

PROJECT REPORT 1999-21

sustainable
forest
management
network

réseau
sur la
gestion durable
des forêts



Effects of Landscape Structure on Distribution, Abundance, and Reproduction of Forest Songbirds

For copies of this or other SFM publications contact:

Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
<http://www.biology.ualberta.ca/sfm/>

ISBN 1-55261-035-7

**Effects of landscape structure on
distribution, abundance, and
reproduction of forest songbirds**

by

Marc-André Villard

Département de biologie
Université de Moncton
Moncton, New Brunswick

May 1999

ABSTRACT

An increasing body of literature indicates that forest songbirds are sensitive to both local and landscape-scale alterations of their habitat. Since recruitment (influx of new individuals) into populations is positively correlated to the previous year's reproductive success, bird population trends are also indicative of longer-term effects of changes in the habitats. Thus, we view birds as excellent indicators of forestry effects on biodiversity.

In this project, we document the distribution, abundance, and reproductive success of forest songbirds in two landscapes (49 km²) with contrasting intensities of timber harvesting. One landscape was moderately harvested (ca. 70% forest cover) and the other was intensively harvested (ca. 45% forest cover). Harvesting intensity was also reflected in the area of clearcuts and partial (selection) cuts, which were substantially larger in the intensively-harvested landscape. In each landscape, we censused birds at 182 to 185 stations distributed systematically in a 7 x 7 km "macro" grid and two 1.75 x 1.75 km "meso" grids. We also compared the reproductive success of eight species at the meso-grid scale using an index based on evidence of reproductive activity. Finally, we measured reproductive success by monitoring the territories and nests of two target species in four 25-ha plots, two in each landscape.

Our results indicate that the intensively-harvested landscape supports lower populations of forest specialists and that reproductive success was significantly lower in three of the eight species examined statistically. One of these, the Ovenbird, was very sensitive to selection cutting, but only in the intensively-harvested landscape. Nesting failure was mainly due to nest predation (67 to 83% of nesting failures). According to marks left on artificial eggs, most of the nest predation was attributable to mammals (Black Bear, Eastern Chipmunk, Red Squirrel). The temporal consistency of Ovenbird response and nest predation patterns will be examined based on data currently being collected.

Our findings suggest a number of precautionary measures to ensure that the reductions we observed in the reproductive success of forest birds do not lead to local or regional extirpations:

- (1) Relatively large blocks of mature, closed-canopy forest should be maintained at all times in forest management units.
- (2) The long-term availability of such blocks will require a drastic reduction in the areas planted with conifers, so that natural regeneration is allowed to take place.
- (3) Selection cutting practices should be altered to ensure the persistence of species requiring open understory conditions, such as the Ovenbird. Application of the first two recommendations to shade-tolerant hardwood stands would protect such species, assuming forest management units are relatively small. Alternatively, the distance between cutting strips or the time between cuts should be increased.

ACKNOWLEDGMENTS

This research project was made possible by the financial support of the Sustainable Forest management Network (SFMN), and by a research grant from the New Brunswick Wildlife Council. I sincerely thank my graduate students, John Gunn and Julie Bourque, and my honours student, Vincent Carignan. Special thanks to Serge Rhéaume, for his ornithological expertise, and to our field assistants Shawn Dubé, Hans Lefebvre, and Julie Marcoux. Jeff Bowman, Mark Edwards, and Peter McKinley (SFMN graduate students) also were instrumental in the realization of this large-scale study. I am indebted to Gilles Couturier, John Jenkins and Steve Young of Fraser Papers Inc. for their continuous logistical and financial support of the project. Finally, I thank Susan Hannon, Pierre Drapeau, Marcel Darveau, and other members of the Landscape Structure and Biodiversity Group for stimulating discussions on the work reported here. Julie Bourque was supported by a NSERC postgraduate scholarship and John Gunn by SFMN scholarships.

INTRODUCTION

Forestry has shaped the landscapes of New Brunswick for decades. No less than 85% of the land area of the province is covered by forests, and virtually all of this area has been harvested at least once. However, harvesting effects on forest biodiversity are still poorly known, with the exception of high-profile species that have direct economic value. Nongame species such as forest songbirds have received very little attention even though (1) they represent a large proportion of terrestrial vertebrate species in forest ecosystems, and (2) they play a major role in the regulation of insect populations, especially phytophagous lepidopteran larvae (Niemi et al. 1998). For example, forest songbird predation on spruce budworm is so intense that it can lengthen the time between outbreaks (Holling 1988). Finally, forest songbirds are very appealing as a target group for monitoring harvesting effects because (1) they can be censused efficiently over large areas through the detection of their vocalizations or drummings, (2) they have been shown to respond both to local (stand level) and landscape-scale changes in their habitat (Franzreb and Ohmart 1978; Askins and Philbrick 1987; Villard et al. 1995; Drapeau et al., in press), and (3) their reproductive success can be measured indirectly (Gibbs and Faaborg 1990; Gunn et al., in press).

