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BREEDING BIRD ASSEMBLAGES INHABITING RIPARIAN BUFFER STRIPS IN NEWFOUNDLAND, CANADA

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Abstract: Throughout most of the North American boreal forest, riparian buffer strips are left during clear-cutting. Although this practice is considered a means to reduce adverse effects of timber harvesting on terrestrial fauna, little research has been conducted to quantify the extent to which buffer strips are used by wildlife. We compared breeding bird assemblages (grouped into 5 habitat guilds) in undisturbed shoreline habitats with those in 20–50-m-wide riparian buffer strips in balsam fir (*Abies balsamea*) forests on insular Newfoundland, Canada. Total avian abundance was higher along buffer strips than undisturbed shorelines because of a greater abundance of ubiquitous species and species associated with clearcut edge habitats. Abundances of forest generalist, interior forest, and riparian species were similar between buffers and controls. Riparian buffer strips provided habitat for a diverse avian assemblage and maintained many riparian and woodland species in areas of intensive clearcutting. Counts of riparian species did not increase in wider buffers, likely due to their association with habitats adjacent to water, which do not increase in proportion to strip width. Total numbers of interior forest birds, many species of which may be declining in northeastern North America, may increase in wider buffers, but these species were rare even in the widest strips sampled (40–50 m) when compared to local interior forest habitat. Furthermore, 3 of 6 species in the interior forest guild were not observed in any buffer strip. While riparian conservation is essential, separate but complementary conservation strategies clearly are required to protect riparian and interior forest species.

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Riparian zones, defined as portions of landscapes influenced by the shorelines of lakes, rivers, and streams, are generally viewed as having high productivity and species diversity in forest ecosystems. Undisturbed riparian zones play an important role in the maintenance of water quality and aquatic habitat, support distinct vegetation communities, and afford high-quality terrestrial wildlife habitat (Thomas et al. 1979, Barton et al. 1985, Naiman et al. 1993, Stoeck 1994). Forest managers have recognized these multiple values and consider the preservation of riparian zones important for minimizing adverse ecological effects of forest harvesting. Consequently, throughout most of North America, buffer strips of standing trees are left between clearcuts and waterbodies (Knopf et al. 1988, Canadian Forest Service 1993).

In addition to maintenance of aquatic habitat

and water quality, riparian buffer strips typically are promoted to minimize the adverse effects of logging on terrestrial and aquatic wildlife. However, specific wildlife conservation objectives are often poorly defined. Presumably, a primary goal is the protection of species preferring riparian habitat. In coniferous and mixed-wood forests, riparian and interior forest habitats each typically support characteristic bird species (Knopf 1985, Small and Hunter 1989, McGarigal and McComb 1992, Murray and Stauffer 1995, Whitaker and Montevecchi 1997). However, resource managers and biologists have often assumed (implicitly or explicitly) that most species prefer or frequent riparian habitats and will consequently use buffer strips (see Hooper 1989). These assumptions likely stem from studies of riparian ecology in arid regions in southwestern North America, where they may be valid (e.g., Szaro and Jakle 1985, Knopf 1986), but such assumptions may be unfounded in northern forest ecosystems (Hooper 1989, Thompson and Welsh 1993).

The view that riparian zones are preferred wildlife habitat has not been questioned by the

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few studies designed to evaluate the conservation potential of buffer strips for forest birds. These studies compared abundances of species inhabiting undisturbed riparian forests to those observed in buffer strips, but they did not consider nonriparian habitats (Johnson and Brown 1990, Triquet et al. 1990, Darveau et al. 1993, 1995). Consequently, these studies provide clear information on avian use of buffer strips, but interpretation is difficult because riparian and interior forest specialists are not identified. More consideration needs to be given to the use of riparian versus interior forest habitats, as the latter are rarely explicitly incorporated in boreal forest management plans.

Researchers often have indicated a need to identify the minimum width of buffer strip necessary to maintain a species assemblage similar to that found along undisturbed shorelines (Johnson and Brown 1990, Darveau et al. 1993, Spackman and Hughes 1995). However, even wide buffer strips (i.e., >100 m) most likely would not support an unaltered bird assemblage. A more productive approach to the development of effective forest management strategies could be to identify patterns of habitat use by the species involved, and then use this information to help explain differences in bird assemblages found along undisturbed shorelines and buffer strips of various widths. Appropriate conservation strategies, which likely involve more than simply altering the width of buffer strips, can then be developed for those species that do not benefit from riparian buffers.

We compared use of undisturbed shorelines and 20–50-m-wide riparian buffer strips by breeding birds inhabiting balsam fir forests on the island of Newfoundland, Canada. As with previous studies, a primary objective was identification of differences in individual species' abundances between buffers and controls. Beyond this objective, we were interested in the effect of strip width on bird assemblage composition. A concurrent study conducted on the same sites described the distribution of each bird species relative to undisturbed shoreline, interior forest, and nonriparian edge habitats in the region (Whitaker and Montevecchi 1997). We used information from this complementary research to assign species to habitat selection guilds that were based on the birds' spatial distribution in the local landscape. This guild classification allowed us to quantify responses of riparian and interior forest specialists and helped

to explain several aspects of the composition of species assemblages observed along buffer strips of various widths.

