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NEOTROPICAL MIGRANT BIRDS AND EDGE EFFECTS AT A FOREST-STREAM ECOTONE

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ABSTRACT.—Species richness, density, and avian diversity were examined along a deciduous-coniferous forest gradient from a ridge crest to a stream bottomland. The study was conducted in Garrett County, Maryland, a region in the central Appalachian Mountains that is 71.2% forested. The 35-ha study area was within a 270-ha core of continuous forest. Bird species were located and habitat sampled using a 35 × 35-m grid that covered a 77-m elevational gradient from a small, second-order stream to a ridge top. Later, twenty-three, 30-m wide elevational bands of 1.26 ha each were defined to relate bird and habitat attributes. Principal components analysis reduced 23 habitat variables to three principal components and provided an ordination of the 23 elevational bands. Four vegetative zones were identified along the main deciduous-coniferous gradient of PC-I, the deciduous zone on the ridge crest, followed by a deciduous/sparse hemlock zone, a hemlock/deciduous zone further downslope, and a hemlock/rhododendron zone at the stream. Based on polynomial regression, the fewest numbers and species of birds were found in the deciduous zone on the ridge. More species occurred with the addition of hemlock at the deciduous-deciduous/sparse hemlock ecotone and markedly more with the addition of rhododendron at the hemlock/rhododendron-stream edge, where rhododendron and total short shrub cover were the highest and deciduous and total canopy cover and deciduous basal area were the lowest. Of 28 breeding bird species, 60.7% were neotropical migrants representing 82.5% of all birds recorded on the study area. Neotropical migrants concentrated near the forest-stream edge as many edge or mixed-habitat species do at forest-field edges. High numbers of cowbirds near the forest-stream edge likely posed a serious threat to these breeding neotropical migrants. These data suggest that conditions at certain forest-stream edges might be conducive to increased nest predation and cowbird parasitism within forested landscapes minimally fragmented by human activities. *Received 2 Oct. 1990, accepted 21 Feb. 1991.*

Breeding bird species richness and density generally are high near edges of forests, particularly at abrupt, shrubby, forest edges bordering fields or other openings (Gates and Gysel 1978, Strelke and Dickson 1980, Chasko and Gates 1982, Morgan and Gates 1982, Hansson 1983). This high diversity reflects the greater number and percent coverage of vegetative strata at these forest edges (MacArthur and MacArthur 1961, MacArthur et al. 1962) and often leads to a high nest density, primarily of edge or mixed-habitat species (Gates and Gysel 1978, Chasko and Gates 1982). Certain human-made forest edges have been characterized as ecological traps for open-nesting passerines, because high numbers of nests near these edges result in high nest mortality from predation and cowbird parasitism (Gates and Gysel 1978). Increase in edge and loss of habitat

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resulting from forest regeneration and fragmentation may reduce reproductive success of many neotropical migrants, particularly those bird species specialized for breeding in mature forest interiors (Wiens 1989).

Bodies of water have been described as openings in forests that lead to changes in the physical and biotic characteristics of the interior, but their effect is not thought to be as great as terrestrial openings (Small and Hunter 1988). Few studies, however, have investigated the potential of riparian ecotones to have a detrimental effect on breeding birds of the forest interior. A major landscape feature of the central Appalachians is the dendritic patterns of streams penetrating the forest interior. Streams could function similarly to human-made corridors within forested landscapes for the birds nesting there. The objectives of this study were (1) to determine whether or not there is a greater bird species diversity near the forest-stream edge than within the interior of a minimally fragmented forested landscape, (2) to determine the composition of the bird assemblage near the forest-stream edge, (3) to ascertain what bird assemblage attributes are associated with the vegetative structure, and (4) to evaluate if conditions at the forest-stream edge are conducive to the formation of ecological traps for birds.

