

Breeding bird assemblages associated with riparian, interior forest, and nonriparian edge habitats in a balsam fir ecosystem

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Abstract: Riparian zones are typically viewed as the highest quality habitat available to wildlife in forested landscapes, and consequently are seen as being the most biodiverse. This perception originated largely from studies conducted in southwestern North America; however, its validity in boreal forests remains relatively untested. We surveyed breeding bird assemblages along transects in riparian edge, nonriparian edge (clearcut or access road), and interior habitat in balsam fir (*Abies balsamea* (L.) Mill.) forests in Newfoundland. Distinct species assemblages were associated with each of these habitat types. Notably, five species were significantly more common in interior forest than along riparian edges. Total abundance and species richness did not differ between riparian and interior forest transects, but were significantly higher on nonriparian edge than riparian transects. Distinct species were characteristic of the two edge types, and no generalist edge species were identified. Based on this and other recent studies, it is apparent that relatively high riparian biodiversity may be the exception for bird assemblages in coniferous and mixedwood forests. Interior forest species, many of which have declined in northeastern North America in recent years, formed an important component of the regional avifauna. These species are likely not afforded adequate protection in boreal forests, where conservation efforts focus on preserving riparian habitat.

Résumé : Les zones riveraines sont typiquement perçues comme les meilleurs habitats disponibles pour la faune dans les paysages forestiers et sont par conséquent considérées comme les plus diversifiés biologiquement. L'origine de cette perception provient en grande partie d'études menées dans le sud-ouest de l'Amérique du Nord, mais sa validité en forêt boréale demeure relativement peu examinée. Nous avons fait l'inventaire d'assemblages d'espèces d'oiseaux nicheurs le long de transects en zone riveraine, non-riveraine (coupe à blanc ou route d'accès) et dans des habitats situés à l'intérieur de forêts de sapin baumier (*Abies balsamea* (L.) Mill.) à Terre-Neuve. Des assemblages distincts d'espèces étaient associés à chacun de ces types d'habitat. Notamment, cinq espèces étaient significativement plus communes à l'intérieur des forêts que le long des bordures riveraines. L'abondance totale et la richesse en espèces à l'intérieur des forêts et le long des bordures riveraines étaient semblables, mais elles étaient significativement supérieures dans les bordures non riveraines comparativement aux transects riverains. Des espèces distinctes étaient caractéristiques des deux types de bordures et aucune espèce généraliste de bordure n'a été identifiée. Selon notre étude et d'autres études récentes, il semble qu'une biodiversité relativement élevée le long des rives soit l'exception dans le cas des assemblages d'espèces d'oiseaux des forêts conifériennes et mixtes. Les espèces vivant à l'intérieur de la forêt, parmi lesquelles plusieurs ont subi un déclin dans le nord-est de l'Amérique du Nord dans les dernières années, formaient une composante importante de l'avifaune régionale. Ces espèces sont probablement l'objet d'une protection inadéquate en forêt boréale, où les efforts de conservation se concentrent sur les habitats riverains.

[Traduit par la Rédaction]

Introduction

The study of riparian (shoreline) ecology in North America has been strongly influenced by research conducted in the southwestern United States since the 1950s (see Johnson and Lowe 1985; Hooper 1989), where wooded mesic riparian zones contrast sharply with more open and arid uplands and consequently support a relatively high abundance and diversity of plants and wildlife (Hubbard 1977; Johnson and Lowe 1985; Szaro and Jakle 1985; Knopf 1986). The ecological importance and limited extent (<1% of land area; Knopf et al. 1988)

of riparian habitat, as well as its high social and economic value, have resulted in riparian zones becoming a focus of research and management activity in the region. Subsequently, generalizations about the importance of riparian habitat in arid regions have had great influence on how riparian habitat is perceived throughout North America (Hooper 1989).

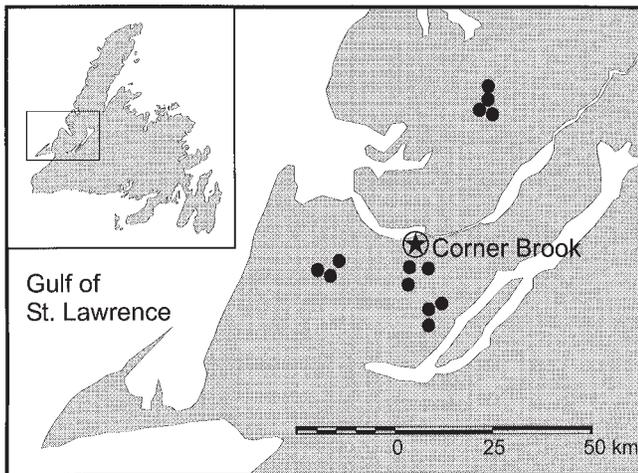
Regulations aimed at protecting riparian habitat are now in place throughout most of North America (Knopf et al. 1988). In the Canadian boreal forest, where 300 000 to 500 000 ha of forest are clear-cut annually, provinces typically require uncut riparian buffer strips to be left along the shorelines of water bodies (Canadian Forest Service 1993). Two properties of riparian zones are generally used to justify their protection during timber harvesting (LaRue et al. 1995). First, through their influence on such factors as water temperature, light incidence, and inputs of sediment, nutrients, and coarse woody debris, riparian zones play an important role in maintaining water quality and fish habitat. Second, riparian zones are viewed as optimal habitat for a disproportionate number of terrestrial wildlife species. However, relatively little research has been