In this project, my students and I are measuring the effects of forest harvesting at the local and landscape scales on the distribution, abundance, and reproduction of forest songbirds. Our specific objectives are to determine (1) how the distribution and abundance of bird species vary with harvesting intensity, and (2) whether silvicultural treatments (harvesting, forest plantation, etc.) affect bird reproductive success at the local and landscape scales. The inclusion of reproductive success among the response variables reflects its importance for the persistence of viable populations in these landscapes. Although juvenile songbirds are known to disperse far from their natal site, a significant correlation has been found between reproductive success and recruitment the following year (Nolan 1978, Holmes et al. 1992, Sherry and Holmes 1992), suggesting that habitat alterations on the breeding grounds cannot be ruled out as a cause of decline in populations of Neotropical migrant birds. Neotropical migrants represent a large proportion of the forest avifauna of northwestern New Brunswick (Erskine 1992, this study).

METHODOLOGY

Study area

This study was conducted in northwestern New Brunswick, north of the village of Plaster Rock (47°11' N, 67°13'W) (Fig. 1). The study area is entirely located on private land owned by our industrial partner, Fraser Papers Inc. Woodland is characterized by a mosaic of shade-tolerant hardwoods dominated by Sugar Maple, American Beech and Yellow Birch on well-drained sites, and coniferous stands along streams and rivers and on poorly-drained sites. The main silvicultural treatments are clearcutting in mixed or coniferous stands, partial (selection)

cutting in hardwood stands (Fraser Papers Inc. 1995), and plantation of conifers in clearcut areas where natural regeneration is deemed insufficient, (Gilles Couturier, Fraser Papers Inc., Plaster Rock, NB, pers. comm.). Herbicides are used to favour young conifers in recent plantations.

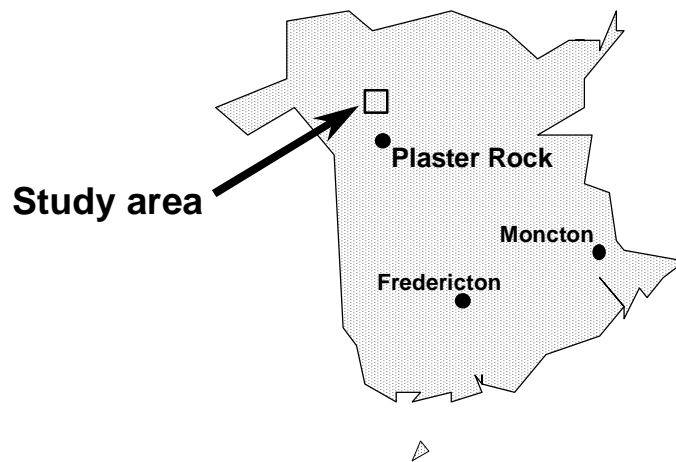


Figure 1: Location of the study area in New Brunswick

Figure. 1

To measure the effects of forest harvesting, we selected two extremes along a gradient of harvesting intensity: a moderately-harvested landscape and an intensively-harvested landscape. Mature forests covered over 70% of the moderately-harvested landscape and approximately 45% of the intensively-harvested landscape. Clearcuts and selection cuts were relatively small (<50 ha and <100 ha, respectively) in the former landscape and much more extensive in the latter (>200 ha and >400 ha, respectively).

In each landscape, we set systematic square grids of 64 points: a 7 x 7 km macro grid, within which were nested two meso grids (1.75 x 1.75 km) (Fig. 2). In the macro grids, points were 1 km apart, whereas this distance was only 250 m in meso grids. The location of meso grids was selected so that they would represent subsamples of the macro grids in terms of stand composition and silvicultural treatments. When accounting for the overlap between some macro and meso points, we surveyed a total of 182 points in the moderately-harvested landscape and 185 points in the intensively-harvested landscape. In each landscape, we measured the