STUDY AREA AND METHODS

The study area was located in a 270-ha core of continuous forest in Garrett County, Maryland, on the watershed of the City of Frostburg (see Gates and Harman 1980). Adjacent habitats included extensive forest to the north, west, and south; and cultivated fields and pasture to the east. Human-made corridors bordering the core area included a 6.1-m-wide county road to the north, with about a 3-m unmowed, grass strip on either side; a 5.2-m-wide access road to the reservoir of the City of Frostburg to the west; and a 9.8-m-wide waterline/powerline corridor to the south. The county is 71.2% forested with clearings in crops (10.0%); pasture (6.9%); other farmland (3.3%); and other land (8.6%), e.g., clear-cuts, corridors, etc. (Frieswyk and DiGiovanni 1988).

The core study area was a mature, northern-hardwood forest community. Sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), cucumber magnolia (*Magnolia acuminata*), and black cherry (*Prunus serotina*) occupied the ridge crest and slope; while along the stream bottomland American hemlock (*Tsuga canadensis*), yellow birch (*Betula lutea*), and red maple (*Acer rubrum*) predominated (Gates and Harman 1980). Blandy Run, a 3.4-m wide, second-order stream flowing generally southeast-northwest, formed a natural corridor and divided the study area into a northern section (approx. 75% of the study area) and a southern section (25%). The stream was bordered by a dense thicket of rosebay rhododendron (*Rhododendron maximum*), an evergreen shrub. Elevations ranged from 740 m at the stream to 817 m on the ridge crest. Soils were loam (0–35% slopes) and silt loam (3–8% slopes), with alluvial soil along Blandy Run (Stone and Matthews 1974). The climate is temperate continental with July (19.8°C) and January (−2.9°C) being, on average, the hottest and coldest months of the year. The average annual precipitation is 114 cm.

The surveyed area totaled 35 ha (420 × 840 m) and was gridded with stake-wire flags set at 35-m intervals. The grid covered a 77-m elevational gradient extending from the stream to the ridge crest and was used in locating bird species and habitat sampling points. Later, the area was divided into twenty-three, contiguous 30-m wide elevational bands with the 420-m axis paralleling the stream. Each band was approximately 1.26 ha, with 19 such bands north and four south of the stream. To reduce edge effects, elevational bands were located at least 100 m from openings other than at the stream, resulting in loss of six ha from the surveyed area. The area was surveyed eight times for breeding bird species between 25 May and 15 July 1981. Birds were located on gridded cover maps of the surveyed area (Kendeigh 1944). A count was begun immediately after sunrise and completed within 4.5 h. Random sampling of habitat variables occurred at two hundred and ninety-six grid intersections. On average, 12.9 (range = 9–17) intersections were located in each band, with 19 bands having 11–14. An ocular tube was used to estimate percent coverage (20 ± readings/intersection, + = contact with a vegetative stratum) of the different vegetative strata: herbaceous, evergreen, and total ground cover; rhododendron, hemlock, deciduous, and total short (>0–1.7 m in height) and tall (>1.7–4.6 m in height) shrub cover; and hemlock, deciduous, and total understory (>4.6–12 m in height) and canopy (>12 m in height) cover. Hemlock, deciduous, snag, and total basal area (m^2/ha) were determined at each point with an angle gauge. Elevation (m) was estimated with a surveying altimeter, and distance (m) from the stream was measured with a tape.

The environmental gradient in the habitat data was examined using principal components analysis (PCA) ordination (SAS Institute 1985, Ludwig and Reynolds 1988). Detrended principal components (DPC) analysis was used to examine nonlinearity, or if any arching pattern existed as a result of relationships among the habitat variables (Ludwig and Reynolds 1988). DPC can be used to detrend the arch into one axis to reflect the underlying environmental gradient. The values of the different habitat variables within the 23 elevational bands were first checked for normality and then transformed, if necessary, before PCA was performed. To interpret the underlying environmental gradient represented by each PC, the habitat variables were correlated with each PC using Pearson product-moment correlation.