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Fig. 1. Map of study area in western Newfoundland (inset). Approximate locations of study blocks are indicated by circles.



done to assess the ecological importance of riparian zones in mesic landscapes, where forests are generally continuous between riparian and upland (i.e., away from shoreline) habitat (Hooper 1989; LaRue et al. 1995; Murray and Stauffer 1995). Further, most research that has been carried out has focused on water quality and fish habitat (Hooper 1989).

The habitat value of riparian zones has often been explained, in part, through edge effects, whereby the juxtaposition of two habitat types (aquatic and terrestrial in this case) leads to an increase in the richness and abundance of wildlife at the interface (Leopold 1933; Odum 1971; Strelke and Dickson 1980). The influence of edges on bird species and communities has received considerable recent attention from researchers, as forest fragmentation and resulting edge effects have been linked to high rates of nest predation (e.g., Small and Hunter 1988; Yahner and Scott 1988; Rudnicki and Hunter 1993) and population declines in several species (see Askins et al. 1990; Robinson et al. 1995). Most studies of edge effects on bird assemblages in forested regions have focused on either unnatural edges created by forest clearing (e.g., Strelke and Dickson 1980; Hansson 1983) or natural riparian edges (e.g., Gates and Giffen 1991; McGarigal and McComb 1992; LaRue et al. 1995), though Small and Hunter (1989) compared these two types of edge.

In the present study, we compare avian assemblages associated with riparian edges, interior forests, and unnatural edges created by forest harvesting. This allows assessment of both the relative importance of riparian habitat to the local avifauna, and of patterns of habitat selection that generate edge effects. Further, the inclusion of nonriparian edges in the study should allow riparian species to be differentiated from generalist edge species. Knowledge of the wildlife communities associated with these habitat types is essential in evaluating current boreal forest utilization and conservation practices, which give priority to protecting riparian habitat and maintaining biodiversity.

Study area

The island of Newfoundland, situated to the east of the Gulf of St. Lawrence and southeast of the Labrador Peninsula, lies at the southeastern limit of the North American boreal forest biome. Climate

on the island is strongly influenced by the surrounding ocean, with less extremes in temperature and precipitation than mainland North America (Robertson 1993).

Study blocks considered representative of the general forest condition were established in mature to overmature woodlands (i.e., 50–100 years old) throughout the Corner Brook Subregion of the Western Newfoundland Ecoregion (Fig. 1; Damman 1983). Landscape in this ecoregion is characterized by heavily forested, rugged topography, with bogs being common on level ground (Damman 1983); elevations of study sites ranged from 250 to 400 m. As a consequence of topography, stream gradients and velocity are generally high; meandering streams, oxbows, and extensive floodplains are uncommon. The climate in the region is wet, with measurable precipitation typically occurring on more than 180 days each year and an average annual total of 1186 mm (Damman 1983; Scruton et al. 1995). Mean annual temperature is 5.2°C (Scruton et al. 1995). The absence of prolonged dry periods has excluded forest fires from most of the region. As a consequence, natural succession is typically insect driven, allowing balsam fir to dominate the forest cover (Meades and Moores 1994), though black spruce, white spruce, white birch, yellow birch, and red maple are also present. Natural forest openings resulting from a hemlock looper (*Lambdina fiscellaria fiscellaria* (Gueene)) outbreak (1983–1988) and wetlands are abundant throughout the region. Forests in the Corner Brook Subregion are some of the most productive on insular Newfoundland (Meades and Moores 1994) and are extensively clear-cut for pulp and paper production, and to a lesser extent for lumber and fuel wood.

Recently adopted environmental protection guidelines for Newfoundland and Labrador require that 20 m wide uncut riparian buffer strips be left along water bodies during forest harvesting (Scruton et al. 1995). The Copper Lake Buffer Zone Study, under which this research was conducted, was initiated to evaluate riparian zone management in the province. A more detailed description of the study area and related research projects has been provided in Scruton et al. (1995).

