

EFFECTS OF EDGE TYPE AND PATCH SHAPE ON AVIAN COMMUNITIES IN A MIXED CONIFER-HARDWOOD FOREST

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ABSTRACT.—Forest bird communities were sampled along line transects in northwestern Wisconsin during June of 1985 through 1992 to determine whether edge type and patch shape affect avian abundance. Landscape structural characteristics quantified along these transects included: (1) edges that defined the habitat patches they separated, (2) fractals to quantify patch shapes, and (3) areal extent of different patches. Three multiple-regression models were constructed for 10 bird species and the mean number of individuals and species using the following sets of independent variables: (1) edge variables and fractals, (2) area variables, and (3) the first six components from a principal components analysis based on all independent variables. Multiple-regression analysis indicated that edge variables and fractal dimension explained the most variation in abundance for Black-capped Chickadees (*Parus atricapillus*), Red-breasted Nuthatches (*Sitta canadensis*), Hermit Thrushes (*Catharus guttatus*), and American Robins (*Turdus migratorius*). In contrast, area variables explained the most variation in abundance for Red-eyed Vireos (*Vireo olivaceus*), Chestnut-sided Warblers (*Dendroica pensylvanica*), and Ovenbirds (*Seiurus aurocapillus*). Abundances of Yellow-bellied Flycatchers (*Empidonax flaviventris*), Common Yellowthroats (*Geothlypis trichas*), and White-throated Sparrows (*Zonotrichia albicollis*) were equally correlated with both edge and area variables. Results of our study show that, for selected species, forest management strategies must be developed that consider not only stand characteristics, but also the edges created between these stands. Received 8 March 1995, accepted 30 August 1995.

EDGE TRADITIONALLY HAS BEEN DEFINED as an abrupt boundary between two structurally distinct habitats, such as a forest and a clearcut (Johnston 1947, Odum 1971, Smith 1980). Many studies examining the effects of edges on bird species have focused on abrupt edges created by clearcuts (Conner and Adkisson 1975, Titterton et al. 1979, Hansson 1983) or powerline corridors (e.g. Gates and Gysel 1978, Kroodsma 1987, Small and Hunter 1989, Askins 1994). In most cases, avian diversity and abundance have been found to be higher at these edges (Conner and Adkisson 1975, Gates and Gysel 1978, Strelke and Dickson 1980); however, some evidence suggests that edges have higher rates of nest predation (Wilcove 1985, Andrén and Angelstam 1988, Paton 1994) and increased brood parasitism (Brittingham and Temple 1983, Paton 1994).

As changes in forest-landscape mosaics resulting from human activities (i.e. logging) continue to lead to replacement of natural vegetation with managed systems of different struc-

ture or composition (Krummel et al. 1987), the type and amount of edge between adjacent habitat patches may become more important. For example, when artificial regeneration is used in forest management, forest composition and habitat types adjacent to each other are largely determined by selection of planting stock (Krummel et al. 1987). Within this context, edge may be redefined as a habitat patch boundary or "an outer band of a habitat patch that has an environment significantly different from the interior of the patch" (Hansen and Urban 1992). Because unique patterns of biodiversity may occur at edges, thereby influencing ecological flows between habitat patches (Angelstam 1992), a greater understanding of the ecology of edges is vital.

Few studies have focused on how edges of varying degrees of contrast (i.e. subtle and intermediate edges) affect forest birds. Bamford (1986) evaluated the importance of deciduous forest edges to bird life within a conifer forest. These subtle edges were important to songbirds, particularly to those species that are most associated with deciduous forests (Bamford 1986). DeGraaf (1992) examined the effects of

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TABLE 1. Total area and frequency of each habitat type delineated along transects based on the interpretation of 1982 black-and-white infrared stereo photographs.

Habitat type	Description	Area (ha)	Frequency*
Upland			
Mature, coniferous (UPCON)	>19 years old, >75% coniferous	15	7
Mature, deciduous (UPDEC)	>19 years old, >75% deciduous	153	19
Mature, mixed (UPMIX)	>19 years old, 25-75% deciduous	88	13
Regenerating (REGEN)	11-19 years old	11	3
Lowland			
Mature, coniferous (LOCON)	>19 years old, >75% coniferous	40	11
Mature, deciduous (LODEC)	>19 years old, >75% deciduous	15	4
Mature, mixed (LOMIX)	>19 years old, 25-75% deciduous	59	13
Alder shrub swamp (ALDER)		18	8
Open sedge/grassy opening (GRASS)		13	10

* Number of sites (of 20) in which habitat type found.

abrupt, intermediate, and subtle edges between even-aged northern hardwood stands and found that stand edges, even of greatly contrasting age or height, were different from field-forest edges. Breeding-bird assemblages in stand edges that were beyond the "abrupt" stage (e.g. pole/sawlog, sawlog/large sawlog) were similar to each other, presumably because of minimal differences in foliage profiles among stands that were more than 30 years old.

The main objectives of our study were to locate and quantify edges (both natural and man-made) of varying degrees of contrast (subtle, intermediate, and abrupt) and shape, and to describe statistical associations between these habitat variables and bird community characteristics found at these edges.

METHODS

Four 4.35-km transects were chosen from a group of randomly selected bird survey transects originally established in northwestern Wisconsin within the Chequamegon National Forest (46°00'N, 91°00'W; Hanowski et al. 1993). The study area is a forested glacial landscape with numerous lakes and wetlands in primarily upland second growth forest. Forest management practices and natural events have resulted in a variety of habitat patches and the creation of many different edge types (Hanowski et al. 1993).