Bird species richness, i.e., the cumulative number of species identified over the eight counts; density, i.e., the mean number of bird observations per count; and the index of bird species diversity (Shannon-Wiener index, H') and evenness (J') were calculated for each 1.26-ha elevational band (Ludwig and Reynolds 1988). The relationships of these values to PC-I and II were determined using polynomial regression analysis. Coefficients of determination (R^2) were calculated for the polynomial curve having the best fit to the data. Density of individual bird-species observations per elevational band also was correlated with PC-I, II, and III to determine the relationship between those observations and the environmental gradient on the study area.

RESULTS

The first three PC's accounted for 77.8% of the total variation in the habitat data correlation matrix, with PC-I accounting for 56.4% (Table 1). Ordination with and without the variables elevation and/or distance from stream gave similar results. DPC produced a non-significant (F ratio = 1.695, df = 2/20, $P > 0.05$) parabolic regression, indicating that the original PCA axes I and II cannot be combined into a single detrended principal component axis; therefore, both PC-I and II were examined separately. Correlation analyses of the original habitat variables with the PC's demonstrated that PC-I represented a deciduous-coniferous forest gradient from the northern hardwood upland to the predominantly hem-

TABLE 1

RESULTS OF PRINCIPAL COMPONENTS AND CORRELATION (*r*) ANALYSES OF HABITAT VARIABLES (N = 23) WITH PC-I, II, AND III

	PC-I	PC-II	PC-III
Eigenvalue	12.965	2.764	2.170
Relative % of the total variance accounted for by the PC's	56.4	12.0	9.4
Cumulative % of total variance accounted for by the PC's	56.4	68.4	77.8
Correlation of habitat variables with the PC's			
Ground cover (%)			
Herbaceous	0.786***	0.288	0.048
Evergreen	0.399	−0.036	0.475*
Total	0.821***	0.313	0.125
Short shrub cover (%)			
Rhododendron	0.746***	−0.458*	−0.220
Hemlock	0.721***	0.012	0.497*
Deciduous	−0.784***	−0.203	0.436*
Total	−0.044	−0.640***	0.577**
Tall shrub cover (%)			
Rhododendron	0.792***	−0.380	−0.208
Hemlock	0.935***	0.075	0.236
Deciduous	−0.954***	−0.141	0.083
Total	−0.617**	−0.390	0.279
Understory cover (%)			
Hemlock	0.885***	0.196	−0.173
Deciduous	−0.964***	−0.059	0.118
Total	−0.789***	0.001	−0.050
Canopy cover (%)			
Hemlock	0.727***	−0.008	−0.128
Deciduous	−0.472*	0.691***	0.436
Total	−0.275	0.781***	0.410
Basal area (m^2/ha)			
Hemlock	0.918***	0.073	0.251
Deciduous	−0.575**	0.568**	−0.252
Snag	0.689***	−0.164	−0.088
Total	0.784***	0.334	−0.346
Elevation (m)	−0.892***	0.019	−0.338
Distance from stream (m)	−0.901***	0.027	−0.369