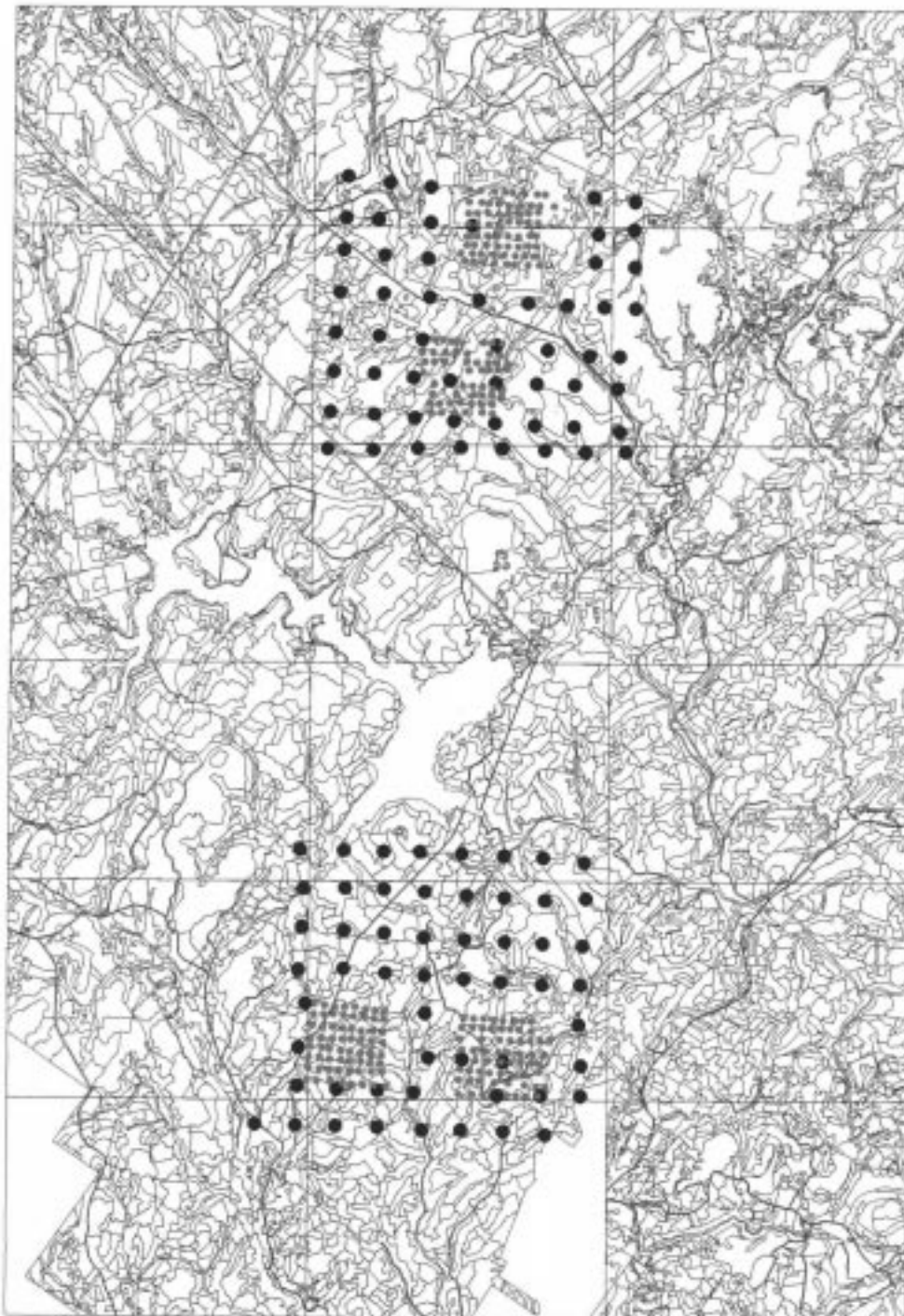


Figure 2: Configuration of macro and meso grid points in the study area. Black dots correspond to macro points and coloured dots represent meso points.

reproductive success of two target species in two 25-ha plots (micro grids): one in a recent (<5 years) selection cut and the other in a stand left uncut for at least 30 years (Fig. 3). Finally, we established 350-m transects perpendicular to the edge between conifer plantations and mature deciduous stands to examine the influence of the former on bird reproductive success in the latter. Along each transect, we installed 12 artificial nests containing plasticine eggs to measure nest predation rates and identify the predators involved. Plasticine eggs were dipped in paraffin to reduce their odour. We installed four transects in each landscape in 1998 and added a fifth transect in 1999.

Field data collection

We surveyed birds and vegetation at all 367 points (stations) during the study. In addition, we collected data on bird reproductive success in three meso grids and in four intensive study plots (25 ha). The intensive study plots, or micro grids, are shown on Fig. 3.

Point counts were conducted at every station. We listed all species detected by sight or sound and estimated their abundance based on the number of simultaneous detections (mainly countersinging males). In 1996, we surveyed the moderately-harvested landscape and in 1997, we surveyed the intensively-harvested landscape and one of the meso grids in the moderately-harvested landscape. Research on reproductive success was mainly conducted in 1997 and 1998, and is currently being completed this summer. We measured reproductive success at the stand level by monitoring the territories of two target species (Black-throated Blue Warbler and Ovenbird) and searching for nests or evidence of success (fledged young) (Bourque and Villard, in prep.). We also indexed reproductive success at the landscape scale by broadcasting a recording of Black-capped Chickadee mobbing calls at each station in meso grids and observing the response of this and other species attracted to the tape. This allowed us to determine evidence of reproductive activity (e.g. adults carrying food) or reproductive success (family groups) (Gunn et al., in press).

We collected detailed data on habitat structure and composition at and around each point count station in 1996 and 1997. Data were collected in three 10 x 20 m plots: one centered on the station and two located 65 m either to the N, SE or SW (randomly-selected direction). These data included the density of all trees, saplings and poles per dbh class, canopy height and closure, ground cover, coarse woody debris, snag density, etc. We also collected vegetation data in a 10 x 10 m plot centered on each nest found in 1997 and 1998.