Vegetation sampling.—A global positioning system Pathfinder Basic receiver was used to provide transect-position information to a ground resolution of 20 to 30 m accuracy (August et al. 1994); these data were transferred to a geographic information system (GIS). Forest maps were created by delineating habitat patches along the transects into one of nine categories (Table 1) based on interpretation of 1:15,840 black-and-white infrared stereo photography taken during

May 1982 (when leaves of deciduous trees were absent). The minimum mapping unit was approximately 450 m². Forest maps were field-verified and updated during spring 1993. Approximately 70% of the delineated habitat patches were verified by ground-truthing and of these 70%, over 90% were classified correctly. Because logging was minimized in the transect area, most vegetation changed little over the 11 years.

Forest maps were digitized using the ARC/INFO 3.4D GIS (ESRI 1987). Using ARC/INFO software, each transect was divided into seven 400-m segments each separated by a 50-m buffer for a total of 28 segments. Spatial autocorrelation tests indicated that a 50-m buffer was sufficient for considering each 400-m segment as an independent experimental unit (Hanowski et al. 1993). Seven segments that had been logged during the study period and one segment that contained two ponds were excluded, leaving 20 segments for use in the analysis. A 100-m buffer was placed around the 200 × 400-m census area of each segment, creating a study site of about 24 ha.

Edges within each site were described by the types of habitat patches they separated and categorized into one of three classes: subtle, intermediate, or abrupt (Table 2). An example of a subtle edge was a mature pine forest next to a mature mixed hardwood forest, while an example of an intermediate edge was a lowland mixed forest next to an alder shrub swamp. The one abrupt edge used in our study was mature forest adjacent to a grassy opening. The total length of each edge type and distribution of each edge among the 20 sites was determined using the edge analysis program from the analysis package APACK (Boeder et al. 1995; Table 2). Rare or infrequent types (those edges less than 100 m in length and/or distributed on fewer than seven sites) were combined with other edges based on similarities in description of the edges and degree of contrast (Table 2). Each of the final nine edge types had a total length of more than 1,000 m and was found on a minimum of seven sites, with the exception of mature forest to regenerating forest,

TABLE 2. Total length and frequency of each edge type. Edges combined into one of nine edge types. Combinations of edges based on similarities in description and degree of contrast. Edges included in each edge type are given in parentheses. "Adjacent to" indicated by slash (/).

Subtle: upland deciduous/upland mixed (UPDEC/UPMIX), ^a 8,153 m ^b (12); ^c upland coniferous/upland mixed (UPCON/UPMIX, UPCON/UPDEC), 2,480 m (8); lowland coniferous/lowland mixed (LOCON/LOMIX, LOCON/LODEC, LOMIX/LODEC), 3,644 m (9).
Intermediate: upland mixed/lowland mixed (UPMIX/LOMIX, UPMIX/LODEC, UPDEC/LODEC, UPDEC/LOMIX, UPCON/LOMIX), 6,527 m (13); upland mixed/lowland coniferous (UPMIX/LOCON, UPDEC/LOCON), 3,893 m (9); upland mixed/alder (UPMIX/ALDER, UPDEC/ALDER), 1,269 m (7); lowland mixed/alder (LOMIX/ALDER, LOCON/ALDER, LODEC/ALDER), 5,126 m (8); mature/regenerating (UPDEC/REGEN, UPMIX/REGEN, LOCON/REGEN), 1,428 m (3).
Abrupt: mature/grass (UPDEC/GRASS, UPMIX/GRASS, UPCON/GRASS, LOMIX/GRASS, LOCON/GRASS), 5,329 m (10).

^a Habitat codes as in Table 1.

^b Total length of each edge type.

^c Number of sites (of 20) in which edge type found.

which was found on only three sites (Table 2). However, this type was retained because of its potential importance.

Areas of different habitat patches found within each site also were calculated using the same nine categories from Table 1. Patch size (area) was quantified so that effects due to the amount of suitable habitat found within the landscape could be distinguished from effects due to edges or a combination of edges and habitat area.

Bird sampling.—A line-transect method (Hanowski et al. 1993) was used to sample bird communities. One census was conducted annually per transect during June of 1985 through 1992. Birds were counted from 0.5 h before to 4.5 h after sunrise on days with little wind (<15 km/h) and no precipitation. One of three experienced observers (> 3 years of experience) conducted the bird census each year; therefore, observer variability was relatively low. Each bird detected within 100 m of the transect center line was identified and its position with respect to the transect recorded. Birds flying above the canopy were not counted.

Estimates of bird species and community param-

eters were obtained for each site using the mean number of individuals and species recorded for the eight-year study period. Significant annual fluctuations in abundance were detected for most birds species (Blake et al. 1994), but these fluctuations likely occurred in response to environmental conditions (e.g. drought and temperature), not to changes in the landscape, because we eliminated logged sites from our analysis. Ten bird species were selected *a priori* for detailed analysis because they were commonly observed along the transects, and their primary habitat associations represent major habitat types found within the study area (Table 3).

Statistical analyses.—Fractal analysis was used to quantify patch shapes within a site. The box-count algorithm method (Morse et al. 1985) was used to calculate an overall fractal dimension estimate (*D*) for each study site (Westman 1993). Values of *D* near 1.0 indicate simple shapes approaching those of a circle, whereas values approaching 2.0 describe more complex shapes (Morse et al. 1985).

