PROJECT REPORT
2000-20
FINAL PROJECT REPORT

sustainable forest management network

réseau sur la gestion durable des forêts

Reducing long-term effects of forest harvesting on indicator species of closed-canopy mature forests

A Network of Centres of Excellence
Un réseau de centres d'excellence

Marc-André Villard

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.ualberta.ca/sfm/

ISBN 1-55261-080-2

Reducing long-term effects of forest harvesting on indicator species of closed-canopy mature forests

by

Marc-André Villard
Département de biologie
Université de Moncton
Moncton, New Brunswick

August 2000

ABSTRACT

Current and projected timber harvesting practices will severely alter landscape structure on New Brunswick forest lands. Extensive spruce plantations are replacing softwood and mixedwood stands and greatly increase landscape contrast. Furthermore, large-scale selection cutting with short return intervals (20-25 yrs) in hardwood stands severely alters their structure. Under this type of management, mature, closed-canopy stands will become rare and sparsely distributed. Forest birds are sensitive to both local and landscape-scale alterations of their habitat. Since recruitment (influx of new individuals) into populations has been shown to be positively correlated to the previous year's reproductive success, bird presence and abundance in a region reflects to a large degree the suitability of their habitat. Thus, birds represent excellent indicators of forestry effects not just at the stand level, but also at the landscape scale.

In this report, I document the major findings of the research conducted by my students and I in the Acadian forest of northwestern New Brunswick (questions 1 to 3 below) and in the boreal mixedwood forest of northern Alberta (question 4). Specifically, we measured the response of two indicator species to harvesting at the stand and landscape scales. Those species were the Pileated Woodpecker (*Dryocopus pileatus*) and the Ovenbird (*Seiurus aurocapillus*). Both species are associated with mature to old forest stands, but the Ovenbird requires closed-canopy stands with an open understory for nesting and foraging. We asked the following questions: (1) do these species persist in intensively-managed landscapes? (2) does harvesting intensity influence Pileated Woodpecker foraging? (3) does the Ovenbird persist in selection cuts within hardwood stands and if so, does it reproduce successfully? (4) does forest harvesting reduce the permeability of the landscape to Ovenbird movements? In New Brunswick, we studied the Pileated Woodpecker in an intensively-harvested landscape with 45% mature forest and extensive conifer plantations and selection cuts, and the Ovenbird in both the intensively-harvested landscape and a moderately-harvested landscape (70% mature forest; small plantations and selection cuts). In Alberta, we measured the permeability of three forest landscape types to Ovenbird movements.

The Pileated Woodpecker was slightly more frequent in the intensively-harvested landscape than in the moderately-harvested landscape, and it did not appear to avoid young or open stands in the former landscape. However, recent foraging excavations were significantly less frequent at intensively-harvested sites than at more moderately harvested sites, suggesting that harvesting reduces the availability of suitable foraging substrates for Pileated Woodpeckers. Also, detailed demographic information would be necessary to determine whether this species can maintain viable populations in intensively-harvested landscapes.

The Ovenbird was less frequent and abundant in the intensively-harvested landscape than in the moderately-harvested landscape, and that it showed a strong preference for mature stands in both landscapes. Reproductive success was significantly lower in selection cuts than in closed-canopy mature stands, and overall productivity per unit area was very low in the former. In

northern Alberta, a moderately harvested landscape (mean: 66% mature forest) was as permeable to Ovenbird movements as a control (naturally patchy) landscape. However, an agricultural landscape (mean: 31% mature forest) was significantly less permeable than the control.

Based on the results outlined in this report, a number of precautionary measures should be taken to ensure that forest birds dependent on mature, closed-canopy forests can persist in managed forest landscapes:

(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 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 should help maintain populations of Ovenbird, Pileated Woodpecker, and ecologically-similar species, assuming forest management units are relatively small. Alternatively, the distance between cutting strips or the time between harvest entries should be increased. Finally, (4) selection cutting should allow for the protection of some large-diameter trees to maintain suitable foraging substrates for Pileated Woodpeckers, in addition to suitable nesting and roosting substrates.