STUDY AREA

Research was conducted on insular Newfoundland, Canada, which lies at the southeastern limit of the North American boreal forest. We established study blocks in 5 watersheds throughout the Corner Brook Subregion of the Western Newfoundland Ecoregion (Damman 1983; Fig. 1). This region supports some of the most productive forests in Newfoundland (Meades and Moores 1994). Balsam fir aged 50–100 years dominated the forest cover on all study sites, and black spruce (*Picea mariana*), white spruce (*P. glauca*), white birch (*Betula papyrifera*), yellow birch (*B. alleghaniensis*), red maple (*Acer rubrum*), pin cherry (*Prunus pensylvanica*), and eastern larch (*Larix laricina*) were found on suitable sites throughout the region. Riparian vegetation zones in this area usually extended from 5 to 50 m upslope from the shoreline and were characterized by high numbers of black spruce, which, in combination with high stem densities of alder (*Alnus crispa*, *A. rugosa*) and other large shrubs, often formed a dense thicket adjacent to waterbodies (Whitaker and Montevecchi 1997).

Industrial clearcuts in the region are widespread, often large (>25 ha), and typically created in close spatial and temporal succession following the creation of new logging roads into a watershed (D. M. Whitaker, personal observation). This cut-as-you-go harvesting style has often resulted in removal of a large proportion of merchantable interior forest in a watershed or valley within a few years. Residual stands are often located on steep slopes, wet soils, or high ground, where tree densities and growth rates are reduced.

METHODS

Data Collection

In 1994, we surveyed breeding birds in undisturbed riparian habitat, buffer strips, bog, interior forest, anthropogenic edges, and clearcuts with and without buffer strips. Using these observations, we established 13 study blocks in 1995, each of which contained a 200-m transect through a riparian buffer strip 20–50 m in width, and another along an undisturbed riparian forest edge. Three pairs of riparian control and buffer strip transects sampled in 1994 (but

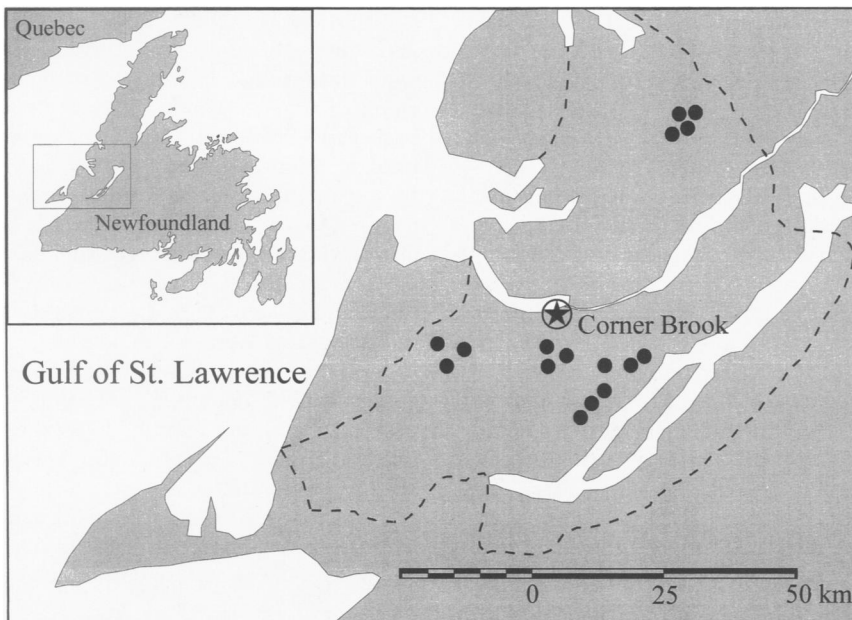


Fig. 1. Study area on the west coast of insular Newfoundland, Canada. Circles indicate the approximate location of study blocks, while the dashed line indicates the approximate boundary of the Corner Brook Subregion of the Western Newfoundland Ecoregion (Damman 1983).

not resampled in 1995) fit the revised study criteria, and data from these sites were added to the 13 pairs sampled in 1995. Thus, we sampled 3,200 m of riparian habitat along control and buffered shorelines.

Nine pairs of transects (1,800 m) were located along lakeshores, and 7 pairs (1,400 m) alongside streams. Streams were 4–15 m wide, and lakes ranged from 2 to 200 ha. Whenever possible, we established these pairs of transects alongside a single waterbody ($n = 5$); otherwise, they were placed on similar waterbodies within the same watershed ($n = 11$). With the exception of small natural openings (e.g., insect kills, bogs), forest cover was continuous for >300 m upslope along undisturbed shorelines. Stream-side controls had intact forest on both banks, and banks opposite streamside buffers also supported undisturbed forests. We selected buffer strips that were adjacent to 3–5-year-old clearcuts (1 at 3 yr, 8 at 4 yr, 7 at 5 yr), were typically >300 m long with adjacent clearcuts >10 ha, and were located in areas of extensive harvesting.

All transects paralleled the shoreline about 20 m into the forest. To avoid traveling along the immediate edges of clearcuts, we placed transects about 5 m within the residual forest cover

when buffer strips were <25 m wide. We placed transects along portions of buffer strips that were relatively constant in width. Strip width was measured at the beginning, middle, and end of each transect, and these 3 values were averaged to obtain mean widths used in data analyses ($\bar{x} = 33.2$ m, $SD = 9.7$, range = 20–52, $n = 16$).

We conducted bird surveys following the line transect method outlined by Bibby et al. (1992). To restrict observations to the habitat being sampled, we included only those birds detected ≤ 30 m from transects. Surveys were conducted by 2 experienced observers from 7 June to 7 July each year, which is the standardized period for breeding bird surveys in the region (Robbins et al. 1986). Each study block was surveyed at the beginning, middle, and end of this period. During a survey, both transects were sampled in random order by a single observer, and observers alternated between visits to a block. Surveys began within 30 min of sunrise (0500–0530) and were completed by 0930 (Skirvin 1981). Transects were walked in 25–30 min, and all birds observed were identified to species by sight or species-specific vocalizations. The distance of each bird from the transect was recorded on a site map; along buffer strips, we

noted whether the bird was in the clearcut or residual forest. We practiced distance estimation and believe we were relatively accurate for birds observed within 50 m of transects. Surveys were not conducted during rain or when winds exceeded 20 km/hr (Robbins 1981).