We limited the number of independent variables to one-half the sample size in the selection multiple-

TABLE 3. Habitat associations of bird species selected for detailed analysis.

Species	Habitat association
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	Coniferous forests and bogs (Brewer et al. 1991)
Black-capped Chickadee (<i>Parus atricapillus</i>)	Deciduous or mixed open forests, suburbs (Niemi and Pfannmuller 1979)
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	Coniferous forests (Brewer et al. 1991)
Hermit Thrush (<i>Catharus guttatus</i>)	Coniferous, mixed, or deciduous forests (Niemi and Hanowski 1984)
American Robin (<i>Turdus migratorius</i>)	Forests, gardens, and parks (Dawson 1979)
Red-eyed Vireo (<i>Vireo olivaceus</i>)	Deciduous forests (Conner and Adkisson 1975)
Chestnut-sided Warbler (<i>Dendroica pensylvanica</i>)	Second-growth deciduous forests, borders (Green and Niemi 1978)
Ovenbird (<i>Seiurus aurocapillus</i>)	Upland forests (Collins et al. 1982)
Common Yellowthroat (<i>Geothlypis trichas</i>)	Marshes, overgrown fields (Harrison 1975)
White-throated Sparrow (<i>Zonotrichia albicollis</i>)	Coniferous or mixed forests, thickets (Titterton et al. 1979)

regression analysis. However, we did not include more than one-third the number of independent variables to sites in any of the final multiple-regression analyses. Moreover, we consider this an exploratory statistical analysis rather than a rigorous test of specific hypotheses. Because 20 study sites and a total of 19 independent variables (10 edge variables and 9 area variables) were used in our study, principal components analysis (PCA) was also performed to reduce the 19 independent variables to a smaller set of orthogonal principal components scores (PCS; Tatsuoka 1971) that combined the edge and area variables. The PCS were then used to complete a multiple-regression analysis using linear combinations of the independent variables.

Hence, three multiple-regression models were constructed for each bird species and each community parameter using the following sets of independent variables: (1) nine edge variables and fractal dimension, (2) nine area variables, and (3) the first six PCA components. Models were constructed using maximum R^2 improvement (MAXR), in which the best one-variable model, the best two-variable model, and so forth was found based on the relative contribution of each variable to the least squares linear regression model (SAS Institute 1988). The level of significance for entering an independent variable into the equation was set at a $P \leq 0.05$. Independent and dependent variables were transformed using square-root or logarithmic transformations, whichever best improved the model assumptions of normality and homogeneity of variances. The final models included those that met model assumptions and had independent variables that were not highly correlated ($P > 0.05$) with each other.

RESULTS

Birds.—We observed 111 species on the study sites during the eight-year study period (for a list of species, see Hanowski et al. 1991). Means of 22 individuals and 10 species were observed per site over all years (Table 4). Of the 10 species selected for analysis, the Red-eyed Vireo (*Vireo olivaceus*) and Ovenbird (*Seiurus aurocapillus*) were observed most often, whereas the Red-breasted Nuthatch (*Sitta canadensis*) and Chestnut-sided Warbler (*Dendroica pensylvanica*) were the least common (Table 4).

Vegetation.—The most common edge type found within the sites was upland deciduous forest adjacent to upland mixed forest, and the least common edge type was upland mixed forest adjacent to alder shrub swamp (Table 2). Upland deciduous forest was the most common habitat type, and regenerating forest was the least common habitat type (Table 1).

TABLE 4. Mean count for 10 individual species and mean number of species and individuals based on 25-min line-transect census in June, 1985–1992. Dash indicates none seen.

Species	Study site																				\bar{x}
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
Yellow-bellied Flycatcher	1.50	—	—	—	0.13	0.38	1.25	0.63	0.25	—	—	—	1.13	1.50	0.50	0.50	—	—	1.50	0.88	0.51
Black-capped Chickadee	0.88	0.13	0.38	—	0.13	1.50	0.88	—	0.38	1.25	—	0.63	1.13	0.25	0.25	0.38	0.25	0.63	—	0.63	0.48
Red-breasted Nuthatch	0.13	0.25	0.25	—	0.25	0.38	0.88	0.25	—	0.25	—	—	—	0.13	—	0.13	—	—	0.13	0.13	0.16
Hermit Thrush	0.88	0.63	—	0.88	0.63	2.00	0.30	0.75	0.13	2.13	1.38	0.38	0.25	0.13	0.25	0.50	0.88	1.13	1.75	0.38	0.77
American Robin	0.75	0.25	—	0.63	0.25	—	—	—	—	0.25	0.13	0.13	—	0.25	0.38	1.25	0.50	0.13	—	—	0.25
Red-eyed Vireo	1.75	3.25	2.88	6.25	4.25	1.00	0.38	2.00	0.38	1.50	2.88	4.25	2.13	1.38	1.63	2.63	4.75	1.50	0.38	1.63	2.34
Chestnut-sided Warbler	0.13	—	3.00	—	4.00	—	—	0.25	4.25	0.13	—	0.13	0.13	—	0.50	—	—	0.63	0.13	—	0.66
Ovenbird	2.50	4.13	1.50	9.25	5.25	4.63	4.00	1.88	2.88	5.75	4.63	4.50	2.75	1.13	0.75	3.00	7.13	5.13	—	4.63	3.77
Common Yellowthroat	1.00	—	0.13	—	0.50	—	—	0.63	0.38	—	—	0.13	—	0.63	0.25	—	—	0.25	—	0.38	0.21
White-throated Sparrow	1.00	—	0.88	—	1.38	0.50	2.88	1.88	3.00	0.25	—	—	0.38	2.75	1.63	—	—	0.50	3.25	—	1.01
No. of individuals	25.60	19.30	16.30	27.00	27.60	21.00	25.10	20.90	22.30	20.60	18.80	16.40	18.00	23.10	17.80	37.50	19.40	18.00	22.90	14.80	21.60
No. of species	14.60	8.50	7.10	7.60	10.80	9.40	11.40	11.60	9.40	10.00	9.50	6.60	10.60	12.30	10.60	15.50	6.40	9.60	8.60	8.00	10.00