ACKNOWLEDGMENTS

This research project was made possible by the financial support of the Sustainable Forest management Network (SFMN), and by a research grants from the New Brunswick Wildlife Council. I sincerely thank my graduate students, Julie Bourque, Jean-François Gobeil, and Vincent Carignan, as well as our numerous field assistants. Special thanks to Serge Rhéaume, for his ornithological expertise, and to our field assistants Greg Campbell, Shawn Dubé, Todd Hunter, Dominique Lavoie, Hans Lefebvre, Julie Marcoux, Mitchell Meredith. 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., and to Stan Boutin and Daryll Hebert of Alberta-Pacific Forest Industries for their logistical and financial support of the subprojects presented in this report. I had stimulating discussions with Susan Hannon, Pierre Drapeau, Marcel Darveau, and other members of the Landscape Structure and Biodiversity Group on the work reported here. Julie Bourque was supported by a NSERC postgraduate scholarship. Jean-François Gobeil was supported by a NSERC-Industry postgraduate scholarship with Alberta-Pacific Forest Industries. Finally, John Gunn was supported 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 (DNRE 1995), 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 relatively 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 (Villard et al. 1995; Bourque and Villard 2000; Drapeau et al., in press), and (3) their reproductive success can be estimated relatively efficiently (Gibbs and Faaborg 1990; Gunn et al. 2000).

Measuring and monitoring the effects of forestry on biodiversity is a major challenge when considering the complexity of forest ecosystems. Even when one focuses on a particular taxon such as forest birds, the diversity of life histories makes it very difficult to rapidly draw management guidelines that will apply to all species or ecological categories. A more sensible approach may be to determine the foreseeable effects of harvesting practices on forest landscapes and to select species associated with stand or landscape characteristics that are at risk of disappearing over the medium or long-term. In New Brunswick, current and projected timber harvesting practices will severely alter landscape structure. Extensive spruce plantations are replacing softwood and mixedwood stands while large-scale selection cutting with short return intervals (20-25 yrs) in hardwood stands severely alters their structure. Under this type of management, mature, closed-canopy stands will become rare and sparsely distributed.

In this project, my students and I measured the effects of forest harvesting at the local and landscape scales on the presence, abundance, and reproduction of two bird species considered as indicators of mature forest, and closed-canopy forest, respectively. The Pileated Woodpecker (*Dryocopus pileatus*) uses large-diameter trees and snags for nesting, roosting and foraging (Bull and Jackson 1995). This species would thus be expected to depend on the protection of sizeable older stands, or at least on the maintenance of large-diameter trees and snags in managed forest landscapes. The Ovenbird (*Seiurus aurocapillus*), a wood-warbler, nests and forages in the leaf litter typically found under a closed canopy of trees or, sometimes, under a dense layer of high shrubs (Van Horn and Donovan 1994; E. Bayne and K. Hobson, University of Saskatchewan, Saskatoon, Saskatchewan, pers. comm.). We addressed four specific questions: (1) do Pileated Woodpeckers and Ovenbirds persist in intensively-managed landscapes? (2) does the intensity of forest harvesting influence Pileated Woodpecker foraging in summer or in winter? (3) does the

Ovenbird persist in selection cuts within hardwood stands and if so, does it reproduce successfully? (4) does forest harvesting reduce the permeability of the landscape to Ovenbird movements?

METHODOLOGY

Study Areas

New Brunswick

This study was conducted in northwestern New Brunswick, approximately 25 km 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. It 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 were clearcutting in mixed or coniferous stands, partial (selection) cutting in hardwood stands, and plantation of conifers in clearcut areas where natural regeneration was deemed insufficient, (Gilles Couturier and John Jenkins, Fraser Papers Inc., Plaster Rock, New Brunswick, pers. comm.). Herbicides are sprayed on recent plantations to favour young conifers.

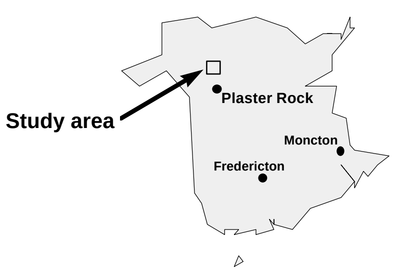

Figure 1: New Brunswick study area

Figure 2: Alberta study areas

To assess the effects of forest harvesting, we selected two extremes along a gradient of harvesting intensity typical of the region. These extremes will hereafter be referred to as the moderately-harvested landscape and the 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 substantially 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) (see Villard 1999, 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 reproductive success of the Ovenbird in two to three 25-ha plots (micro grids): one or two in recent (<5 years) selection cuts and another in a stand left uncut for at least 30 years (Fig. 4).

Alberta

The Alberta study area is located in the boreal mixedwood forest (Fig. 2). It comprises three forest landscapes: one fragmented by agriculture (Meanook region, 54°35'N, 113°20'W), another altered by forestry (Calling Lake region, 55°15'N, 113°20'W), and a naturally-patchy landscape (Owl River region, 54°54'N, 111°53'W). Although we tried to reduce the variation in the proportion of mature woodland, this characteristic did vary substantially among landscape types. The proportion of mature woodland in the agricultural landscape was 30.6±0.5% (mean ± standard error), compared to 66.2±0.4% in the harvested landscape, and 90.3±0.8% in the naturally-patchy landscape (control).