For each species and transect, the greatest number of adults observed during the 3 surveys was assumed to represent the population. We believe the highest count represents a minimum estimate of bird numbers along a transect because more birds unlikely will be observed than occupy nesting territories within the area (Bibby et al. 1992). We realize this assumption is invalid for nonterritorial species (e.g., cardueline finches), but pine siskin was the only such species we observed during surveys (see Table 1 for scientific names of bird species). Adult counts were not confounded by the presence of juveniles, because very few young had fledged by the end of the survey period, and these were readily identified by plumage and behavior.

An assumption of avian community studies is that all birds are equally detectable. Consequently, observed numerical differences between species or habitats reflect real differences in abundance. Comparisons of abundance may be misleading when detectability varies among species (e.g., due to vocalizations or behavior) or between habitats (e.g., due to vegetation structure or ambient noise). We believe we minimized any effects of differential detectability because we restricted sampling to within 30 m of transects, within which distance most quiet species were readily detected (D. M. Whitaker, personal observation). Also, vegetation structure within buffer strips was similar to control shorelines (Whitaker 1997), and Hooper (1991) reported that stream noise does not decrease avian census efficiency at a distance of 25 m from turbulent water.

Data Analyses

We had previously assigned bird species to habitat guilds via local comparisons of abundance between undisturbed riparian, interior forest, and nonriparian (clearcut) edge habitats (Whitaker and Montevecchi 1997) and published information (Erskine 1977, Welsh 1981, Hooper 1991, Parker et al. 1994, Darveau et al. 1995, Murray and Stauffer 1995). These 2 sources of information were in good agreement, and we identified 5 guilds: (1) forest generalists were those inhabiting wooded areas but whose

distributions were not influenced by riparian or anthropogenic edges; (2) interior forest species were those found in forested habitats but rare along riparian and anthropogenic edges; (3) riparian species were those associated with shorelines, riparian vegetation, or both but rarely observed in the forest interior or along clearcut edges; (4) open-edge species were those associated with nonforested terrestrial habitats such as clearcuts or the interfaces between these nonforested habitats and woodlands; (5) ubiquitous species were those found in all of the above mentioned habitat types. We used these guilds, which contained 5–11 species each, to obtain general and broadly applicable information on effects of riparian forest management on bird communities.

To test if type of waterbody influenced avian abundance, we used a Mann-Whitney *U*-test to compare counts between control lakeshores and streams for individual species, guilds, and all species combined (Mann-Whitney *U*-test; Minitab [Ryan and Joiner 1994]). Similarly, we compared bird observations between lacustrine and riverine buffer strips, using width of buffer strips (as a covariate), type of waterbody, and the interaction between the 2 as explanatory variables (PROC GLM in Minitab). If we found no effect of waterbody type on avian assemblages, lake and stream transects were pooled in subsequent analyses. Because of the small number of 1994 blocks, we were unable to test for any differences between years; however, all trends observed on the 1995 blocks also were evident on 1994 blocks, and 1994 counts were within the range observed in 1995. Consequently, data from both years were pooled in all analyses.

Count data typically follow a Poisson distribution, so we compared species and guild counts between control and buffer strip transects via a generalized linear model with a Poisson error distribution and log-link function (McCullagh and Nelder 1989, using PROC GLM in S-plus; Venables and Ripley 1994). We obtained 95% confidence limits for the treatment means from the 2.5 and 97.5 percentiles of 10,000 randomly generated means from a Poisson distribution having the same mean and sample size as the observed data (SAS Institute 1989). We modeled total relative abundance (i.e., all bird observations combined) and species richness (no. of species) via a paired-comparison analysis of variance (Sokal and Rohlf

1995; Minitab [Ryan and Joiner 1994]) because the Poisson distribution approaches normality as the mean value increases (Haight 1967). We evaluated the fit of generalized linear models and analyses of variance by visual inspection of residual error plots. Generalized linear models were unacceptable when <6 individuals had been observed, and we do not present statistical tests for these uncommon species. To further describe avian community structure, we generated rarefaction and relative abundance curves via pooled observations from all buffer strip or control transects (James and Rathburn 1981).

All of the preceding comparisons of bird observations between control shorelines and buffer strips were conducted twice. In the first analysis, we included all observations obtained within 30 m of the transects. However, clearcuts adjacent to buffer strips often extended within this sampling area, likely leading to underestimation of the density of forest-dwelling species within buffer strips. Consequently, we conducted a second series of analyses after excluding observations obtained in the clearcut adjacent to each buffer strip (i.e., considering only forested habitat). To standardize the area sampled for statistical tests, we also excluded observations obtained in an equal-sized strip along the upslope side of each paired riparian control. Both analyses are reported: probability values designated P_{30m} report analyses including all sightings within 30 m of transects, whereas those denoted by P_B refer to analyses of the buffer-sized area only. Because of the overlap in datasets tested in these 2 analyses, we used the Bonferroni method to determine the appropriate significance level ($\alpha = 0.025$; Sokal and Rohlf 1995).

To assess the influence of buffer strip width on bird counts, we regressed counts obtained within buffer strips (i.e., excluding sightings from clearcuts) against the width of the buffer strips for each of the 5 guilds and for all species combined ($\alpha = 0.05$; PROC REGRESS in Minitab [Ryan and Joiner 1994]).