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

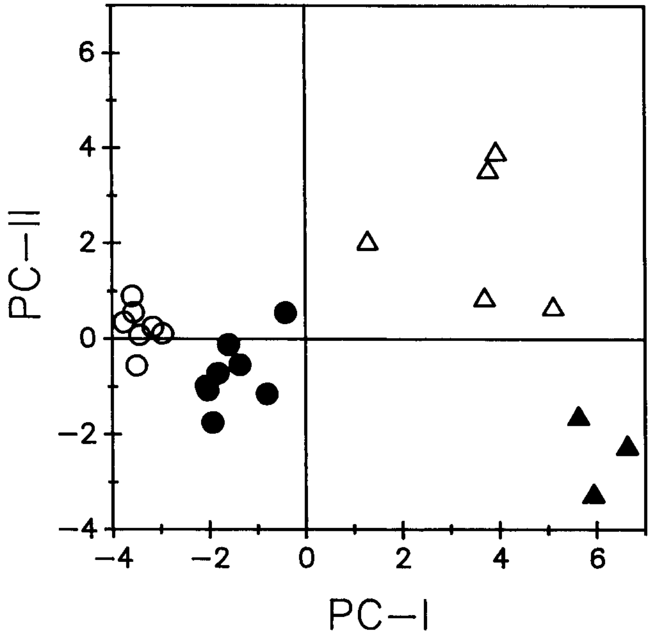

FIG. 1. Principal components ordination of 23 elevational bands within a northern hardwood forest in western Maryland. The deciduous-coniferous forest gradient was partitioned into four vegetative zones; deciduous (open circle), deciduous/sparse hemlock (solid circle), hemlock/deciduous (open triangle), and hemlock/rhododendron (solid triangle).

lock bottomland along Blandy Run (Table 1). This deciduous-coniferous gradient was superimposed on the elevation/moisture gradient. Along the deciduous-coniferous gradient, four vegetative zones, two deciduous and two coniferous, were delineated based on field observations of similarities as well as clustering of elevational bands along PC-I (Fig. 1). A deciduous zone on the ridge crest (approximately 360–690 m from the stream) had the lowest ground cover and the highest deciduous cover and basal area. Continuing downslope toward the stream (120–360 m away), a deciduous/sparse hemlock zone contained more ground cover, higher hemlock shrub cover, and high deciduous cover and basal area. A hemlock/deciduous zone located farther downslope (60–120 m from the stream) was characterized by less deciduous and more hemlock and rhododendron shrub cover, and a decrease in deciduous cover and basal area with a corresponding increase in that of hemlock. Finally, a hemlock/rhododendron zone nearest the stream (0–60 m) was characterized by high ground cover, high rhododendron and hemlock cover, and high hemlock and snag basal area. Observable ecotones occurred between the deciduous and deciduous/sparse hemlock zones with the addition of hemlock, and between the hemlock/rhododendron zone and the stream with the addition of streamside rhododendron shrub cover. PC-II separated the two coniferous zones and was a measure of certain deciduous patches within the coniferous portion of the gradient that were characterized by low rhododendron and total short shrub cover, and high deciduous and total canopy cover and deciduous basal area. PC-III represented other patches of high evergreen ground cover and hemlock, deciduous, and total short shrub cover.

The three measures, species richness, density, and diversity index, used to characterize the breeding bird assemblage were strongly associated with PC-I and II based on polynomial regression analyses. Using sequential sums of squares to determine when additional polynomial terms were unnecessary, the cubic polynomial curve was found to provide the best fit of the data to PC-I (Fig. 2). The bird assemblage was most sparse in the deciduous zone on the ridge, increased with the addition of hemlock at the ecotone and markedly increased with the addition of rhododendron at the forest-stream edge. Evenness showed a slight linear relationship ($R^2 = 0.20$, $P < 0.05$) with PC-I, indicating that observations of species were more equitable near the stream. A quadratic polynomial curve provided the best fit of species richness and diversity index to PC-II; however, a cubic polynomial curve gave a slightly better fit of density of bird observations to PC-II (Fig. 3). The highest values occurred within the coniferous zones, particularly where rhododendron and total short shrub cover were the highest, and deciduous and total canopy cover and deciduous basal area were the lowest. There was no relationship ($R^2 = 0.001$, $P > 0.05$) of evenness with PC-II.

Of the 28 breeding bird species, 60.7% were neotropical migrants (Whitcomb et al. 1981, Robbins et al. 1989) representing 82.5% of the total number of birds recorded on the study area. Seventeen species occurred in sufficient numbers ($\geq$nine observations) and across enough elevational bands (≥ 4) to make correlation analysis worthwhile (Table 2). Those neotropical migrants found on only one elevational band or occurring in low numbers included Great Crested Flycatcher (*Myiarchus crinitus*), Hooded Warbler (*Wilsonia citrina*), Black-and-white Warbler (*Mniotilta varia*), Northern Waterthrush (*Seiurus noveboracensis*), and Louisiana Waterthrush (*Seiurus motacilla*). Resident/short distance migrants that also were infrequently observed included Pileated Woodpecker (*Dryocopus pileatus*), American Crow (*Corvus brachyrhynchos*), Blue Jay (*Cyanocitta cristata*), Cedar Waxwing (*Bombycilla cedrorum*), Common Yellowthroat (*Geothlypis trichas*), and Mourning Dove (*Zenaida macroura*). Based on correlation analysis, two main groups of neotropical migrants were identified; one associated with the deciduous upland and another asso-