Field Data Collection

New Brunswick

We surveyed birds and vegetation at all 367 points (stations) during the study. In addition, we collected data on bird reproductive success in two (1997) to five (1999) intensive study plots (25 ha) (Fig. 3).

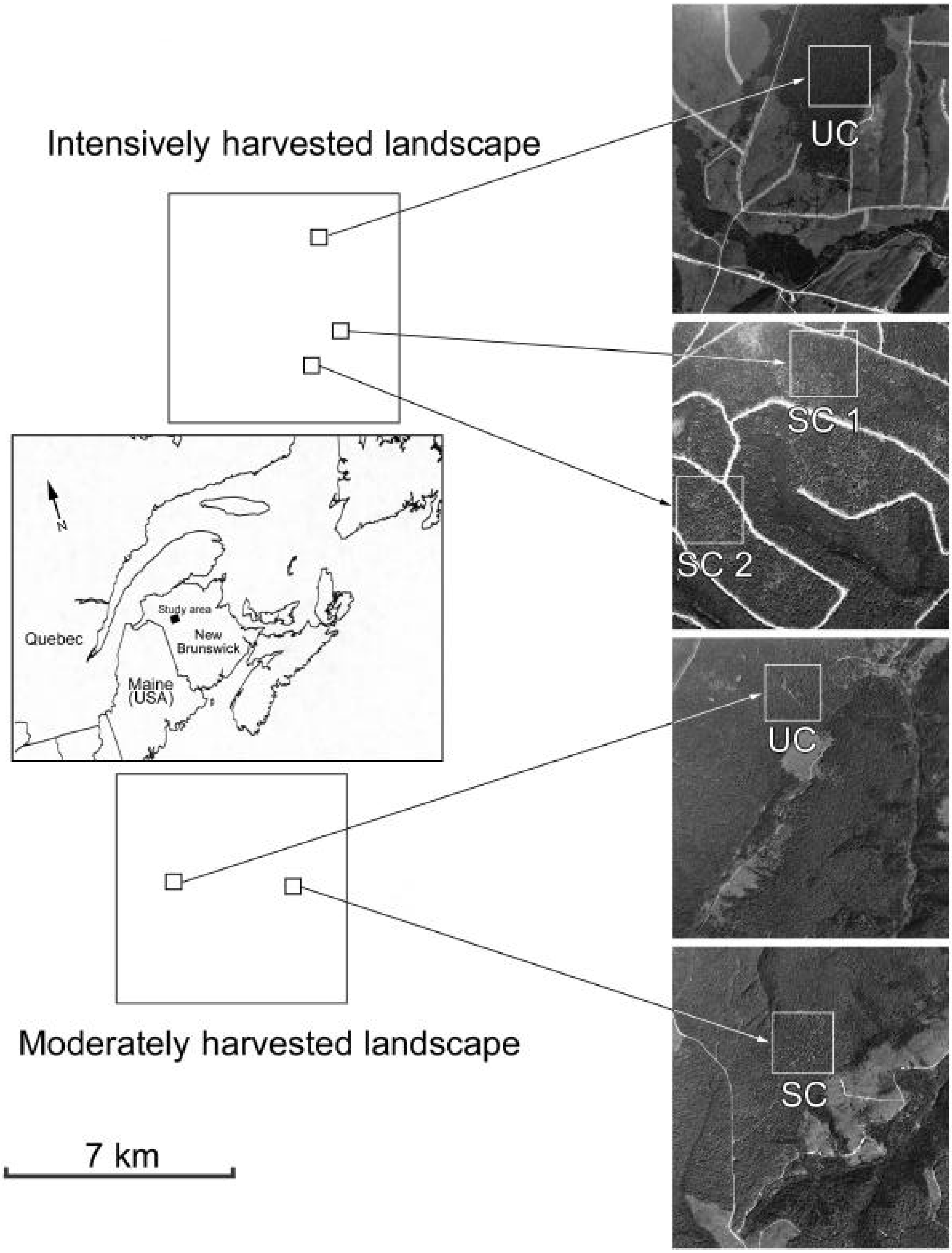

Figure 3: Study plots in uncut (UC) stands and selection cuts (SC) where we mapped Ovenbird territories and measured reproductive success (modified from Bourque and Villard 2000).