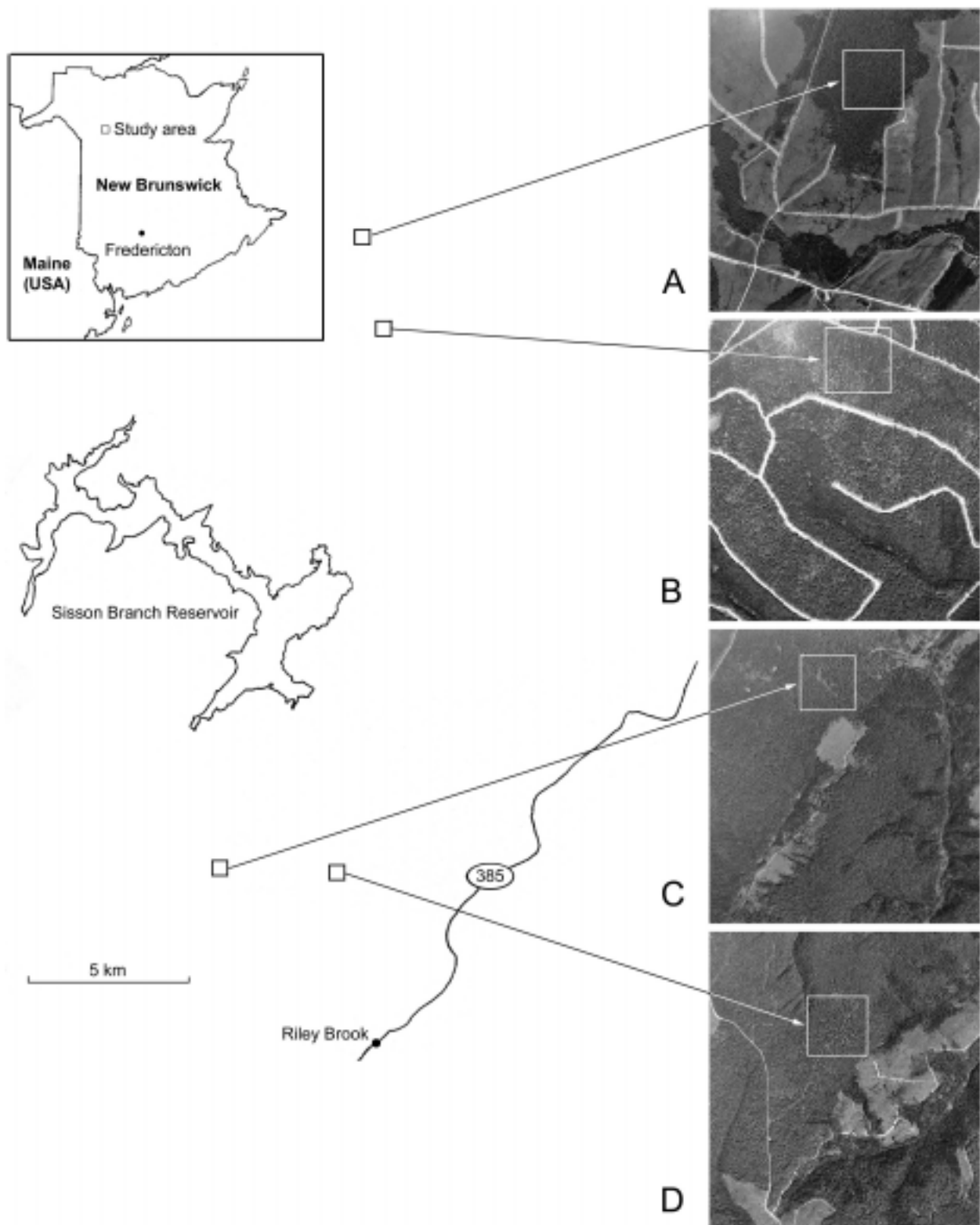


Figure 3.

Data analysis

We compiled point count data to obtain the frequency of occurrence of each species at each station, and its average abundance. Since stations sampled a variety of habitats, the data presented in Table 1 only are an indication of the trends in relative abundance in the two landscape types surveyed. Data will then be related to local habitat variables and landscape-scale characteristics to determine whether harvesting intensity influenced the structure of bird assemblages beyond the effects of local habitat conditions.

We compared the reproductive success of our target bird species at the local and landscape scales. Comparisons at the local scale were conducted at several levels: (1) proportion of males that were paired; (2) proportion of territories fledging young, (3) daily probability of predation on nests found. For Black-throated Blue Warblers, we also used the proportion of older males (>2 yrs or older) as an index of habitat quality (after Holmes et al. 1996). Comparisons at the landscape scale were made for all species responding strongly to song playbacks which were common enough to allow statistical analyses.

RESULTS

Distribution and abundance

The most common species in each landscape are listed in Table 1. It can readily be seen that the structure of the bird communities is very distinct between the two landscapes. The five most common species in the intensively-harvested landscape are typical of open or semi-open habitats, reflecting the lower forest cover and larger area of openings. In contrast, the five most common species in the moderately-harvested landscape are typically found in closed-canopy forests. The White-throated Sparrow, which was the most common species in the intensively-harvested landscape, only occupies the 16th rank in the moderately-harvested landscape. Likewise, the American Robin is 5th in the former and only 19th in the latter.

Table 1: the twenty most frequent bird species in each landscape. Species codes are listed in the appendix.