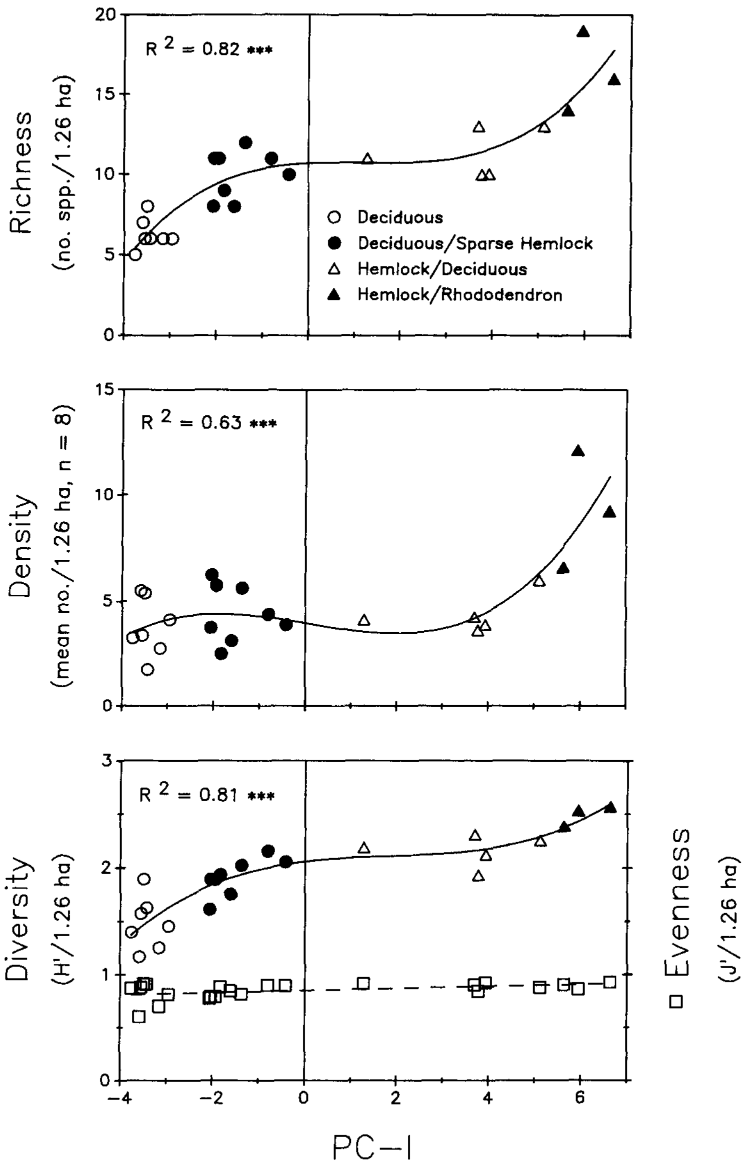

FIG. 2. The association of the bird assemblage attributes of species richness, density, and diversity with PC-I determined by polynomial regression (*** $P < 0.001$).