Methods

Data collection

Transects 200 m in length were established in three habitat types (treatments): undisturbed Riparian Forest Edge (RIP), Interior forest (INT), and Nonriparian Forest Edge (NFE). Promising locations for study sites were identified using a library of aerial photographs of recent clearcuts, which is maintained by the Newfoundland and Labrador Forest Service. Ground checks were then made and appropriate sites selected based on accessibility, location, continuity of forest cover, forest age, and proximity to a buffer strip (for an associated study, see Whitaker 1997). Riparian transects paralleled forested shorelines at a distance of 10–20 m. Interior forest transects ran parallel to riparian transects 150 m away from the shoreline and at least 150 m from other forest edges. Nonriparian edge transects were set in forests at a distance of 10–20 m from edges created by woodland access roads or clearcuts, and more than 150 m from riparian habitat. Many bird species demonstrate high site fidelity across breeding seasons and consequently when displaced by clear-cutting may move into the adjacent forest (see Darveau et al. 1995; Hagan et al. 1996). To avoid this short-term “packing” of birds around clearcuts, all nonriparian edges used had been present for at least 4 years, which should have been sufficient time for populations to stabilize (see Darveau et al. 1995; Hagan et al. 1996). The high number of openings in the forest made it difficult to sample interior habitat at distances greater than 150 m from shoreline edges, as has been done in similar studies (e.g., Small and Hunter 1989; Gates and Giffen 1991; Hooper 1991; McGarigal and McComb 1992; LaRue et al. 1995; Murray and Stauffer 1995). This sampling is, however, representative of interior habitat on the scale at which it occurs in the region. Because habitat to be

protected under riparian forest management legislation in Newfoundland only extends to 20 m from the shoreline, the riparian transect approximates protected riparian habitat, while interior transects represent habitat vulnerable to harvesting.

Transects were established such that they could be grouped into blocks containing one transect representing each treatment. The non-riparian edge transect was located as close as possible to the other two, which were paired. Thirteen complete study blocks were established, providing a total of 2600 m of transects through each habitat type. Blocks were placed in five watersheds throughout the Corner Brook Subregion, thus minimizing the risk of local conditions biasing observations. Five (1000 m) of the nonriparian edges followed forest access roads, while eight (1600 m) were located alongside clearcuts. Roadbeds were separated from forest edges by deforested (but vegetated) habitat greater than 20 m in width. Five (1000 m) riparian edges bordered streams, while eight (1600 m) were situated adjacent to lakes. Streams were 4–15 m wide and lakes ranged from approximately 2–200 ha.

For habitat comparisons, plots measuring 10 × 20 m (200 m²) were sampled at the 0-, 100-, and 200-m points along each transect. Plots were oriented perpendicularly to transects, with a 10 m side along the edge of the forest habitat on both the riparian and nonriparian edge transects. On each habitat plot, all trees and shrubs, which were distinguished by growth form rather than height or stem diameter, reaching breast height (1.3 m) were tallied by species. Diameter at breast height (DBH; 2 cm size classes) was recorded for trees and used to calculate basal area (m²/ha) by species. Vegetation sampling was carried out in late July and early August, after bird surveys were completed.

Line transect surveys were used to census bird assemblages (see Bibby et al. 1992). In an attempt to restrict sightings to the habitat being sampled, counts were truncated such that only birds detected within 30 m of transects were included in data analyses. Counts were conducted from 7 June until 7 July (1995), the standardized period for surveying breeding birds in the region (Robbins et al. 1986). Three rounds of surveys were completed, with all blocks being visited at the beginning, middle, and end of the survey period. Surveys began within 30 min after sunrise (05:00), as breeding birds are most vocal during early hours of daylight, vocalizing less often as the morning progresses (Skirvin 1981). Surveys were not carried out during rain or when winds exceeded 20 km/h, as poor weather reduces the activity and detectability of birds (Robbins 1981). Transects were traveled slowly (25–30 min/transect), and all birds heard or seen were recorded. To reduce variability entire blocks were surveyed by a single observer in a morning, and blocks were not sampled by the same person on consecutive visits. Also, transects within each block were visited in a different order in each of the three surveys. It was assumed that birds were equally detectable between stream, lake shore, and nonriparian sites; Hooper (1991) found that stream noise did not reduce avian census efficiency at a distance of 25 m from the shoreline of turbulent streams in Maine.

Data analyses

Analyses were conducted to assess whether habitat structure differed between riparian forest edge, interior forest, and nonriparian forest edge transects. Tree basal areas (m²/ha) were compared using analyses of variance, followed by Tukey's test for differences between pairs of treatment means (Sokal and Rohlf 1995; Day and Quinn 1989; one-way procedure, Minitab Inc., State College, Pa.). Similar analyses were carried out comparing shrub density (number of stems/200 m²) between treatments. However, since these data were non-normally distributed, an equivalent nonparametric test (Kruskal–Wallis) was used (Sokal and Rohlf 1995; Kruskal–Wallis procedure, Minitab). A Steel–Dwass test was then used to check for differences between pairs of treatments (Day and Quinn 1989). The significance level for all statistical analyses was set at 95% (i.e., $\alpha = 0.05$).

For each bird species, the highest count from the three surveys of a transect was used for data analyses. This does not lead to an overes-

timate of abundance because all individuals will not always be detected, and it is unlikely that more birds will be counted on any one visit than occupy territories within the area (Bibby et al. 1992).