TABLE 5. Quantification of structural characteristics. Fractal-dimension value (D) and length of edges (m) found within each study site. Dash indicates edge type was not found in that site.

Site	D	Edge type ^a								
		Subtle			Intermediate				Abrupt	
		UPDEC/ UPMIX	UP- CON/ UPMIX	LOCON/ LOMIX	LOMIX/ ALDER	UPMIX/ LOMIX	UPMIX/ LOCON	MA- TUR/ REGEN	UPMIX/ ALDER	MATUR/ GRASS
1	1.20	467	472	—	153	—	369	—	380	—
2	1.30	1,181	49	345	—	676	233	56	—	—
3	1.11	—	935	—	—	—	—	—	—	—
4	1.05	—	—	—	—	—	—	—	—	—
5	1.19	—	—	—	—	321	—	—	—	989
6	1.20	—	—	19	—	311	384	—	—	194
7	1.26	312	488	375	—	456	1,009	—	—	—
8	1.28	—	—	1,090	737	453	—	—	162	3
9	1.17	—	—	—	753	480	—	—	—	—
10	1.22	497	172	—	—	—	—	—	—	971
11	1.26	948	—	—	—	—	—	—	—	1,226
12	1.30	1,366	111	—	317	—	352	—	239	210
13	1.31	415	—	879	—	791	812	—	—	51
14	1.34	576	—	—	1,372	258	—	853	63	133
15	1.28	—	—	26	1,006	688	141	519	125	—
16	1.18	519	—	—	138	529	—	—	232	117
17	1.05	—	—	—	—	—	—	—	—	—
18	1.22	384	118	172	—	240	216	—	—	800
19	1.19	123	—	534	—	316	375	—	—	—
20	1.27	718	—	205	651	1,009	—	—	70	—

^a Habitat codes as in Table 1.

Fractal dimension values for the 20 sites ranged from 1.05 to 1.34 (Table 5). The lowest value described two sites that were comprised entirely of contiguous, upland deciduous forest (i.e. lacked edges as defined by this study). Sites that had a higher proportion of lowland edges, such as LOMIX/ALDER, had relatively higher fractal dimension values than those sites having a higher proportion of upland edges, such as UPCON/UPMIX (Table 5).

PCA identified six components (eigenvalue > 1.0), which accounted for 89% of the variance. The first two components explained 46% of the variance in the 19 habitat variables and contrasted two different landscapes within the study area. Sites that had high scores of PC 1 generally had high fractal-dimension values and a high proportion of lowland edges and habitats. Sites that had high values of PC 2 generally had a high proportion of upland edges and habitats. Values for PC 1, fractal dimension, and the amount of lowland edges or habitats found within a site were highly positively correlated with each other.

Species related with edges.—Models constructed using edge variables and fractal dimension values explained the most variation in abundance for Black-capped Chickadees (*Parus atri-*

capillus), Red-breasted Nuthatches, Hermit Thrushes (*Catharus guttatus*), and American Robins (*Turdus migratorius*), as well as the most variation in number of species observed (Fig. 1). The model constructed using the amount of edge habitat of upland mixed forest adjacent to lowland coniferous forest explained 23% of the variation and was the best predictor for number of Black-capped Chickadees (Table 6, Fig. 1A; $P = 0.03$). The model constructed using the amount of edge habitat of upland mixed forest adjacent to lowland mixed forest and upland coniferous forest adjacent to upland mixed forest explained 35% of the variation in Red-breasted Nuthatch numbers (Table 6, Fig. 1B; $P = 0.03$). The best predictor for number of Hermit Thrushes was the model constructed using the amount of edge habitat of lowland mixed forest adjacent to alder shrub (Table 6, Fig. 1C; $P = 0.03$), which explained 25% of the variation. The model constructed using fractal dimension and the amount of edge habitat created between upland mixed forest and alder shrub explained 49% of the variation and was the best predictor for number of American Robins (Table 6, Fig. 1D; $P = 0.003$).

Species related with area.—Models constructed using area variables explained most of the variation in abundance for the Red-eyed Vireo,

TABLE 6. Best models for multiple regression (using all possible subsets of habitat variables). Maximum R^2 used as selection criterion. Adjusted R^2 is R^2 for model after adjustment made for corresponding degrees of freedom.