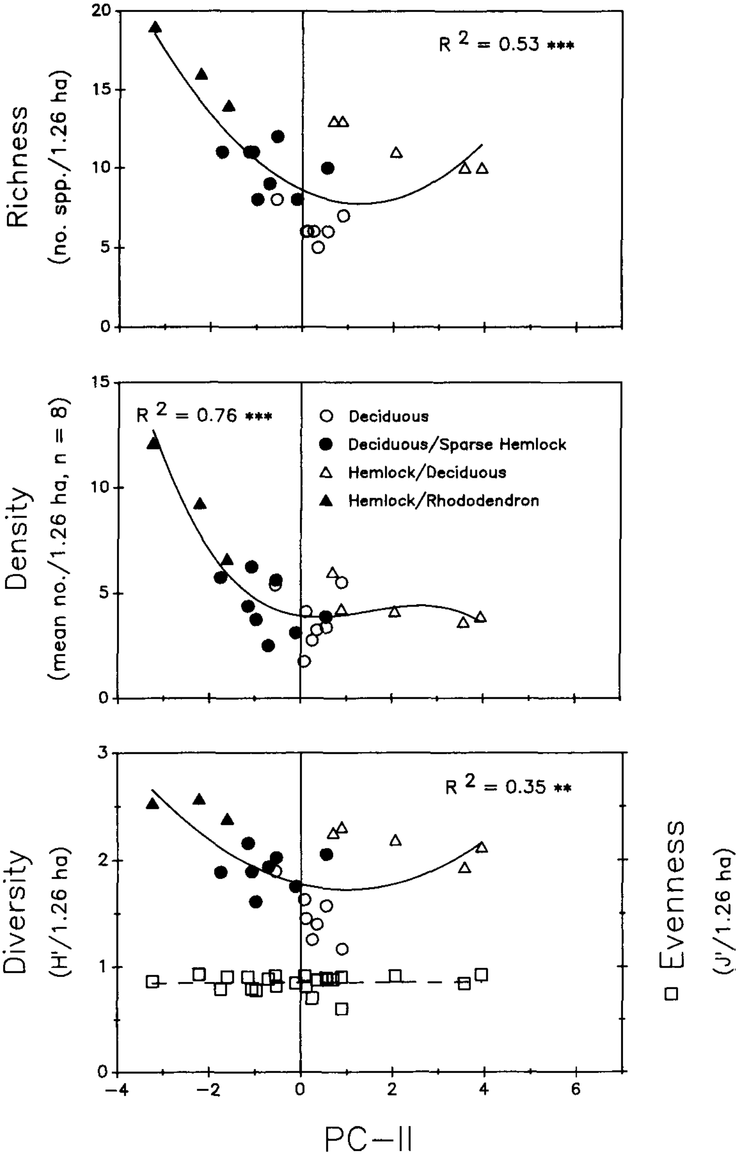

FIG. 3. The association of the bird assemblage attributes of species richness, density, and diversity with PC-II determined by polynomial regression (** $P < 0.01$, *** $P < 0.001$).

TABLE 2

Correlation (r) Analysis of Density of Bird Species Observations (Mean Number Per 1.26 ha, N = 8) within Each Elevational Band (N = 23) with PC-I, II, and III

	PC-I	PC-II	PC-III
Neotropical migrants			
Eastern Wood-Pewee (*Contopus virens*)	−0.775***	−0.258	−0.127
Acadian Flycatcher (*Empidonax virescens*)	0.392	−0.550**	0.286
Veery (*Catharus fuscescens*)	0.509*	−0.182	−0.267
Wood Thrush (*Hylocichla mustelina*)	0.691***	−0.336	0.116
Red-eyed Vireo (*Vireo olivaceus*)	−0.660***	−0.116	−0.138
Solitary Vireo (*V. solitarius*)	0.933***	0.016	−0.015
Black-throated Green Warbler (*Dendroica virens*)	0.287	0.136	−0.036
Black-throated Blue Warbler (*D. caerulescens*)	0.456*	−0.463*	0.056
Canada Warbler (*Wilsonia canadensis*)	0.723***	−0.544**	−0.292
Nashville Warbler (*Vermivora ruficapilla*)	0.689***	−0.520*	−0.242
Ovenbird (*Seiurus aurocapillus*)	0.333	0.216	0.489*
Scarlet Tanager (*Piranga olivacea*)	−0.435*	−0.277	−0.382
Resident/short distance migrants			
Hairy Woodpecker (*Picoides villosus*)	0.391	−0.386	−0.261
Black-capped Chickadee (*Parus atricapillus*)	0.638**	−0.371	−0.208
Tufted Titmouse (*P. bicolor*)	0.313	−0.140	0.344
White-breasted Nuthatch (*Sitta carolinensis*)	−0.395	0.186	−0.004
Brown-headed Cowbird (*Molothrus ater*)	0.576**	0.254	0.274