RESULTS

We found no differences when comparing individual species, guild, or total bird counts between lake and stream shorelines for either control or buffer strip transects. Consequently, we pooled lacustrine and riverine transects in subsequent analyses.

Avian assemblages differed between the control and buffer strip shorelines. The total num-

ber of birds observed in buffer strips was greater than in the riparian controls for both the analysis of all sightings within 30 m ($F_{1,15} = 8.33$, $P_{30m} = 0.011$), and after the exclusion of clearcut habitat ($F_{1,15} = 16.35$, $P_B = 0.001$; Table 2). Total counts were larger in buffer strips because of the greater abundance of birds in the open-edge ($\chi^2_1 = 33.70$, $P_{30m} < 0.001$; $\chi^2_1 = 12.09$, $P_B < 0.001$) and ubiquitous guilds ($\chi^2_1 = 5.75$, $P_B = 0.017$), whereas counts for other guilds were similar between buffer strip and control shorelines (Table 1). Several species from the open-edge and ubiquitous guilds were more abundant along buffer strip transects, whereas no species from any guild was significantly less abundant (Table 1). Species richness in buffers and controls did not differ either with ($F_{1,15} = 1.07$, $P_{30m} = 0.317$) or without ($F_{1,15} = 4.44$, $P_B = 0.052$) the inclusion of sightings from clearcut areas (Table 2). Rarefaction curves for the entire plots indicated that as numbers of birds increased, species accumulated more rapidly along undisturbed shorelines than buffered shorelines (Fig. 2A). This pattern was not evident following the restriction of observations to the buffer area (Fig. 2B). Relative abundance curves were similar for buffered and undisturbed shorelines (Fig. 3).

Comparisons of analyses including all birds seen within 30 m of the transects to analyses of those seen within the buffer strip alone reflected differences in patterns of habitat selection among guilds (Table 1). The difference between buffers and controls was more pronounced for the open-edge guild when clearcut habitat was included in the analyses. Two species from this guild, magnolia warbler ($\chi^2_1 = 9.02$, $P_{30m} = 0.003$) and white-throated sparrow ($\chi^2_1 = 5.28$, $P_{30m} = 0.022$), were significantly more abundant along the buffer strip transects only when observations from clearcut habitat were included. The opposite was true for the ubiquitous guild, where the frequency of observation was higher for the guild ($\chi^2_1 = 5.75$, $P_B = 0.017$) only when counts were restricted to forested habitat. The initial comparison (i.e., including clearcut habitat) of forest generalists between treatments suggested lower numbers along buffer strips ($\chi^2_1 = 3.13$, $P_{30m} = 0.077$); however, after the exclusion of deforested habitat, there was no such indication ($\chi^2_1 = 0.33$, $P_B = 0.566$).

We found a weak, positive relation between the total number of birds observed within buf-

Table 1. Mean frequency of bird observations on transects following undisturbed riparian edges and riparian buffer strips in Newfoundland, Canada, 1994–95. Treatments were compared via a generalized linear model with Poisson error distribution. Two analyses were conducted: (1) all individuals within 30 m (P_{30m}), and (2) individuals detected in the buffer area only (P_b).