Analyses were carried out to test for differences between the bird assemblages found on riparian transects located alongside streams and those located alongside lakes. No differences were detected in either total avian abundance (individuals/transect) or species richness (species/transect) when compared between shoreline types using a general linear model (glm procedure, Minitab). Further, comparisons of counts of each bird species also revealed no differences between streams and lakes (Mann–Whitney *U*-test; Sokal and Rohlf 1995; Mann–Whitney procedure, Minitab). Consequently, shoreline type was not considered in subsequent analyses of bird counts. A similar series of tests was made comparing nonriparian edge transects located beside clearcuts with those located alongside roads. Again no differences were detected, and consequently nonriparian forest edge type (road or clearcut) was not controlled for in further analyses.

To assess the distributional patterns of individual bird species, comparisons were made between pairs of treatments (RIP:INT, INT:NFE, RIP:NFE). Analyses were carried out using generalized linear models that included treatment and block as explanatory variables (McCullagh and Nelder 1989; glm procedure, S-plus, Math Soft Inc., Seattle, Wash.). As the response variable consisted of counts (individuals/transect), a Poisson error distribution and log-link function were used (McCullagh and Nelder 1989). In generalized linear models, the probability value for each explanatory variable is related to the reduction in residual deviance that results from its inclusion in the model (McCullagh and Nelder 1989). This follows a χ^2 distribution and is reported as such.

A similar series of tests was conducted to evaluate the influence of habitat type on both species richness (number of species/transect) and total avian abundance (number of individuals/transect). However, the data could not be fit to a theoretical error distribution, and so for these analyses a nonparametric randomization test was used (Crowley 1992; Adams and Anthony 1996; SAS Inc., Cary, N.C.). In this test, values of the response variable (counts) were randomly reassigned to the treatment levels without replacement. *F*-statistic values for each explanatory variable were then calculated from the redistributed data. Three thousand iterations of this procedure were carried out. The proportion of the 3000 randomized *F*-statistic values exceeding the *F*-statistic value obtained from the original distribution of the data set was used as the probability estimate for each explanatory variable (i.e., treatment and block).

Based on both the observed distribution of sightings between treatments and published information (Godfrey 1966; Erskine 1977; DeGraff et al. 1980; Welsh 1981; Hooper 1991; Parker et al. 1994; Darveau et al. 1995; Murray and Stauffer 1995), each bird species was assigned to one of five habitat selection guilds: (1) forest generalist species, found in forested habitats but showing no clear preferences within these; (2) interior forest species, found in forested habitats but not along riparian, and in some cases, anthropogenic edges; (3) riparian species, associated with shorelines and (or) riparian vegetation; (4) open or edge species, associated with nonforested terrestrial habitats (e.g., clearcuts) or interfaces between forested and nonforested habitats; (5) ubiquitous species, those showing no clear patterns of selection between the habitat types considered in this study. Totals from these guilds were used to subdivide plots of both species richness and total abundance, thereby illustrating some differences in the composition of the avian assemblage associated with each habitat type.

Results

Habitat

Vegetational characteristics differed among treatments (Tables 1 and 2). The basal area of black spruce was significantly greater

Table 1. Summary of analyses of variance comparing tree basal area between habitat types.

	Mean basal area (m ² /ha) ± SE*			ANOVA summary (α = 0.05)		
	RIP	INT	NFE	MS	F _[2,114]	p
Coniferous trees						
Balsam fir (<i>Abies balsamea</i> (L.) Mill.)	21.7±1.7	26.6±2.1	22.6±1.8	256.75	1.87	
Black spruce (<i>Picea mariana</i> (Mill.) BSP)	7.7±1.0a	3.6±1.0b	2.4±0.7b	296.00	9.16	<0.001
White spruce (<i>Picea glauca</i> (Moench) Voss)	1.3±0.4	1.3±0.4	1.7±0.4	2.13	0.34	
Subtotal	30.7±1.5	31.6±1.8	26.7±1.9	258.00	2.19	
Deciduous trees						
White birch (<i>Betula papyrifera</i> Marsh.)	1.6±0.3a	3.4±0.7a	3.5±0.7a	42.03	3.14	0.047
Red maple (<i>Acer rubrum</i> L.)	0.4±0.2	0.2±0.1	0.2±0.1	0.62	0.49	
Subtotal	2.2±0.4	3.9±0.8	3.7±0.7	33.00	2.07	
Total	32.9±1.6	35.4±1.7	30.4±1.9	241.50	2.10	
Standing deadwood	9.0±1.1a	14.3±1.3b	7.8±1.0a	461.25	9.24	<0.001

Note: Pairs of means were compared using Tukey's test. Values followed by the same letter or no letter are not statistically different. Eastern larch (*Larix laricina* (Du Roi) K. Koch), yellow birch (*Betula lutea* Michx. f.), and pin cherry (*Prunus pensylvanica* L.f.) were also occasionally found on vegetation plots, and are included in appropriate totals.

*RIP, INT, and NFE are riparian forest edge, interior forest, and nonriparian forest edge habitat, respectively.