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ciated with the hemlock bottomland (Table 2). The deciduous upland group included the Eastern Wood-Pewee, Red-eyed Vireo, and Scarlet Tanager (scientific names appear in Table 2, if not given in text); the hemlock bottomland group included the Veery, Wood Thrush, Solitary Vireo, Black-throated Blue Warbler, Canada Warbler, and Nashville Warbler. The Acadian Flycatcher and Ovenbird were associated with particular patches along the deciduous-coniferous gradient. The Acadian Flycatcher was more abundant in areas near the stream characterized by high amounts of rhododendron and total short shrub cover, but with low deciduous and total canopy cover and deciduous basal area. These areas were generally open in the middle vegetative strata. The Ovenbird was more abundant where evergreen ground cover and hemlock, deciduous, and total short shrub cover were high. These patches provided high amounts of cover near the ground. The Black-throated Green Warbler was not significantly associated with any of the PC's. The resident/short distance migrants also were typically not associated with any of the PC's. The Black-capped Chickadee and Brown-headed Cowbird were recorded more frequently in the hemlock/rhododendron vegetative zone. Cowbird numbers within the hemlock/rhododendron zone were 1.27 times higher than that in the hemlock/deciduous zone and 4.14 times higher than that in the deciduous/sparse hemlock zone. At >240 m from the stream and within the deciduous zone, they were essentially absent.

DISCUSSION

Although edge effects are often considered an anathema to neotropical migrants, the high values of richness, density, and diversity near the forest-stream edge were due to the presence of breeding neotropical migrants, most of which are characterized as forest-interior or area-sensitive species (Whitcomb et al. 1981, Robbins et al. 1989). Regression of the three attributes of the bird assemblage on PC-I demonstrated the importance of the deciduous-deciduous/sparse hemlock ecotone and then the hemlock/rhododendron-stream edge to the overall pattern. Compared to the adjacent deciduous forest, the increase in coverage of vegetative strata, particularly that of evergreens; horizontal vegetative patchiness resulting from canopy gaps formed by dead trees, i.e., snags; and moisture near the stream likely resulted in a more varied and productive habitat with many foraging and nesting substrates (Wiens 1989).

The natural forest-stream edge had certain characteristics in common with some edges created by human disturbance, e.g., forest-field and forest-powerline corridor edges (Gates and Gysel 1978, Chasko and Gates 1982). Although not to the extent found at some human-made edges, the contrast at the hemlock/rhododendron-stream edge was high, and the width as characterized by the rhododendron shrub border was generally narrow. However, the forest-stream edge was sinuous rather than linear. The dense border of shrubby vegetation was similar between forest-stream and forest-field edges contributing to the "edge wall" of foliage formed by many vegetative layers. Furthermore, bird assemblages at forest-field and forest-corridor edges are dominated by edge or mixed-habitat species; whereas forest-interior birds contributed to the edge effect at the forest-stream edge (Gates and Gysel 1978, Chasko and Gates 1982).

Given these vegetative characteristics, we might predict that birds nesting near the forest-stream edge would suffer comparable high mortality as birds near similarly structured forest-field and forest-corridor edges.