Intensively-harvested landscape (n=185)					Moderately-harvested landscape (n=182)				
Rank	Species	Freq.	%Freq.	Mean ab./stn	Rank	Species	Freq.	%Freq.	Mean ab./stn
1	WTSP	139	75,14	2,18	1	NOPA	173	95,05	1,53
2	MNWA	138	74,59	1,25	2	SWTH	171	93,96	1,61
3	COYE	127	68,65	1,29	3	REVI	162	89,01	1,82
4	HETH	126	68,11	0,89	4	BGNW	147	80,77	1,35
5	AMRO	110	59,46	0,64	5	YBSA	144	79,12	0,86
6	REVI	110	59,46	1,07	6	RBGR	143	78,57	1,01
7	WIWR	110	59,46	0,74	7	BTBW	141	77,47	1,23
8	OVEN	105	56,76	1,08	8	OVEN	135	74,18	1,49
9	NOPA	102	55,14	0,72	9	AMRE	134	73,63	1,22
10	YRWA	98	52,97	0,70	10	HETH	122	67,03	0,89
11	BGNW	93	50,27	0,72	11	BCCH	116	63,74	0,42
12	NAWA	91	49,19	0,70	12	BLWA	115	63,19	0,90
13	BTBW	90	48,65	0,83	13	MNWA	114	62,64	1,07
14	CSWA	83	44,86	0,55	14	YRWA	109	59,89	0,72
15	LEFL	82	44,32	0,79	15	UNWO	107	58,79	0,52
16	AMRE	80	43,24	0,63	16	WTSP	96	52,75	1,10
17	LISP	80	43,24	0,71	17	WIWR	93	51,10	0,60
18	YBSA	80	43,24	0,44	18	LEFL	89	48,90	0,81
19	DEJU	77	41,62	0,55	19	AMRO	81	44,51	0,42
20	ALFL	74	40,00	0,65	20	CSWA	80	43,96	0,61

We are currently measuring landscape attributes around all meso and macro grid stations to characterize the cover and configuration of the different habitat types present. Once these data are available, we will examine how local and landscape-scale habitat characteristics allow us to predict species presence. We will also compare species occurrence and abundance in similar stands between the two landscapes to determine whether the differences between bird communities apparent in Table 1 are attributable to a combination of local and landscape effects of harvesting or simply to local stand characteristics. For example, if landscape characteristics influence species distribution and abundance, we would expect to see significant differences between the bird community of a shade-tolerant hardwood stand located in the intensively-managed landscape and one located in the moderately-managed landscape.

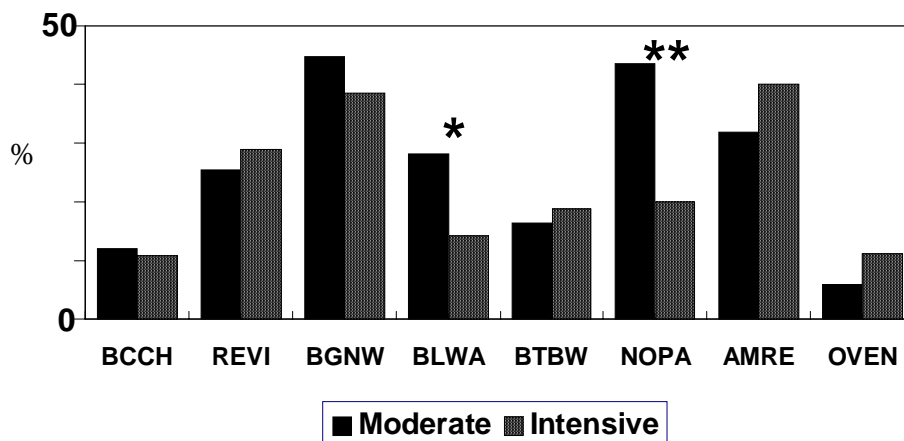
Reproductive success

According to our intensive studies on the Black-throated Blue Warbler and Ovenbird, 67 to 83% of nesting failures were attributable to nest predation in 1997 and 1998, respectively (Bourque and Villard, in prep.). Other nesting failures were attributable to abandonment by adults due to weather events (e.g. very cold nights, severe rainstorms) or for no apparent reason. We recorded no case of starvation of nestlings.

According to tooth marks left on plasticine eggs in artificial nests, mammals were responsible for 84% of cases of nest predation. The main mammalian nest predators were the Black Bear, Eastern Chipmunk, and Red Squirrel (Carignan and Villard, unpublished data). We are repeating our artificial nest experiment this year to examine the temporal consistency of this pattern.

Landscape scale

Our results at the scale of meso grids (306 ha) indicate that two species had a significantly lower index of reproductive success in the intensively-managed landscape: the Blackburnian Warbler and the Northern Parula (Fig. 4). For both species, the proportion of stations occupied by territorial male(s) where signs of reproductive activity were detected in the moderately-harvested landscape was roughly twice that obtained in the intensively-harvested landscape.



Kruskal-Wallis test, * P'0.05; **P'0.01

Figure X: percentage of stations with evidence of reproduction

Figure 4.