Table 2. Density of shrubs in the three habitat types.

	Mean density (stems/200 m ²) ± 95% C.I.			p
	RIP	INT	NFE	
Alder*	30.2±14.3a	0.7±1.3b	1.9±2.8b	<0.001
Mountain maple (<i>Acer spicatum</i> Lamb.)	13.2±8.0ab	6.7±5.6a	29.0±11.8b	0.007
Mountain ash (<i>Sorbus americana</i> Marsh.)	6.5±2.7a	1.1±0.8b	4.1±2.1ab	0.001
Other shrubs†	16.0±6.6a	1.4±1.3b	13.4±7.0a	<0.001
Total	65.8±16.7a	9.9±6.6b	48.3±16.5a	<0.001

Note: The effect of treatment was assessed using a Kruskal–Wallis test, and the corresponding probability (p) is reported. Analyses for differences between pairs of treatments were made using a Steel–Dwass test. Values followed by the same letter are not significantly different.

*Mountain alder (*Alnus crispa* (Ait.) Pursh) and speckled alder (*Alnus rugosa* (Du Roi) Spreng.).

†Common species included beaked hazelnut (*Corylus cornuta* Marsh.), Canadian yew (*Taxus canadensis* Marsh.), chuckley pear (*Amelanchier* spp.), red elderberry (*Sambucus pubens* Michx.), red-osier dogwood (*Cornus stolonifera* Michx.), wild raisin (*Viburnum cassinoides* L.), and squashberry (*Viburnum edule* (Michx.) Raf.).

on riparian forest edge transects than on those located in interior forest or nonriparian edge habitats. A significant effect of treatment on white birch was also detected, where the average basal area in riparian habitat was less than half of that in either interior forest or nonriparian edge habitat. Standing deadwood was significantly more abundant along interior forest transects than either of the other two treatments. Mean densities of all classes of shrubs were greater along riparian transects than in interior forest (Table 2); mountain maple was the only species for which this difference was not significant. The comparison between nonriparian edge and interior forest transects yielded similar results, but in this case the difference for mountain maple was significant, whereas the differences for alder and mountain ash were not. Densities of alder were significantly greater on riparian transects than on nonriparian edge transects.

Bird assemblages

Distinctive bird species were associated with each of the habitat types sampled. In total, 34 species of bird were identified during 117 transect surveys (Table 3). Total species richness and total avian abundance were significantly higher along nonriparian edges than riparian edges (Fig. 2; Table 4). Only one species, northern waterthrush, was significantly more common

on riparian transects than either nonriparian edges or interior forest transects. Spotted sandpiper, belted kingfisher, black-and-white warbler, yellow warbler, and rusty blackbird were found exclusively along riparian transects, though numbers were low. Yellow-bellied flycatcher, black-throated green warbler, and ovenbird were significantly more common along interior forest than riparian transects, and intermediate in abundance along nonriparian edge transects. Red-breasted nuthatch and Swainson's thrush were significantly more common along interior forest transects than either riparian or nonriparian edge transects. Gray jay and dark-eyed junco were significantly more common on nonriparian edge transects than on riparian transects. White-throated sparrows were more common on nonriparian edge transects than on interior forest transects.

Discussion

Habitat

Balsam fir was the dominant tree species on all transects, although clear vegetation differences existed between the three treatments. Riparian habitat was characterized by relatively low basal areas of white birch and standing deadwood, a high mean basal area of black spruce, and high densities of shrubs,

Table 3. Mean frequency of bird observations on thirteen 200 × 60 m survey transects in three habitat types.

