLIMKIEWICZ, AND D. BYSTRAK. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest, p. 125–206. *In* R. L. Burgess and D. M. Sharpe [EDS.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.

APPENDIX 1. Species included in statistical analyses of individual species' distributions.

Neotropical migrants	
Prothonotary Warbler	*Protonotaria citrea*
Acadian Flycatcher	*Empidonax virescens*
Red-eyed Vireo	*Vireo olivaceus*
Great-crested Flycatcher	*Myiarchus crinitus*
Yellow-billed Cuckoo	*Coccyzus americanus*
Indigo Bunting	*Passerina cyanea*
Eastern Wood-pewee	*Contopus virens*
Yellow-throated Vireo	*Vireo flavifrons*
Summer Tanager	*Piranga rubra*
American Redstart	*Setophaga ruticilla*
Wood Thrush	*Hylocichla mustelina*
Northern Parula	*Parula americana*
Short-distance migrants	
Blue-gray Gnatcatcher	*Polioptila caerula*
Common Yellowthroat	*Geothlypis trichas*
Permanent residents	
Carolina Chickadee	*Parus carolinensis*
Carolina Wren	*Thryothorus ludovivianus*
Downy Woodpecker	*Picoides pubescens*
Pileated Woodpecker	*Dryocopus pileatus*
White-breasted Nuthatch	*Sitta carolinensis*
Eastern Tufted Titmouse	*Parus bicolor*
Red-bellied Woodpecker	*Melanerpes carolinus*
Northern Cardinal	*Cardinalis cardinalis*