Predator activity is often concentrated at the interface between adjacent habitats (Bider 1968, Gates and Gysel 1978, Chasko and Gates 1982, Gates, 1991). Streams also concentrate predator activity and are frequently used as travel corridors by mammals, e.g., raccoon (*Procyon lotor*) and mink (*Mustela vison*) (Harris 1984, Forman and Godron 1986, Gates, pers. obs.). Additionally, predators increase their search intensity in response to discovering occupied nests (Martin 1988). However, birds nesting in large patches of vegetation, e.g., rhododendron thickets, may have higher nesting success than those nesting in smaller habitat patches, e.g., isolated rhododendron shrubs; because, the number of potential nest sites that predators must search would be greater in larger patches (Chasko and Gates 1982, Martin and Roper 1988, Møller 1988). Additionally, if the edge is wide enough, birds may be able to disperse their nests, thereby reducing the probability of a chance encounter with a nest predator.

Besides potential impacts from predators, known impacts on breeding neotropical migrants come from two disparate sources. Expansion of the breeding range and populations of the Brown-headed Cowbird have been associated with declines of populations of neotropical migrants (Brittingham and Temple 1983, Wiens 1989). The higher number of Brown-headed Cowbird observations near the hemlock/rhododendron-stream edge was noteworthy, as cowbirds are habitat generalists, and their presence is dependent upon host-nest density (McGeen 1972). The abundance of snags near the hemlock/rhododendron-stream edge as well as canopy gaps serve as attractants to cowbirds (Brittingham and Temple 1983, Robbins et al. 1989). Because forest habitat does not provide sufficient open foraging sites for this ground-foraging bird, cowbirds utilizing forest interiors often maintain separate breeding and foraging ranges (Brittingham and Temple 1983). Foraging areas in nearby open fields and clearings allow cowbirds to penetrate deeply into forest interiors and utilize even small canopy openings as sites from which to parasitize nests of forest-interior birds. Susceptibility is known to be high among the neotropical migrant species nesting near the hemlock/rhododendron-stream edge (Friedmann 1963, 1971; Brittingham and Temple 1983; Gates, pers. obs.).

We noted an even more insidious threat to neotropical migrants breeding in the hemlock/rhododendron zone: habitat alteration by white-tailed deer (*Odocoileus virginianus*) (Alverson et al. 1988, Gates, pers. obs.). Deer concentrate in hemlock and rhododendron cover in the central Appalachians during severe winter weather (Gates and Harman 1980, Lang and Gates 1985). Prolonged use of this habitat leads to a browse line at about 2 m in height, below which there is little vegetation. In some localities, reproduction of hemlock and rhododendron has been completely eliminated by deer browsing (Alverson et al. 1988, Gates, pers.

observ.). Many of these neotropical migrants nest on or near the ground in open nests (Whitcomb et al. 1981). Besides immediate loss of nesting habitat and concealing nest cover, there is potential for elimination of the hemlock/rhododendron habitat type in many localities and possibly with it the associated bird assemblage. Additionally, fragmentation of rhododendron thickets by deer browsing could increase the probability of predation by reducing the number of available nest sites (Martin and Roper 1988).

In conclusion, the hemlock/rhododendron-stream edge contributed significantly to the high diversity of neotropical migrants. These birds appeared to be responding in a similar manner to the narrow, high-contrast, multi-layered edge occurring at the forest-stream interface as more typical edge or mixed-habitat species respond to narrow, high-contrast, multilayered forest-field edges. It seems likely that no species assemblage can be classified as truly edge species; but, many birds can inhabit different edge habitats, including numerous neotropical migrants associated with forest interiors. The hemlock/rhododendron-stream edge could function as an ecological trap (Gates and Gysel 1978, McKearnan and Gates, unpubl. data); however, composition and structure of the habitat within and on either side of the edge would have a controlling influence on the bird species assemblage as well as on competitors, predators, and nest parasites by influencing distributional patterns and permeability of the edge. The forest-stream edge did lack the usual array of mixed-habitat competitors associated with shrubby forest edges. However, this result was likely due to the fact that this edge bordered a narrow stream corridor within a forested region rather than an extensive terrestrial opening.

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