Guild and species	Total count	Mean frequency (individuals/200 m transect)			Pairwise comparisons $p(\chi^2, 1 \text{ df})$		
		RIP	INT	NFE	RIP:INT	INT:NFE	RIP:NFE
Forest generalist							
Ruffed grouse (<i>Bonasa umbellus</i> L.)	2	0	0	0.15			
Black-backed woodpecker (<i>Picoides arcticus</i> Swainson)	4	0.08	0.08	0.15			
Downy woodpecker (<i>Picoides pubescens</i> L.)	7	0.23	0.23	0.08			
Hairy woodpecker (<i>Picoides villosus</i> L.)	4	0.08	0.08	0.15			
Black-capped chickadee (<i>Parus atricapillus</i> L.)	12	0.31	0.23	0.39			
Boreal chickadee (<i>Parus hudsonicus</i> Forster)	26	0.69	0.69	0.62			
Winter wren (<i>Troglodytes troglodytes</i> L.)	9	0.23	0.15	0.31			
Golden-crowned kinglet (<i>Regulus satrapa</i> Lichtenstein)	8	0.23	0.15	0.23			
Ruby-crowned kinglet (<i>Regulus calendula</i> L.)	58	1.23	1.69	1.54			
Black-and-white warbler (<i>Mniotilta varia</i> L.)	2	0.15	0	0			
Pine grosbeak (<i>Pinicola enucleator</i> L.)	4	0.15	0.15	0			
Pine siskin (<i>Carduelis pinus</i> Wilson)	33	0.85	0.62	1.08			
Purple finch (<i>Carpodacus purpureus</i> Gmelin)	2	0	0.08	0.08			
Subtotal	171	4.23	4.15	4.78			
Interior							
Yellow-bellied flycatcher (<i>Empidonax flaviventris</i> Baird & Baird)	4	0.54	1.54	1.23	0.011 (6.52)		
Red-breasted nuthatch (<i>Sitta canadensis</i> L.)	8	0.08	0.46	0.08	0.047 (3.96)	0.047 (3.96)	
Hermit thrush (<i>Catharus guttatus</i> Pallas)	9	0.08	0.39	0.23			
Swainson's thrush (<i>Catharus ustulatus</i> Nuttall)	11	0.08	0.62	0.15	0.013 (6.20)	0.049 (3.86)	
Black-throated green warbler (<i>Dendroica virens</i> Gmelin)	49	0.77	1.62	1.39	0.046 (4.00)		
Ovenbird (<i>Seiurus aurocapillus</i> L.)	13	0.08	0.62	0.31	0.013 (6.20)		
Subtotal	133	1.63	5.25	3.39			
Riparian							
Spotted sandpiper (<i>Actitis macularia</i> L.)	4	0.31	0	0			
Belted kingfisher (<i>Ceryle alcyon</i> L.)	1	0.08	0	0			
Northern waterthrush (<i>Seiurus noveboracensis</i> Gmelin)	15	0.85	0.08	0.23	0.002 (9.75)		0.027 (4.86)
Yellow warbler (<i>Dendroica petechia</i> L.)	2	0.15	0	0			
Rusty blackbird (<i>Euphagus carolinus</i> Müller)	2	0.15	0	0			
Subtotal	24	1.54	0.08	0.23			
Open-edge							
Gray jay (<i>Perisoreus canadensis</i> L.)	10	0	0.23	0.54			0.002 (9.70)
Magnolia warbler (<i>Dendroica magnolia</i> Wilson)	10	0.15	0.15	0.46			
Mourning warbler (<i>Oporornis philadelphia</i> Wilson)	13	0.15	0.31	0.54			
Dark-eyed junco (<i>Junco hyemalis</i> L.)	10	0	0.23	0.54			0.002 (9.71)
White-throated sparrow (<i>Zonotrichia albicollis</i> Gmelin)	35	0.77	0.46	1.46		0.008 (7.10)	
Lincoln's sparrow (<i>Melospiza lincolni</i> Audubon)	4	0	0	0.31			
Subtotal	82	1.07	1.38	3.85			
Ubiquitous							
American robin (<i>Turdus migratorius</i> L.)	43	1.08	0.92	1.31			
Blackpoll warbler (<i>Dendroica striata</i> Forster)	9	0.23	0.23	0.23			
Yellow-rumped warbler (<i>Dendroica coronata</i> L.)	78	1.92	2.15	1.92			
Fox sparrow (<i>Passerella iliaca</i> Merrem)	3	0	0.08	0.15			
Subtotal	133	3.23	3.38	3.61			

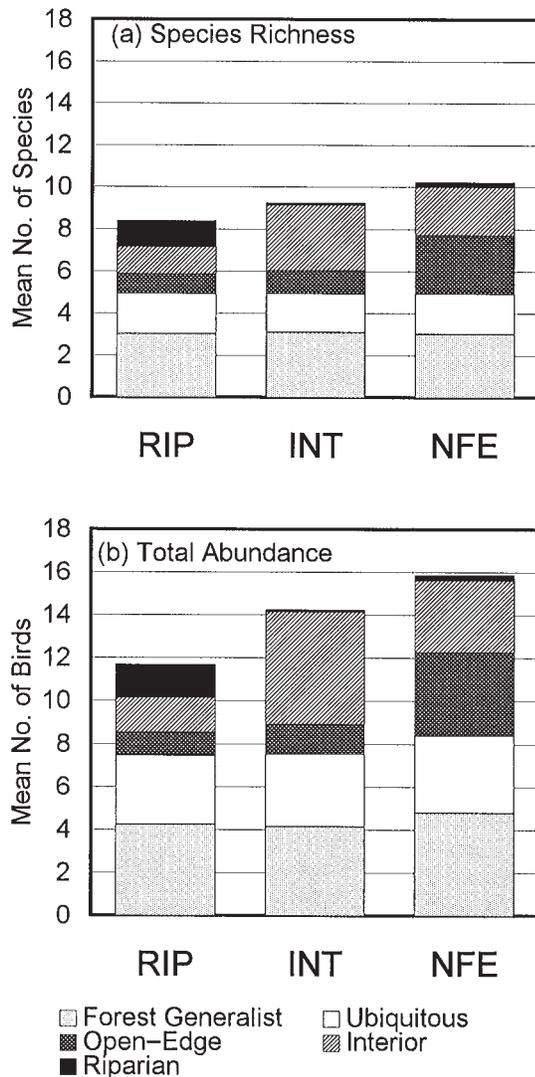
Note: Pairs of treatments were compared using a generalized linear model with poisson error distribution and a log-link function ($\alpha = 0.05$). Based on the observations reported here, as well as published information (see text), species were separated into five habitat selection guilds and are grouped as such. Statistical tests were not run on guild subtotals.