Habitat selection guild Species	All birds within 30 m					Birds in buffer area only				
	Undisturbed		Buffer strip		χ^2_1 ^a	Undisturbed		Buffer strip		χ^2_1 ^a
	\bar{x}	95% CI	\bar{x}	95% CI		\bar{x}	95% CI	\bar{x}	95% CI	
Forest generalist										
Black-backed woodpecker (<i>Picoides arcticus</i>)	0.06	0.00–0.19	0.06	0.00–0.19		0.06	0.00–0.19	0.06	0.00–0.19	
Downy woodpecker (<i>P. pubescens</i>)	0.19	0.00–0.44	0.13	0.00–0.31		0.06	0.00–0.19	0.13	0.00–0.31	
Hairy woodpecker (<i>P. villosus</i>)	0.13	0.00–0.31	0.00			0.13	0.00–0.31	0.00		
Black-capped chickadee (<i>Parus atricapillus</i>)	0.25	0.06–0.50	0.19	0.00–0.44	0.15	0.703	0.00–0.31	0.06	0.00–0.19	
Boreal chickadee (<i>P. hudsonicus</i>)	0.56	0.25–0.94	0.88	0.44–1.38	1.10	0.294	0.13–0.81	0.75	0.38–1.19	1.34
Winter wren (<i>Troglodytes troglodytes</i>)	0.19	0.00–0.44	0.13	0.00–0.31		0.06	0.00–0.19	0.06	0.00–0.19	0.247
Golden-crowned kinglet (<i>Regulus satrapa</i>)	0.19	0.00–0.44	0.00			0.13	0.00–0.31	0.00		
Ruby-crowned kinglet (<i>R. calendula</i>)	1.06	0.63–1.56	0.88	0.44–1.38	0.30	0.584	0.25–1.06	0.81	0.44–1.31	0.40
Black-and-white warbler (<i>Mniotilta varia</i>)	0.13	0.00–0.31	0.00			0.06	0.00–0.19	0.00		
Pine grosbeak (<i>Pinicola enucleator</i>)	0.13	0.00–0.31	0.00			0.13	0.00–0.31	0.00		
Pine siskin (<i>Carduelis pinus</i>)	0.94	0.50–1.44	0.44	0.13–0.81	2.98	0.084	0.38–1.19	0.38	0.13–0.69	2.05
Subtotal	3.81	2.91–4.81	2.69	1.94–3.50	3.13	0.077	1.81–3.38	2.25	1.56–3.00	0.33
Interior										
Yellow-bellied flycatcher (<i>Empidonax flaviventris</i>)	0.56	0.25–0.94	0.69	0.31–1.13	0.20	0.652	0.06–0.62	0.56	0.25–0.94	1.16
Red-breasted nuthatch (<i>Sitta canadensis</i>)	0.06	0.00–0.19	0.00			0.00		0.00		
Hermit thrush (<i>Catharus guttatus</i>)	0.06	0.00–0.19	0.19	0.00–0.44		0.00		0.13	0.00–0.31	
Swainson's thrush (<i>C. ustulatus</i>)	0.13	0.00–0.31	0.00			0.06	0.00–0.19	0.00		
Black-throated green warbler (<i>Dendroica virens</i>)	0.63	0.25–1.06	0.38	0.13–0.69	1.01	0.313	0.13–0.69	0.38	0.13–0.69	<0.01
Ovenbird (<i>Seiurus aurocapillus</i>)	0.06	0.00–0.19	0.00			0.00		0.00		
Subtotal	1.50	0.94–2.13	1.25	0.75–1.81	0.37	0.544	0.38–1.19	1.06	0.63–1.56	0.87
Riparian										
Spotted sandpiper (<i>Actitis macularia</i>)	0.31	0.06–0.62	0.19	0.00–0.44	0.51	0.470	0.06–0.62	0.19	0.00–0.44	0.51
Belted kingfisher (<i>Ceryle alcyon</i>)	0.06	0.00–0.19	0.00			0.06	0.00–0.19	0.00		
Northern waterthrush (<i>Seiurus noveboracensis</i>)	0.88	0.44–1.38	0.69	0.31–1.13	0.37	0.564	0.38–1.19	0.56	0.25–0.94	0.43
Wilson's warbler (<i>Wilsonia pusilla</i>)	0.00		0.13	0.00–0.31		0.00		0.13	0.00–0.31	
Yellow warbler (<i>Dendroica petechia</i>)	0.13	0.00–0.31	0.00			0.00		0.00		
Rusty blackbird (<i>Euphagus carolinus</i>)	0.13	0.00–0.31	0.06	0.00–0.19		0.13	0.00–0.31	0.06	0.00–0.19	
Subtotal	1.50	0.94–2.13	1.06	0.63–1.56	1.20	0.272	0.75–1.81	0.94	0.50–1.44	0.72
Open-edge										
Olive-sided flycatcher (<i>Contopus borealis</i>)	0.00		0.13	0.00–0.31		0.00		0.13	0.00–0.31	
Gray jay (<i>Perisoreus canadensis</i>)	0.00		0.25	0.06–0.50		0.00		0.25	0.06–0.50	
Magnolia warbler (<i>Dendroica magnolia</i>)	0.13	0.00–0.31	0.81	0.44–1.31	9.02	0.003	0.00–0.31	0.44	0.13–0.81	2.94
Mourning warbler (<i>Oporornis phyladelphia</i>)	0.13	0.00–0.31	0.75	0.38–1.19	7.93	0.005	0.00–0.19	0.44	0.13–0.81	5.06
Dark-eyed junco (<i>Junco hyemalis</i>)	0.00		0.19	0.00–0.44		0.00		0.13	0.00–0.31	

Table 1. Continued.

Habitat selection guild Species	All birds within 30 m					Birds in buffer area only				
	Undisturbed			Buffer strip		Undisturbed			Buffer strip	
	\bar{x}	95% CI		\bar{x}	95% CI	\bar{x}	95% CI		\bar{x}	95% CI
White-throated sparrow (<i>Zonotrichia albicollis</i>)	0.75	0.38–1.19		1.63	1.06–2.31	0.75	0.38–1.19		1.19	0.69–1.75
Lincoln's sparrow (<i>Melospiza lincolni</i>)	0.06	0.00–0.19		0.19	0.00–0.44	0.06	0.00–0.19		0.06	0.00–0.19
Subtotal	1.06	0.63–1.56		4.06	3.13–5.06	1.00	0.56–1.50		2.63	1.88–3.44
Ubiquitous										
Northern flicker (<i>Colaptes auratus</i>)	0.00			0.06	0.00–0.19	0.00			0.06	0.00–0.19
American robin (<i>Turdus migratorius</i>)	0.94	0.50–1.44		0.88	0.44–1.38	0.75	0.38–1.19		0.63	0.25–1.06
Blackpoll warbler (<i>Dendroica striata</i>)	0.25	0.06–0.50		0.56	0.25–0.94	0.160	0.00–0.31		0.56	0.25–0.94
Yellow-rumped warbler (<i>D. coronata</i>)	1.75	1.13–2.44		2.31	1.63–3.13	1.31	0.81–1.88		2.25	1.56–3.00
Fox sparrow (<i>Passerella iliaca</i>)	0.00			0.31	0.06–0.62	0.00			0.13	0.00–0.31
Subtotal	2.94	2.13–3.81		4.12	3.19–5.13	2.19	1.50–2.94		3.63	2.75–4.63

^a Statistical comparisons were not conducted if <6 birds were observed.

fer strips and buffer width ($r^2 = 0.35$, $P = 0.017$, $n = 16$; Table 3). At the guild level, no comparisons were significant ($P > 0.05$; Table 3).

DISCUSSION

Riparian forest management practices are intended to protect species dependent on riparian habitat. Consequently, the response of these species is of primary concern when evaluating the effectiveness of riparian management practices. Buffers were effective in that counts of riparian species at the guild level were similar between control shorelines and buffer strips (Table 1). In contrast to findings in Maine (Johnson and Brown 1990), we found no evidence that northern waterthrush were less abundant along buffers than undisturbed shorelines ($\chi^2_1 = 0.37$, $P_{30m} = 0.564$; $\chi^2_1 = 0.43$, $P_B = 0.511$). However, Johnson and Brown's (1990) study was unreplicated, making it difficult to separate harvesting effects from intrinsic variability between 2 lakeshores (e.g., Lewis 1998).