The Blackburnian Warbler is a species requiring conifers for successful reproduction. However, it was never recorded in conifer plantations. Instead, it was found in mature mixed or coniferous stands. The difference in reproductive success probably reflects the greater availability of conifer-dominated mature stands in the moderately-managed landscape. This interpretation will be verified using local and landscape-scale habitat data. The Northern Parula, on the other hand, is not as strongly related to conifers. This species is found in relatively moist stands, whether they are deciduous, mixed, or coniferous. This species is also strongly associated with beard-lichens (*Usnea* spp.), which it almost always uses to build its nest (Erskine 1992, Gauthier and Aubry 1995). At this point we ignore why there was such a large difference in the apparent reproductive success of this species between the two landscapes. Our working hypothesis is that microclimate may be less favourable for the development of beard-lichens in the intensively-harvested landscape. We will run transects to estimate the abundance of beard-lichens this fall and compare this abundance between the two landscapes.

We also used our direct measurements of reproductive success to examine whether our target species were influenced by harvesting intensity at that scale. In 1997 and 1998, we mapped and monitored all territories of our two target species, the Black-throated Blue Warbler and the Ovenbird, in 25 ha plots within uncut tolerant hardwood stands (Fig. 3A and C). Reproductive success did not differ significantly between the two landscapes for either of the target species or years, which is consistent with the results obtained with our index of reproductive success for these species (Fig. 4).

Stand level

In 1998, we added a plot in each landscape (Fig. 3B and D) to assess the simultaneous effects of harvesting at the stand level (selection cuts) and at the landscape scale. Reproductive success did not differ significantly for the Black-throated Blue Warbler, whether we considered pairing success or fledging success (Fig. 5). For the Ovenbird, however, both pairing and fledging success were significantly lower in the selection cut within the intensively-harvested landscape (Fig. 3D), suggesting a cumulative effect of harvesting at both scales (Bourque and Villard, in prep.). Julie Bourque's preliminary analyses of vegetation around Black-throated Blue Warbler nests and at random points suggest that selection cuts provide large patches of suitable nesting habitat for this species. For the Ovenbird, our results show the opposite effect. This species, which nests on the ground and mainly forages in the leaf litter, requires patches of open understory (Van Horn and Donovan 1994), which are rather sparsely distributed in selection cuts (Bourque and Villard, in prep.). Ovenbird pairing and fledging success were significantly lower in the selection cut within the intensively-harvested landscape (Fig. 5). The much greater pairing and fledging success observed in Ovenbird territories in the selection cut within the moderately-harvested landscape (Fig. 5) may reflect differences in the landscape contexts of the two sites (Fig. 3B and D). The selection cut in the intensively-harvested landscape was embedded in an extensive complex of selection cuts, whereas the selection cut in the moderately-harvested

landscape was mainly surrounded by uncut mature stands favourable to Ovenbirds. The former may have suffered from a low influx of females from the surroundings.