especially alders. In some cases a narrow (<3 m) ericaceous shrub and (or) graminoid (grasses, sedges, rushes) vegetation band separated the woody vegetation from the waters' edge (D.M.W., personal observation). These characteristics are not unexpected, given the increased soil moisture and light availability along shorelines. Although we did not measure the ex-

tent of the riparian vegetation zone, the transition to upslope, interior forest was generally distinct and occurred within 5–50 m of the shoreline (D.M.W., personal observation).

Interior forests typically had the highest balsam fir and standing deadwood basal areas, and lowest shrub densities. Others have also found that standing deadwood increased

Fig. 2. Mean species richness (a) and mean abundance of birds (b) on riparian forest edge (RIP), interior forest (INT), and nonriparian forest edge (NFE) transects. Subdivisions of each bar indicate the mean for each of five habitat selection guilds.



away from shorelines (McGarigal and McComb 1992; Murray and Stauffer 1995). One might expect the distribution of tree basal areas to be similar between interior forest and nonriparian edge transects, as nonriparian edges were interior forest prior to the adjacent harvesting. Total basal area was, however, somewhat lower along nonriparian edge transects, largely because of lower conifer basal area. Also, standing deadwood basal area was significantly lower. It is likely that these reductions reflect disturbance related to harvesting, primarily wind-throw, which causes high losses along unnatural forest edges in Newfoundland (Robertson 1993). Well-developed shrub communities were characteristic of deforested areas and often extended a short distance into forests.

Bird assemblages

Bird assemblages associated with riparian habitat had several distinct species. Northern waterthrush was significantly associated with riparian transects; spotted sandpiper, belted king-

fisher, yellow warbler, and rusty blackbird were found there exclusively (in low numbers). All are generally associated with riparian habitat in boreal forests (Godfrey 1966; Erskine 1977; LaRue et al. 1995). The few sightings of black-and-white warbler were also limited to riparian transects, although this species is not generally associated with shorelines (Erskine 1977; Murray and Stauffer 1995). In addition to these terrestrial riparian birds, several species of water birds, which typically nest in riparian habitat, were seen in the study area: common loon (*Gavia immer* Brünnich), Canada goose (*Branta canadensis* L.), American black duck (*Anas rubripes* L.), ring-necked duck (*Aythya collaris* Donovan), greater scaup (*Aythya marila* L.), common goldeneye (*Bucephala clangula* L.), and merganser (*Mergus* sp.). Though not considered in this study, these species are important components of regional riparian bird assemblages.

Several species were significantly more common along interior forest transects than along riparian edges. Within this group two distributional patterns were evident: (1) Red-breasted nuthatch and Swainson's thrush were significantly more common along interior transects than either riparian or nonriparian edge transects and so are considered true "interior" (i.e., edge-avoiding) species in the context of this study. (2) Yellow-bellied flycatcher, black-throated green warbler, and ovenbird were also significantly more common along interior than riparian transects, but were intermediate in abundance along nonriparian edges. With the exception of Swainson's thrush, which was associated with riparian habitat in Oregon (McGarigal and McComb 1992), all of these species have been associated with interior forest habitat in other regions (Derleth et al. 1987; Hooper 1991; LaRue et al. 1995; Murray and Stauffer 1995; Hagan et al. 1996). Hermit thrush, a species often associated with interior forest (Hooper 1991; LaRue et al. 1995), was most abundant along interior forest transects, but was uncommon. Interior forest habitat thus contributed greatly to the diversity of bird communities in the study area. In total, these six interior species accounted for approximately 37% of bird observations along interior forest transects, and 24% of all observations.

In addition to the occurrence of several "interior" species, other aspects of the avian assemblages observed along nonriparian forest edges were distinctive. White-throated sparrow was observed significantly more frequently here than in the interior forest, and its abundance along nonriparian edges was approximately twice that on riparian edges. Both dark-eyed junco and gray jay were significantly more common along nonriparian forest edges than along riparian edges, and rare in interior forests. Other species associated with early successional openings and edges were most abundant along nonriparian edges (e.g., magnolia warbler, mourning warbler, Lincoln's sparrow).

Riparian habitat supports the most diverse and dense bird assemblages in arid regions (e.g., Hubbard 1977; Johnson and Haight 1985; Szaro and Jakle 1985; Knopf 1986) and in mesic broadleaf forests in eastern North America (Hair et al. 1978; Hooper 1991; see also Gates and Giffen 1991). Zones of riparian vegetation are typically narrow in boreal forests, and the present study found neither avian species richness nor total abundance to differ between riparian and interior forest habitats. While in contrast with the widely held assumption that riparian zones provide the highest quality wildlife habitat in

Table 4. Comparisons of avian community parameters between habitat types.