Although we detected no differences in abundance between control shorelines and buffer strips for the 5 remaining riparian species, all were rarely observed during surveys; thus, any effect would have gone undetected (Table 1). Regression analysis showed no association between counts of riparian species and buffer strip width (Table 3). This lack of relation likely stems from the association of riparian species with habitat found along the shoreline, which would not increase in proportion to buffer width. Thus, increasing the width of buffer strips beyond the riparian vegetation zone would not likely increase their use by riparian birds.

The general rarity of riparian birds in riparian habitat was unexpected. In comparison, however, these species were almost entirely absent in the forest interior (Table 4). We propose 2 nonexclusive explanations for the low numbers of riparian birds observed. First, riparian species occupy long, narrow shoreline territories, thereby reducing the number of breeding pairs observed. Manuwal (1986) described the shapes of bird territories along streams in Montana. While some species typically occupied symmetric territories spanning riparian and forested upland vegetation, others had elongated territories that fell almost entirely within riparian vegetation. Similarly, several of the riparian species we observed appeared to occupy linear shoreline

Table 2. Mean abundance and species richness of avian assemblages observed along 16 pairs of 200-m transects placed along undisturbed riparian edges and riparian buffer strips in Newfoundland, Canada 1994–95. Two analyses were conducted: (1) all individuals within 30 m (P_{30m}), and (2) individuals detected in the buffer area only (P_B).

	Undisturbed		Buffer strip		ANOVA summary		
	\bar{x}	SE	\bar{x}	SE	MS	$F_{1,15}$	P
All sightings							
Total relative abundance	10.7	0.9	13.2	1.1	50.00	8.33	$P_{30m} = 0.011$
Species richness	8.1	0.6	8.6	0.5	2.00	1.07	$P_{30m} = 0.317$
Buffer area only							
Total relative abundance	7.9	0.9	10.5	1.2	60.50	16.35	$P_B = 0.001$
Species richness	6.2	0.7	7.2	0.5	8.00	4.44	$P_B = 0.052$

territories. These species, particularly spotted sandpiper, belted kingfisher, northern waterthrush, and rusty blackbird were regularly seen traveling long distances along shorelines, but they were rarely seen away from water. Such a pattern of habitat use by riparian species could result in low encounter rates by observers using linear or point sampling techniques, as much of each territory could extend beyond the area sampled. Furthermore, one would be less likely to sample >1 territory of a species along a transect, as often occurred with nonriparian species during our study. A second explanation is that riparian habitat in the region is of low quality and consequently supports low densities of riparian birds. Northern waterthrush was the most common riparian species in the region and was observed on most waterbodies, whereas the presence of other riparian species was much less predictable. Other studies in eastern balsam fir forests also have reported low densities for most of these species (Darveau et al. 1995, LaRue et al. 1995). We suggest that a combination of low abundance and linear shoreline territories was responsible for the low numbers of riparian birds we observed during surveys. Studies of riparian species probably require

more extensive sampling than is typically necessary in studies of species selecting other (i.e., nonlinear) habitat types.

Darveau et al. (1995) suggested narrow buffer strips were unfavorable habitat for forest-dwelling birds because numbers of these species observed within 80 m of shorelines having buffers 20–40 m wide were lower than on forested controls. Woodland species would not, however, be expected to inhabit deforested areas; hence, analyses including sampling in clearcuts are likely biased. Analyses considering buffer area only indicated that in Newfoundland, as in Quebec (Darveau et al. 1995), densities of forest generalists remained relatively unchanged within narrow buffer strips (Table 2). Thus, in the boreal forest, we suggest that riparian buffers of widths >20 m may be beneficial to forest generalists. In both our study and Darveau et al.'s (1995), many forest generalist species were found in areas that would have been unsuitable without buffer strips (Triquet et al. 1990; D. M. Whitaker, unpublished data). However, lack of association between buffer strip width and counts of forest generalists was unexpected, given that the habitat area available to these species (as we have de-

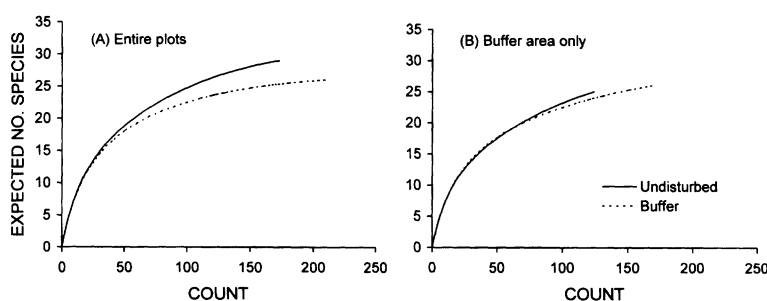


Fig. 2. Rarefaction curves for avian assemblages observed along riparian buffer strips and undisturbed shorelines in Newfoundland, Canada. Figures include (A) all birds detected within 30 m of transects, and (B) birds detected in a buffer-sized area only. Curves predict the rate of species accumulation with increasing numbers of individuals, up to the observed values (James and Rathburn 1981).