Model ^a	R^{2b}
Abundance	
Yellow-bellied Flycatcher (PC1)	0.45 (0.42)***
Black-capped Chickadee (UPMIX/LOCON)	0.23 (0.19)*
Red-breasted Nuthatch (UPMIX/LOMIX [0.18] UPCON/UPMIX [0.17])	0.35 (0.27)*
Hermit Thrush (LOMIX/ALDER)	0.25 (0.21)*
American Robin (FD [0.27] UPMIX/ALDER [0.22])	0.49 (0.43)**
Red-eyed Vireo (UPDEC [0.31] LOMIX [0.13])	0.44 (0.38)*
Chestnut-sided Warbler (UPCON [0.15] LOCON [0.13] UPMIX [0.08] LOMIX [0.08])	0.44 (0.29)
Ovenbird (UPDEC [0.51] ALDER [0.10])	0.61 (0.57)***
Common Yellowthroat (ALDER) ^c	0.48 (0.45)***
Common Yellowthroat (LOMIX/ALDER)	0.46 (0.43)***
White-throated Sparrow (UPDEC [0.23] UPMIX [0.19])	0.42 (0.34)**
White-throated Sparrow (FD [0.26] UPDEC/UPMIX [0.15])	0.41 (0.34)**
No. of individuals (UPDEC)	0.19 (0.14)
No. of species (UPMIX/ALDER)	0.26 (0.22)*

^{*}, $P < 0.05$; ^{**}, $P < 0.01$; ^{***}, $P \leq 0.001$.

^a Habitat codes as in Table 1.

^b Adjusted R^2 given in parentheses.

^c Both sets of area and edge variables resulted in significant models with similar R^2 s for the Common Yellowthroat and White-throated Sparrow.

Chestnut-sided Warbler, and Ovenbird, as well as the most variation in number of individuals observed (Fig. 2). The model constructed using the amount of upland deciduous forest and the amount of lowland mixed forest explained 44% of the variation in Red-eyed Vireo numbers (Table 6, Fig. 2A; $P = 0.01$). The model constructed

using the amount of lowland mixed and upland coniferous forest, and the amount of lowland coniferous and upland mixed forest, explained 44% of the variation and was the best predictor for number of Chestnut-sided Warblers (Table 6, Fig. 2B); the model approached statistical significance, with a P of 0.056. The best predictor

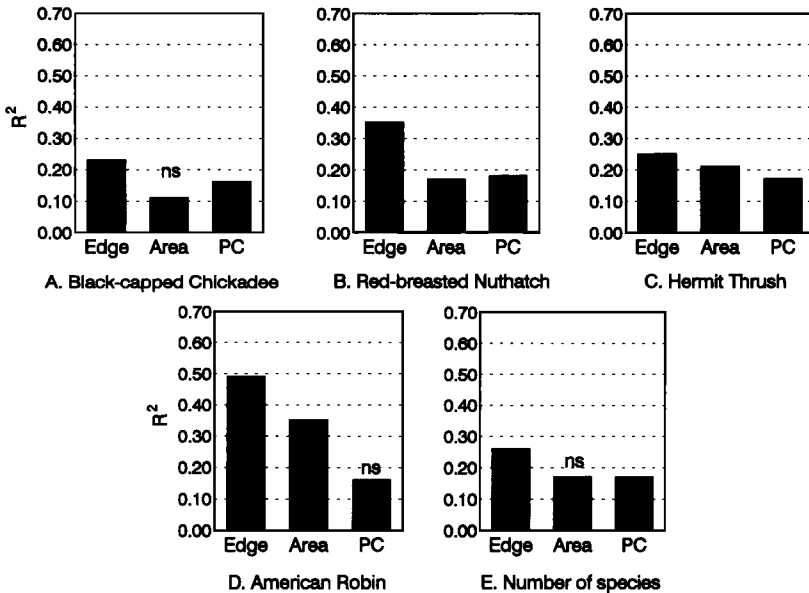


FIG. 1. Summary of explained variation (R^2) for species primarily related with edge and fractal variables for three sets of independent variables: (1) edge and fractal dimension (Edge), (2) habitat area (Area), and (3) principal components (PC) based on 19 independent variables; "ns" above bar indicates that the set did not result in a significant ($P < 0.05$) model.

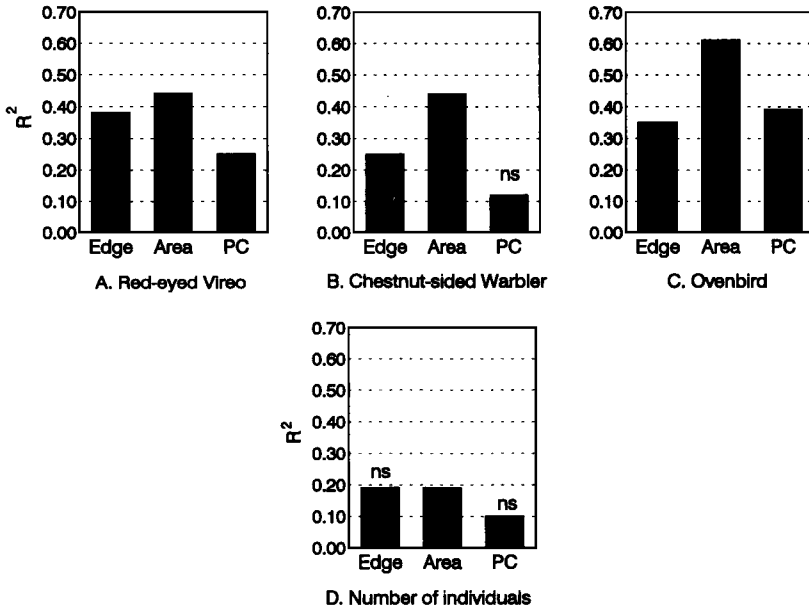


FIG. 2. Summary of explained variation (R^2) for species primarily related with habitat area for three sets of independent variables: (1) edge and fractal dimension (Edge), (2) habitat area (Area), and (3) principal components (PC) based on 19 independent variables; "ns" above bar indicates that the set did not result in a significant ($P < 0.05$) model.

for number of Ovenbirds was the model constructed using the amount of upland deciduous forest and the amount of alder shrub, which explained 61% of the variation (Table 6, Fig. 2C; $P < 0.001$).