	Mean (<i>n</i> /200 m transect) ± SE			<i>p</i>		
	RIP	INT	NFE	RIP:INT	INT:NFE	RIP:NFE
Species richness	8.4±0.7	9.2±0.7	10.2±0.8			0.037
Total abundance	11.6±0.9	14.3±1.1	15.9±1.2			0.004

Note: Values for total abundance represent the mean number of birds observed per transect (all species combined), while species richness values represent the mean number of species per transect. Pairs of treatments were compared using randomization tests (3000 iterations, $\alpha = 0.05$).

forested landscapes, these findings are consistent with most other studies conducted in coniferous and mixed coniferous–deciduous forests (Knopf 1985; Small and Hunter 1989; Hooper 1991; McGarigal and McComb 1992; Murray and Stauffer 1995; Haché 1996).

Unlike most findings from coniferous forests, LaRue et al. (1995) found species richness and abundance to be greatest in riparian portions of balsam fir – white-cedar (*Thuja occidentalis* L.) stands in Quebec. However, they categorized birds occurring within 200 m of the shoreline as being associated with riparian habitat (LaRue et al. 1995). Other studies (Hooper 1991; Murray and Stauffer 1995; Haché 1996), including the present one, have found that the shift from riparian to interior forest bird assemblages occurred well within 200 m of the shoreline. It seems likely that the lower resolution “riparian” plots of LaRue et al. (1995), through the inclusion of both riparian and interior species, overestimated the species richness of riparian assemblages. Indeed, all bird species we identified as being associated with interior forest habitat were common on both riparian and nonriparian forest plots sampled by LaRue et al. (1995).

Edge effects

Bird species richness and total abundance along anthropogenic forest edges (NFEs) were significantly greater than along riparian forest edges (Table 4, Fig. 2). Two factors seem to be responsible for this: (1) Many “interior” species, which were rare along riparian edges, were common along nonriparian edges (i.e., yellow-bellied flycatcher, hermit thrush, black-throated green warbler, ovenbird). The mechanism responsible for this difference was not tested but is likely linked to structural differences between the two edge types. For example, the zone of increased black spruce, which was typical of riparian edges, was not present along nonriparian edges and may act as a “barrier” to the movements of species selecting interior forest vegetation types. In boreal forests black-throated green warbler, ovenbird, and red-breasted nuthatch have been shown to be characteristically associated with fir, but not found in spruce stands (Erskine 1977). (2) Avian assemblages along nonriparian edges include more open, edge, and mixed habitat species than those along shorelines (Small and Hunter 1989; Gates and Giffen 1991). Present findings support this pattern, with the highest counts of these species (gray jay, magnolia warbler, mourning warbler, dark-eyed junco, white-throated sparrow, Lincoln’s sparrow) occurring along nonriparian edges (Fig. 2). In contrast, aquatic habitat adjacent to riparian edges contributed relatively little to the terrestrial riparian bird assemblage with the exception of aquatic foragers (belted kingfisher, spotted sandpiper, and northern waterthrush). Indeed, most riparian species were relatively rare and may restrict themselves to

the narrow riparian vegetation zone (see Manuwal 1986; Whitaker 1997).

The inclusion of nonriparian edge transects in the study should have allowed generalist edge species to be distinguished from riparian edge species; however, no species appeared to select both edge types over interior forest habitat. Consequently, none of the species selecting riparian edges over interior forest were provided with alternate habitat along edges created by forest clearing (see also Small and Hunter 1989). Bird assemblages associated with intrinsic riparian edges are distinct from those associated with anthropogenic nonriparian forest edges.

Management implications

The high density and species richness typically attributed to riparian wildlife assemblages is often used to justify protecting riparian habitat (e.g., Naiman et al. 1993; LaRue et al. 1995). In the present study riparian bird assemblages in balsam fir forests were similar in species richness and abundance to those associated with interior forests. This should not, however, be taken as an argument against protecting riparian habitat. The presence of several terrestrial riparian bird species (spotted sandpiper, belted kingfisher, northern waterthrush, yellow warbler, rusty blackbird) as well as several species of water birds in the study area indicates that riparian habitat is important to the diversity of the regional avifauna.

From management and conservation perspectives, one of the most important findings of this study is that concern for the protection of interior birds is warranted (see also Hagan et al. 1996). Populations of several of these species, including black-throated green warbler and ovenbird, have declined significantly in much of northeastern North America (Robbins et al. 1989; Askins et al. 1990; Sauer and Droege 1992). Typically, riparian buffers, which are presumably implemented to maintain habitat for riparian species, are viewed as inadvertently benefiting nonriparian species; however, this assumption is unfounded (Thompson and Welsh 1993). Little has been done to either assess the need for or to develop conservation strategies for boreal forest interior species. The habitat requirements of interior forest species deserve detailed consideration by researchers, managers, and conservationists working in boreal forests.

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