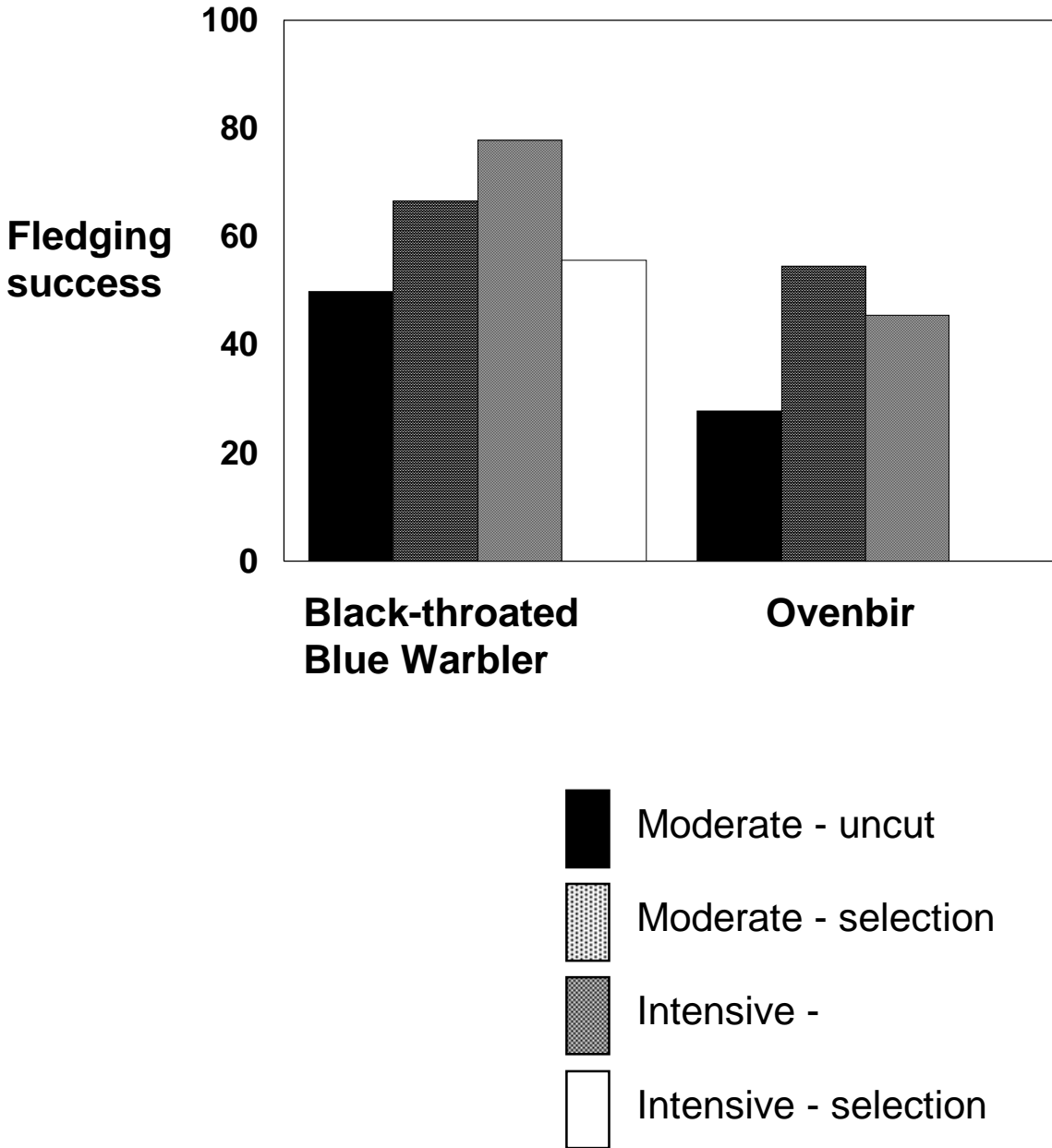


Figure 5. Percentage of territories where at least one young fledged

SUMMARY

Not surprisingly, our point count data indicate that the intensively-harvested landscape supports lower populations of forest specialists. It remains to be shown whether untreated mature stands maintain similar populations of forest birds irrespective of harvesting intensity. We will address this question as soon as our landscape analyses are completed.

Three of the eight forest bird species examined showed significant negative effects of harvesting intensity on their reproductive success: the Blackburnian Warbler, Northern Parula, and Ovenbird (three wood-warbler species). The Ovenbird showed a sensitivity to local harvesting (selection cutting) when combined with high-intensity harvesting at the landscape scale. We are currently repeating our intensive work in the same plots and in an additional plot within the intensively-harvested landscape to further investigate Ovenbird response to harvesting.

Finally, artificial nests and eggs allowed us to examine the composition of the nest predator community in each landscape under study. We are currently collecting a second year of data to draw more robust conclusions but, based on 1998 results, it appears that mammalian predators are dominant over avian nest predators.

MANAGEMENT APPLICATIONS

The history of agriculture should bring home clear lessons about the dangers of extensive alteration and oversimplification of ecosystems. In New Brunswick, there is a strong trend toward intensive silviculture whereby virtually all stands are managed to some degree. Coniferous and mixedwood stands are gradually converted into spruce plantations with the help of herbicides, although the Forest Habitat Program of the Department of Natural Resources and Energy provides some protection to mature coniferous habitat (Anonymous 1995). Meanwhile, shade-tolerant hardwoods are quickly turned into extensive partial (or selection) cuts. On Fraser Papers' forest lands, these selection cuts remove 30% of the basal area every 20 years or so (Fraser Papers Inc. 1995). These selection cuts are performed using feller-bunchers, which create strips 18-22 m apart. Our results indicate that the combination of these silvicultural treatments can already be shown to have an effect on the occurrence and reproductive success of some forest songbird species. The important point here is that effects on reproductive success can ultimately translate into local and regional extirpations if we do not treat these early signs seriously.

Our results suggest a number of precautionary measures that could be taken to reduce impacts on songbirds:

1. Harvest plans should maintain relatively large blocks of mature forest at all times in forest management units. Blocks of closed canopy forest are important for species requiring relatively open understories such as the Ovenbird and possibly the Swainson's Thrush.

2. Cutblock size and shape, and postcut site treatments should be designed to favour rapid *natural* regeneration of mixedwood stands rather than conifer monocultures. In our study area, conifer plantations are still too young to assess their suitability for bird species typical of mature coniferous stands. However, it is highly unlikely that these plantations will provide suitable habitat for these species given the expected frequency of harvesting in these plantations and the low compositional and structural diversity which characterizes them.
3. Selection cuts should maintain an intermediate level of structural heterogeneity similar to that observed in old-growth remnants in northeastern forest region (see Lorimer and Frelich 1994). Our results clearly show that some species strongly depend on certain structural components of forest stands for nesting. For example, the Black-throated Blue Warbler nests in patches of dense shrubs and saplings associated with canopy gaps while the Ovenbird apparently cannot nest successfully in the absence of patches of closed-canopy forest (with the associated open understory). Under the current selection cutting practices, the latter species will be severely affected. Both species could persist if cutting cycles were extended to longer periods, or if cutting strips were more widely spaced.