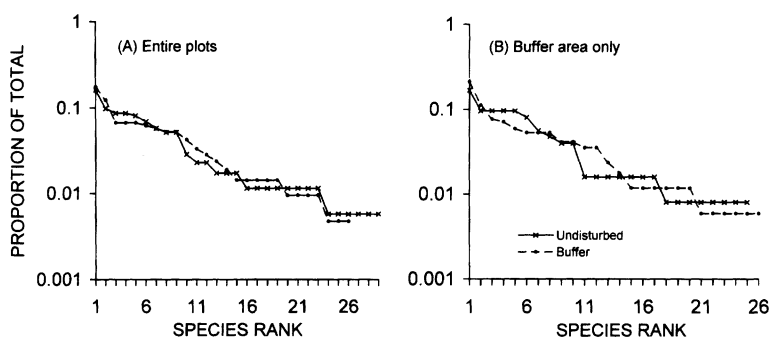


Fig. 3. Relative abundance curves for avian assemblages observed along riparian buffer strips and undisturbed shorelines in Newfoundland, Canada. Figures include (A) all birds detected within 30 m of transects, and (B) birds detected in a buffer-sized area only. The ordinate indicates the proportion of all observations accounted for by each species (log scale), and the abscissa is the rank from most common (yellow-rumped warbler, in all cases) to least common species.

fined it) should increase with buffer width. Possibly, the range of buffer widths sampled was not great enough to detect a response.

Interior forest species are an important component of forest bird assemblages in western Newfoundland (Table 4; Whitaker and Montevecchi 1997). As with forest generalists, no difference in abundance was detected for the interior forest guild between control shorelines and buffer strips (Table 1). Consideration of data from shoreline habitats alone might lead to the conclusion these species are adequately protected in buffers. However, the rarity of these species resulted from their general absence in riparian habitat, not overall rarity in the region. The mean frequency of sightings in interior forest habitat (i.e., 150 m from the shoreline) in the study area was >3 times that observed along either riparian controls or buffer strips (Table 4; Whitaker and Montevecchi 1997). Also, 3 of 6 interior species were not observed along any buffer strip. Thus, both undisturbed shorelines and buffer strips are likely poor or marginal habitat for these species.

Regression analysis indicated buffer width was not a significant factor influencing numbers of interior forest birds and accounted for little

of the observed variation in counts ($r^2 = 0.19$, $P = 0.095$, $n = 16$; Table 3). However, both our sample size and the range of buffer widths sampled were limited. If wide enough, buffers may provide adequate interior forest conditions to support greater numbers of birds selecting this habitat. Nevertheless, even the widest buffers we sampled (40–50 m) supported densities <50% of that observed in interior forest habitats. In Newfoundland, as with much of the boreal forest, surface water is abundant. Consequently, the economic effects of setting aside riparian buffers wide enough to support populations of interior forest species would be high (Bren 1995). Core interior forest habitat (>100 m from any edge; Temple 1986) can only be preserved by setting aside large, relatively symmetric reserves, not extensive linear buffers. Thus, separate (but complementary) conservation strategies clearly are required to maintain riparian and interior species in extensively harvested forests. Under such a management scenario, riparian buffer strips would likely play an important role as travel corridors linking large forest blocks and thereby facilitating movement and dispersal of woodland birds (Haas 1995,

Table 3. Regressions of bird counts for avian guilds and all birds combined against buffer strip width. Counts include only those birds observed within buffer strips ($\alpha = 0.05$).

Habitat selection guild	Slope	95% CI	Intercept	r^2	$F_{1,14}$	P
Forest generalists	0.02	−0.07–0.11	1.61	0.02	0.23	0.641
Interior forest	0.04	−0.01–0.09	0.41	0.19	3.21	0.095
Riparian	0.03	−0.03–0.09	−0.01	0.07	1.01	0.332
Open-edge	0.07	−0.06–0.20	0.22	0.09	1.44	0.250
Ubiquitous	0.12	0.00–0.24	−0.22	0.24	4.40	0.055
Total count	0.28	0.06–0.50	1.20	0.35	7.41	0.017

Table 4. Abundance of riparian and interior forest birds along 200-m transects located in riparian and interior forest habitats in Newfoundland, Canada 1994–95 (from Whitaker 1997)^a.

Habitat selection guild Species	Riparian		Interior forest		$\chi^2_{1^b}$	P
	\bar{x}	95% CI	\bar{x}	95% CI		
Interior forest						
Yellow-bellied flycatcher	0.54	0.15–1.00	1.54	0.92–2.23	6.52	0.011
Red-breasted nuthatch	0.08	0.00–0.23	0.46	0.15–0.85	3.96	0.047
Hermit thrush	0.08	0.00–0.23	0.39	0.08–0.77	2.91	0.088
Swainson's thrush	0.08	0.00–0.23	0.62	0.23–1.08	6.20	0.013
Black-throated green warbler	0.77	0.31–1.31	1.62	1.00–2.31	4.00	0.046
Ovenbird	0.08	0.00–0.23	0.62	0.23–1.08	6.20	0.013
Subtotal ^c	1.63	1.00–2.31	5.25	4.08–6.54		
Riparian						
Spotted sandpiper	0.31	0.08–0.62	0.00			
Belted kingfisher	0.08	0.00–0.23	0.00			
Northern waterthrush	0.85	0.38–1.38	0.08	0.00–0.23	9.75	0.002
Wilson's warbler ^d	0.00		0.00			
Yellow warbler	0.15	0.00–0.38	0.00			
Rusty blackbird	0.15	0.00–0.38	0.00			
Subtotal ^c	1.54	0.92–2.23	0.08	0.00–0.23		

^a Bird surveys were conducted concurrently on most of the same sites as research presented here, and surveys followed the same methodology. Interior transects were placed parallel to riparian transects (13 pairs), 150 m upslope from the shoreline.
^b Statistical tests were conducted as for individual species presented in this paper; comparisons were not conducted if <6 birds were observed.
^c Not tested statistically, because species were assigned to guilds based in part on these observations.
^d Seen only along buffer strip transects.