Species related with both edges and area.—The best predictor for number of Yellow-bellied Flycatchers (*Empidonax flaviventris*) was the model constructed using the six PCs, which explained 45% of the variation (Fig. 3A; $P = 0.001$). Abundance of this species was positively

correlated with PC 1 (Table 6), which represented sites that had high fractal dimension values and a high proportion of lowland edges and habitats (Table 5). Models constructed using both edge and area variables explained similar amounts of variation in abundance for Common Yellowthroats (*Geothlypis trichas*) and White-throated Sparrows (*Zonotrichia albicollis*; Fig. 3B, C). The two models constructed using the amount of alder and the amount of edge between lowland mixed forest and alder shrub

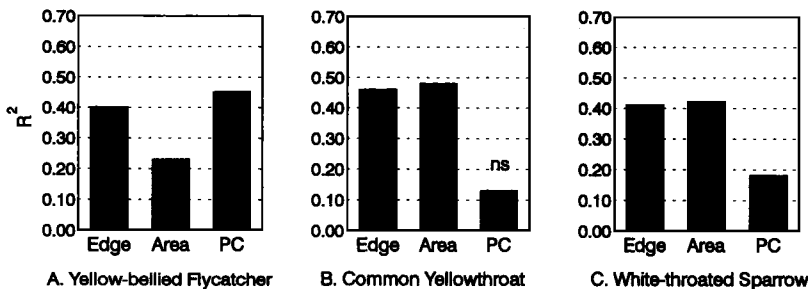


FIG. 3. Summary of explained variation (R^2) for species primarily related with both edge and habitat area for three sets of independent variables: (1) edge and fractal dimension (Edge), (2) habitat area (Area), and (3) principal components (PC) based on 19 independent variables; "ns" above bar indicates that the set did not result in a significant ($P < 0.05$) model.

explained 46 and 48%, respectively, of the variation in Common Yellowthroats (Table 6, Fig. 3B; $P = 0.001$). The model constructed with the amount of upland deciduous forest to upland mixed forest edge habitat and fractal dimension, and the model constructed with the amount of upland deciduous and upland mixed forest, were the best predictors for number of White-throated Sparrows. These models explained 41 and 42%, respectively, of the variation in White-throated Sparrows (Table 6, Fig. 3C; $P = 0.01$).

Community parameters.—The best predictor for number of species observed was the model constructed using the amount of edge habitat created between upland mixed forest and alder shrub, which explained 26% of the variation (Table 6, Fig. 1E; $P = 0.02$). The model constructed using the amount of upland deciduous forest was the best predictor for number of individuals observed, explaining 19% of the variation (Table 6, Fig. 2D; $P = 0.057$).

DISCUSSION

Patch size, isolation, and habitat diversity are components of variation in biodiversity among bird communities (Forman et al. 1976, Roth 1976, Lynch and Whitcomb 1978, Ambuel and Temple 1983). Our results suggest that birds also are associated with edges between habitat patches of varying composition, age, structure, and vegetative diversity. The characteristics of a species' life history (e.g. nesting and foraging habits, dispersal ability, and sensitivity to fragmentation) are mechanisms that underlie avian community dynamics at these edges.

Black-capped Chickadee.—The Black-capped Chickadee is a secondary cavity nester that breeds in a variety of mature and successional forest types, including deciduous, mixed, and coniferous, with little evidence of preference for a particular type (Niemi and Pfannmuller 1979, Noon et al. 1979, Temple et al. 1979, Brewer et al. 1991). It appears to have a relatively high tolerance for many types of disturbances due to human activities, as long as suitable nest cavities are present.

Black-capped Chickadees were more abundant in areas with edges between upland mixed forest and lowland coniferous forest. Perhaps the vertical complexity at the interface of these two mature forest types creates a suitable habitat for this species. Further work will be need-

ed to address this issue, but intermediate edges within this forest landscape appear to be important areas for the Black-capped Chickadee.

Red-breasted Nuthatch.—The Red-breasted Nuthatch is a secondary cavity nester that breeds in mature and successional upland and lowland coniferous and upland mixed forests (Green and Niemi 1978, Dawson 1979, Niemi and Pfannmuller 1979, Noon et al. 1979). The species' preference for unbroken canopies (Langelier and Garton 1986) and the greater number of nesting cavities available in older stands may be reasons for Probst et al. (1992) finding it to be more common in mature forest. Temple et al. (1979) found presence of Red-breasted Nuthatches to be positively correlated with the amount of pine (*Pinus* spp.) in the forest, probably because of the species' dependence on conifer seeds as a food source.

We found that Red-breasted Nuthatches responded positively to subtle edges with a conifer component and a closed canopy (upland mixed to lowland mixed forest, and upland coniferous to upland mixed forest). This species may respond to a more complex landscape mosaic consisting of a variety of habitat patches, rather than to a homogeneous forest.