REFERENCES

- Anonymous. 1995. Management of forest habitat in New Brunswick. Forest Habitat Program, Fish and Wildlife Branch, Department of Natural Resources and Energy, Fredericton, NB.
- Askins, R.A. and Philbrick, M.J. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. *Wilson Bull.* 99: 7-21.
- Bourque, J., and Villard, M.-A. In prep. Relative effect of stand and landscape-level harvesting on the reproductive success of two Neotropical migrant bird species in northwestern New Brunswick. Submitted to *Conservation Biology*, 4 March 1999.
- Drapeau, P., Leduc, A., Giroux, J.-F., Savard, J.-P., Bergeron, Y., and Vickery, W.L. In press. Landscape-scale disturbances and changes in bird communities of eastern boreal mixed-wood forests. *Ecology*.
- Erskine, A.J. 1992. Atlas of the breeding birds of the Maritime Provinces. Nimbus Publishing and Nova Scotia Museum, Halifax, Nova Scotia. P. 161.
- Franzreb, K.E. and Ohmart, R.D. 1978. The effects of timber harvesting on breeding birds in a mixed coniferous forest. *Condor* 80: 431-441.
- Fraser Papers Inc. 1995. New Brunswick Timberlands, 1995-1999 Forest Resources Management Plan. Edmundston, Alberta. Pp. 31-33.
- Gauthier, J. and Aubry, Y. 1995. Les oiseaux du Québec: Atlas des oiseaux nicheurs du Québec méridional. Association québécoise des groupes d'ornithologues, Société québécoise de protection des oiseaux, Service canadien de la faune, Environnement Canada, Région du Québec, Montréal, Québec. Pp. 862-865.

- Gibbs, J.P., and Faaborg, J. 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conserv. Biol.* 4: 193-196.
- Gunn, J.S., Desrochers, A., Villard, M.-A., Bourque, J., and Ibarzabal, J. In press. Playback of Black-capped Chickadee mobbing calls as a method to estimate reproductive success of forest birds. *J. of Field Ornithol.* (accepted 27 May 1999).
- Holling, C.S. 1988. Temperate forest insect outbreaks, tropical deforestation, and migratory birds. *Mem. Ent. Soc. Can.* 146: 21-32.
- Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple-brooding, nesting success, and annual productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109: 321-333.
- Holmes, R.T., Marra, P.P., and Sherry, T.W. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *J. of Anim. Ecol.* 65: 183-195.
- Lorimer, C.G., and L.E. Frelich. 1994. Natural disturbance regimes in old-growth northern hardwoods: Implications for restoration efforts. *J. For.* 92: 33-38.
- Niemi, G., Hanowski, J., Helle, P., Howe, R., Monkkonen, M., Venier, L., and Welsh, D. 1998. Ecological sustainability of birds in boreal forests. *Conserv. Ecol.* 2 (2): 17 (<http://www.consecol.org/vol2/iss2/art17>).
- Nolan, V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithological Monograph No.26. American Ornithologists' Union, Washington, D.C.
- Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance Neotropical migrant: demographic evidence for the importance of breeding season events in the American Redstart. Edited by J.M. Hagan III and D.W. Johnston. *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, DC. Pp. 431-442.
- Van Horn, M.A., and Donovan, T.M. 1994. Ovenbird (*Seiurus aurocapillus*). The birds of North America No.88. Edited by A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologist's Union, Washington, DC.
- Villard, M.-A., Merriam, G., and Maurer, B.A. 1995. Dynamics in subdivided populations of Neotropical migratory birds in a fragmented temperate forest. *Ecology* 76: 27-40.

APPENDIX

Meaning of bird species codes used in the text and scientific names

ALFL	Alder Flycatcher	<i>Empidonax alnorum</i>
AMRE	American Redstart	<i>Setophaga ruticilla</i>
AMRO	American Robin	<i>Turdus migratorius</i>
BCCH	Black-capped Chickadee	<i>Poecile atricapillus</i>
BGNW	Black-throated Green Warbler	<i>Dendroica virens</i>
BLWA	Blackburnian Warbler	<i>Dendroica fusca</i>
BTBW	Black-throated Blue Warbler	<i>Dendroica caerulescens</i>
COYE	Common Yellowthroat	<i>Geothlypis trichas</i>
CSWA:	Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>
DEJU	Dark-eyed Junco	<i>Junco hyemalis</i>
HETH	Hermit Thrush	<i>Catharus guttatus</i>
LISP	Lincoln's Sparrow	<i>Melospiza lincolni</i>
MNWA	Magnolia Warbler	<i>Dendroica magnolia</i>
NAWA	Nashville Warbler	<i>Vermivora ruficapilla</i>
NOPA	Northern Parula	<i>Parula americana</i>
OVEN	Ovenbird	<i>Seiurus aurocapillus</i>
RBGR	Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
REVI	Red-eyed Vireo	<i>Vireo olivaceus</i>
SWTH	Swainson's Thrush	<i>Catharus ustulatus</i>
UNWO	Unknown Woodpecker	
WIWR	Winter Wren	<i>Troglodytes troglodytes</i>
WTSP	White-throated Sparrow	<i>Zonotrichia albicollis</i>
YBSA	Yellow-bellied Sapsucker	<i>Sphyrapicus varius</i>
YRWA	Yellow-rumped Warbler	<i>Dendroica coronata</i>