Machtans et al. 1996, Desrochers and Hannon 1997, Schmiegelow et al. 1997).

The most pronounced changes in avian assemblages were observed in the open-edge and ubiquitous guilds, both of which were more common along buffer strips than along undisturbed shorelines (Table 1). Similar increases in many of these species were observed in buffer strips in Maine and Quebec (Johnson and Brown 1990, Darveau et al. 1995). The change in open-edge species is not surprising given their preferred habitats have been created in areas that previously supported continuous forest cover. Correspondingly, the difference between controls and buffers was more pronounced with the inclusion of observations obtained in clearcut habitat. Counts of open-edge species showed no response to increasing buffer strip width ($r^2 = 0.09$, $P = 0.250$, $n = 16$; Table 3). As with the riparian guild, lack of response to strip width is likely related to use of adjacent habitat types and ecotones, which do not increase with increasing buffer width. The mixed habitat along buffer strips seemed to be favorable to species we classified as ubiquitous. Counts of these species, which were most often seen within buffers rather than in adjacent clearcuts, may be positively related to strip width ($r^2 = 0.24$, $P = 0.055$, $n = 16$; Table 3). Given that ubiquitous species were less abun-

dant along control shorelines, where forests extended >300 m upslope, there may be an optimal buffer width beyond which numbers of these birds would stabilize or decline.

Mixed results were obtained regarding the biodiversity of avian assemblages on the undisturbed and buffer strip shorelines, with different indices suggesting contrasting trends. Considering entire sampling plots (i.e., including clearcuts), species accumulated more rapidly along undisturbed shorelines than buffer strips, typically a sign of higher biodiversity (Fig. 2A). However, the lower rate of species accumulation along buffered shorelines was offset by the greater number of birds observed, which resulted in species richness being similar for the 2 shoreline types (Table 2). Conversely, the near significant increase in species richness observed within buffer strips ($F_{1,15} = 4.44$, $P_B = 0.052$; Table 2) resulted from the greater number of birds they supported, because species accumulated at a similar rate within buffers and undisturbed shorelines (Fig. 2B). Relative abundance curves suggest assemblages along the 2 shoreline types are similar in structure and evenness (Fig. 3). The higher total number of birds along buffers (Table 2) is not surprising because species in 2 guilds became more abundant, whereas no guild or individual species was significantly less abundant in this habitat (Table 1).

The possibility that this increase could be explained through packing of birds that originally inhabited the harvested forest into the residual buffer strip (e.g., Darveau et al. 1995) is unlikely for 2 reasons. First, the time since harvesting (≥ 3 yr) on buffer strip plots should have been long enough for densities of breeding birds to stabilize. Darveau et al. (1995) found that populations of boreal forest birds in buffer strips returned to approximately preharvest levels within 3 years. Second, a large portion of the observed increase can be attributed to species in the open-edge guild, which are associated with clearcut habitat that was created by timber harvesting.

Other research we have conducted demonstrated that bird assemblages along nonriparian forest edges created by clearcutting differed from undisturbed riparian shorelines in having greater species richness and bird abundance, primarily due to greater numbers of open ground and edge-associated birds (Whitaker and Montevecchi 1997). Thus, the juxtaposition of natural riparian and clearcut forest edges along the length of narrow buffer strips resulted in bird assemblages containing the characteristic species of both edge types. In addition, some ubiquitous species became more abundant than they were along either type of edge alone.

MANAGEMENT IMPLICATIONS

Riparian buffer strips 20–50 m wide were used by a relatively abundant and diverse forest bird assemblage that included species from a variety of habitat guilds. Buffer strips in boreal forests also may have important ecological roles as dispersal and movement corridors, particularly for juvenile birds during the postbreeding season (Haas 1995, Machtans et al. 1996, Desrochers and Hannon 1997, Schmiegelow et al. 1997). However, although buffer strips clearly help to maintain avian biodiversity in areas of extensive clearcutting, riparian buffers are not a panacea for mitigating effects of forest harvesting on wildlife. Many riparian species apparently restrict their activities to riparian vegetation, and it seems unlikely that their populations can be augmented by increasing buffer strip widths. In addition, we observed extensive tree blowdowns in many buffers, which can reduce their value as woodland habitat within a few years (Darveau et al. 1993). Silvicultural practices which make buffers more wind resistant, such as removing some large trees from

the clearcut edge of the strip, are necessary in regions where blow-downs are common.

Furthermore, distinct and separate conservation strategies are required for interior forest birds. Recently, there has been concern over the status of populations of many interior forest birds in northeastern North America (Robbins et al. 1989, Askins et al. 1990, Sauer and Droege 1992). Although the status of interior forest birds is uncertain (James et al. 1996), long-term data are extremely limited for northern forests, and a cautionary approach is warranted. Even very wide buffer strips (>100 m) may not provide adequate interior forest conditions and could act as ecological traps (Gates and Gysel 1978) compelling these species to breed in areas where nest predation rates are high (Vander Haegen and DeGraaf 1996, Darveau et al. 1997, Lewis 1998). Given the concern over the status of interior forest wildlife and the extent of clearcutting in the boreal forest, preservation of large tracts of interior forests should be incorporated into regional harvesting plans. Finally, information is needed on such aspects of riparian buffering as the effects of forest type and waterbody size, of harvesting along both banks of streams, of the size of adjacent clearcuts, relations between buffer width and nest predation rate, use during the postbreeding season, lengths of buffer strips, and, particularly, the broader effects on wildlife of extensive harvesting throughout watersheds.

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