Hermit Thrush.—The Hermit Thrush is a ground nester that breeds in mature and successional lowland coniferous (Niemi and Hanowski 1984) and upland mixed and deciduous forests (Dawson 1979, Niemi and Pfannmuller 1979, Noon et al. 1979, Probst et al. 1992). Temple et al. (1979) found the species' presence to be positively correlated with the amount of pine found in the forest. Although the Hermit Thrush has been characterized as a generalist in its response to edge and patch size (Hansen and Urban 1992), it also has been classified as a forest-interior species (Gillespie and Kendeigh 1982). We found that the Hermit Thrush was negatively associated with a lowland, intermediate edge (lowland mixed forest to alder shrub) within our study area. Lowland edges are important in predicting the abundance of Hermit Thrushes.

American Robin.—The American Robin nests in trees, shrubs, and artificial structures within suburban areas and a wide range of forested habitat types and age classes, including mature and successional, upland and lowland, coniferous and deciduous forests (Dawson 1979). Robins were associated with intermediate edges

within a northern hardwood forest where the species was observed at the interfaces of all edge types (DeGraaf 1992). Thus, it is not surprising that the species was associated with intermediate forest edges that are comprised of a mature forest patch on one side and a shrub habitat on the other (upland mixed forest to alder shrub habitat). The species' negative correlation with high fractal dimension values may be because the species is less common in lowland habitats (Robbins et al. 1989); in our study, high fractal dimension values were highly correlated with lowland habitats.

Red-eyed Vireo.—The Red-eyed Vireo is a shrub, subcanopy, and canopy nester that breeds primarily in mature upland deciduous forest (Conner and Adkisson 1975, Howe 1979, Niemi and Pfannmuller 1979). It also has been found in mature upland coniferous forest (Howe 1979) and successional (Niemi and Pfannmuller 1979) or recently cut areas with a closed canopy layer (Conner and Adkisson 1975). The critical forest size estimated by Robbins et al. (1989) to maintain a viable breeding population of Red-eyed Vireos was 101 ha. The species was found to be positively correlated with forest area, canopy cover, and canopy height, and it generally is considered to be a forest-interior species that responds positively to patch size (Robbins et al. 1989, Hansen and Urban 1992). The Red-eyed Vireo responded positively to the amount of mature, upland deciduous forest within the study area and was less common in lowland forest, especially those with a conifer component. The high densities of Red-eyed Vireos in mature upland forest suggest that the amount of suitable forest habitat is important to them.

Chestnut-sided Warbler.—The Chestnut-sided Warbler is a shrub nester that is associated with early successional forests, young saplings, and brushy edges (Niemi and Pfannmuller 1979, Noon et al. 1979). The species requires a dense shrub layer (Dawson 1979, Temple et al. 1979, Niemi and Hanowski 1984) because it is an understory foliage gleaner.

The Chestnut-sided Warbler responded to habitat area (positively with upland coniferous and lowland mixed forest, and negatively with lowland coniferous and upland mixed forest) within the landscape. Upland coniferous forests within our study area tend to be open-canopy stands, with a well-developed understory of regenerating aspen to which the Chestnut-sided

Warbler may have been responding. The species' relatively high densities observed in lowland mixed forests and relatively low densities observed in lowland coniferous and upland mixed forest also may be due to its association with a well-developed shrub layer or small openings in the forest.

Growing evidence suggests that Chestnut-sided Warblers are associated with forest patch size. Robbins et al. (1989) found it to be positively associated with forest cover, and Niemi et al. (unpubl. data) found it to be associated more with contiguous forest area than with fragmented forest landscapes. If logged areas had been included in the analysis, models constructed for the Chestnut-sided Warbler also may have reflected the species' preference for early successional habitats. The amount of forest with a well-developed shrub layer, a common feature in the forests of northern Wisconsin, is important in predicting the abundance of Chestnut-sided Warblers.

Ovenbird.—The Ovenbird is a ground nester that breeds primarily in upland deciduous, mixed, and coniferous forests (Collins et al. 1982, Probst et al. 1992). It also has been found in lowland (Dawson 1979) and successional forests (Niemi and Pfannmuller 1979, Noon et al. 1979). The species generally is considered to be a forest-interior species that responds positively to patch size, a closed canopy (Collins et al. 1982, Robbins et al. 1989, Hansen and Urban 1992), and ground cover (Robbins et al. 1989). The Ovenbird has been shown to be negatively associated with a moisture gradient (Robbins et al. 1989); therefore, it is not surprising that the species responded positively and was most abundant in mature, upland deciduous forest and less common in lowland habitats.

Common Yellowthroat.—The Common Yellowthroat is a low-shrub nester that breeds in wetland shrub habitat, open bog, open marshlands, and semiopen lowland coniferous forests with few or no trees (Niemi and Pfannmuller 1979, Collins et al. 1982). It is positively associated with ground and shrub cover and negatively associated with a closed canopy (Collins et al. 1982, Robbins et al. 1989). For these reasons, Common Yellowthroats are seldom observed in mature forest stands in north-central forests (Noon et al. 1979). This species responded positively to a lowland habitat (alder shrub) and an intermediate lowland edge (lowland mixed

forest to alder shrub) in our study. It is likely that yellowthroats favor a more complex landscape mosaic consisting of a variety of habitats.

White-throated Sparrow.—The White-throated Sparrow is a ground nester that breeds in a wide variety of habitats including recently logged areas (Niemi and Hanowski 1984), successional habitats (Niemi and Pfannmuller 1979, Noon et al. 1979), lowland coniferous forests (Dawson 1979, Niemi and Pfannmuller 1979), and upland mixed forests with shrubby openings. The species seldom ventures far from dense cover and is often uncommon or absent in mature upland forests that lack a well-developed shrub layer.

Lack of a well-developed shrub layer may be a reason why White-throated Sparrows were negatively associated with two mature upland habitats (upland deciduous and upland mixed forest) and a subtle upland edge (upland deciduous to upland mixed forest). On our study sites, the mature upland habitats have a relatively open shrub layer. White-throated Sparrows were positively correlated with high fractal dimension values, which was indicative of lowland habitats within the study area. The amount of lowland habitats, as well as the distribution of edges within the landscape, are important in predicting the abundance of White-throated Sparrows.

Yellow-bellied Flycatcher.—The Yellow-bellied Flycatcher is a ground nester that breeds almost exclusively in mature, lowland coniferous forests (Dawson 1979, Niemi and Pfannmuller 1979, Niemi and Hanowski 1984), but occasionally it occurs in upland coniferous habitats (Niemi 1977, Niemi and Pfannmuller 1979). Temple et al. (1979) found the species to be positively correlated with the amount of spruce (*Picea* spp.) or fir (*Abies* spp.) within the forest.

Proximity to mature stands of lowland coniferous forest, where a substantial layer of moss has developed, may be necessary for the Yellow-bellied Flycatcher because it nests on the ground in a layer of moss (Harrison 1975). Perhaps because of the species' affinity for lowland habitats, the abundance of Yellow-bellied Flycatcher was correlated with PC 1, which represented the lowland edges and habitats within the study area.

Community parameters.—Species diversity has been shown to be related to habitat complexity (MacArthur and MacArthur 1961, Probst 1976,

James and Wamer 1982). Because habitat structure is important in determining the distribution and abundance of breeding birds, it is probable that a complex landscape composed of a variety of habitats and edges would support a more diverse bird community than would a more homogeneous landscape.

In our study, species diversity was associated with the abundance of an intermediate edge, i.e. upland mixed forest to alder shrub. The link between the complexity of the foliage at this interface and species diversity is consistent with results of the studies listed above. The number of individuals observed was related to the patch size of the most abundant habitat type found within the study area, upland deciduous forest. This association occurred because the two most abundant species observed within the study area, the Red-eyed Vireo and the Ovenbird, were found primarily in upland deciduous forests, and four additional species of the 10 also were found predominantly within this forest type. When Red-eyed Vireos and Ovenbirds were not included in the analysis, the best predictor for the number of individuals observed was the model constructed using three lowland habitats (LOCON, ALDER, and LOMIX) and a lowland edge (LOMIX/ALDER), which explained a smaller percentage of the variation.

Fractal dimension values.—Sites that had low fractal dimension values and were comprised of a high percentage of upland habitats generally had been modified through forest management practices (i.e. conifer plantation). Sites that had high fractal dimension values and were composed of a high percentage of lowland edges generally were unmanaged areas within the landscape (i.e. alder shrub swamp). Although there may be a greater number of landscape patches and ecosystem types in a disturbed landscape (Mladenoff et al. 1993), human-influenced landscapes often exhibit simpler patterns than natural landscapes (Turner 1989).

Because lowland habitats tended to be the less managed habitats within the study area, fractal dimension values were higher for study sites that had a high number of lowland patches. Fractal dimension was highly correlated with these habitats. Any potential relationship between patch shape (as measured by fractal dimension) and bird-species composition may have been masked by this strong correlation between patch shape and lowland habitats. The

species that responded to patch shape (Yellow-bellied Flycatcher, American Robin, and White-throated Sparrow) probably were responding to the lowland habitats associated with this more complex landscape.

Conclusions.—Birds may respond to either the extent of edge within a landscape, the amount of suitable habitat present, or a combination of the two. As fragmentation of the forest continues and patch juxtaposition is determined largely by forest management practices, the type of edge created may become more important than habitat composition. Modifications of habitat connectivity or patch shape can have an effect on species movement patterns. For example, patch shape may have more importance in subtle-edged habitats that have moderate to high permeability to dispersers, compared with abrupt-edged habitats, where low permeability results in decreased species movement (Stamps et al. 1987). As we increase our understanding of forest edges, forest management strategies may be developed that consider not only stands in forest planning, but also the edges created between these stands.

Examining edges is a challenge because edges are complex landscape features and difficult to quantify. What a person delineates as an "edge" may not be a feature that an organism is responding to as an "edge," and what a person describes as a abrupt edge actually may be perceived as a subtle edge by some organisms. In future studies, it would be useful to examine how the three classes of edges (subtle, intermediate, and abrupt) separately influence bird species composition. For example, edge length within a site could be calculated in two ways, with and without the inclusion of subtle and intermediate edges. Results of the two analyses could then be compared to determine whether subtle and intermediate edges are as important as abrupt edges, or even perceived as an edge by certain species.

ACKNOWLEDGMENTS

We thank JoAnn Hanowski, Patrick Collins, John Blake, Philip Polzer, and Joseph Whittaker for their involvement in the collection of field data. Members of the GIS Laboratory at the Natural Resources Research Institute, in particular John Bonde, were extremely patient and helpful in providing assistance with GIS analyses. We gratefully acknowledge Ann Lima and Ronald Regal for providing assistance with

the statistical analysis. Funding for this project was provided by the Department of Defense, Illinois Institute of Technology, ELF Project. Additional funding was provided by the U.S. Forest Service, Chequamegon National Forest, and the Minnesota State Legislature through the Minnesota Environment and Natural Resources Trust Fund as recommended by the Legislative Commission on Minnesota Resources.

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