Point counts were conducted at every station from May to July each year. 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. In addition, we surveyed Pileated Woodpeckers four times at each macro-grid point in the intensively-harvested landscape. These surveys were conducted between the last week of May and the first week of July 1999 using playbacks of calls and drummings. Research on Ovenbird reproductive success was conducted from 1997 to 1999 in both landscapes. We monitored all territories detected from our spot maps (Bibby et al. 1992) and searched for nests or evidence of success (fledged young) (Bourque and Villard 2000). 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 an 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. 2000).

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 data on all substrates excavated by Pileated Woodpeckers within 100 m of the 64 macro points surveyed in the intensively-harvested landscape. At each point, we walked 100-m transects in each cardinal direction and recorded the following characteristics for each excavated substrate: type and height of substrate, tree species and diameter at breast height or width (for logs), degree of decomposition, number, and relative age of cavities (from presence or absence of wood chips).

Alberta

In each landscape, male Ovenbirds were captured on territory, banded using a unique combination of plastic colour bans, and translocated 1.5-2.7 km (mean: 2.0 km) away within a sound-proof box, and released in similar habitat. We determined the proportion of successfully returning males and their return speed by monitoring the territories of translocated males every 24 hours for the first 48 hours following the translocation (Gobeil and Villard, in prep.). This work was conducted in 1998 and 1999.

Data Analysis

New Brunswick

We compiled point count data to obtain the frequency of occurrence of each species in each landscape and its average abundance per station. Since stations sampled a variety of habitats, we classified stations according to their dominant vegetation, as determined from our habitat sampling. For the Pileated Woodpecker, we considered a station to be occupied if an individual was detected at least once within approximately 500 m of the observer. We realize that this survey may include areas used by transient individuals (e.g. juveniles not settled on a territory).

We determined the effects of stand level and landscape-scale harvesting intensity on Ovenbird reproduction by comparing their fledging success per territory and the overall productivity of each plot. We used a loglinear model to determine the effects of local harvest treatment (selection cutting vs. none) and landscape-scale harvesting intensity (intensive vs. moderate) on fledging success per territory.

Alberta

For each translocated male, we mapped the location of capture and release and calculated an ellipse using these two points as foci. We then characterized landscape structure (percentage of mature woodland and woodland configuration metrics) in rectangles drawn to encompass each ellipse using digitized aerial photographs and Alberta-Pacific's and inventories. Calculations were performed using ArcView GIS and FRAGSTATS.

The variables influencing the ability of Ovenbirds to return to their territory were examined using logistic regression models. We initially built univariate models with the following independent variables: percent forest cover, translocation distance, density of forest edges, the number of forest fragments, mean nearest neighbour distance among fragments, as well as the translocation scenario (for individuals translocated to and from similar areas). Based on variables with significant effects on the probability of return, we built multivariate models comparing translocations performed in each fragmented landscape (agricultural or harvested) to the naturally-patchy landscape. The probability of return was determined based on the status of translocated birds after 24 hours (i.e. whether they had returned or not). We also used survival analysis (Cox regression models) to determine the influence of landscape characteristics on the speed of return of Ovenbirds in the 48 hours following their translocation.

RESULTS

Distribution and Abundance

Pileated Woodpecker

Based on the point count surveys, the Pileated Woodpecker was slightly more frequent in the intensively-harvested (IH) landscape (14.1% of stations) than in the moderately-harvested (MH) landscape (9.4%). However, the difference was not statistically significant (G-test, P=0.43). In the summer of 1999, we detected the presence of this species at 28.1% of the same macro-grid points in the intensively-harvested landscape. This time, we used playbacks of calls and drummings. However, we did not survey the moderately-harvested landscape.

Pileated Woodpeckers responded negatively to local-scale harvesting intensity. We classified macro-grid points according to harvesting intensity within a 100-m radius using the data we obtained from our 1997 habitat survey. In the spring of 2000, recent signs of foraging (i.e. foraging substrates with wood chips) were significantly less frequent within 100 m of stations where harvesting intensity was classified as very intensive or intensive than where harvesting was moderate or absent.

Within the intensively-harvested landscape, Pileated Woodpeckers foraged on a wide variety of substrates, but mainly on snags or logs, and only occasionally on stumps. Diameter at breast height (or width of logs) ranged from 11,5 to 77,2 cm (mode: 20-30 cm). Seventy nine percent (79%) of the 186 substrates could be identified to genus or species. Of these, 50% were Balsam Firs, Sugar Maples and spruces. However, they tended to use deciduous species, especially Sugar Maple, more frequently than expected from their availability, whereas conifer (except Eastern Cedar) were used less frequently than expected (Fig. 4).

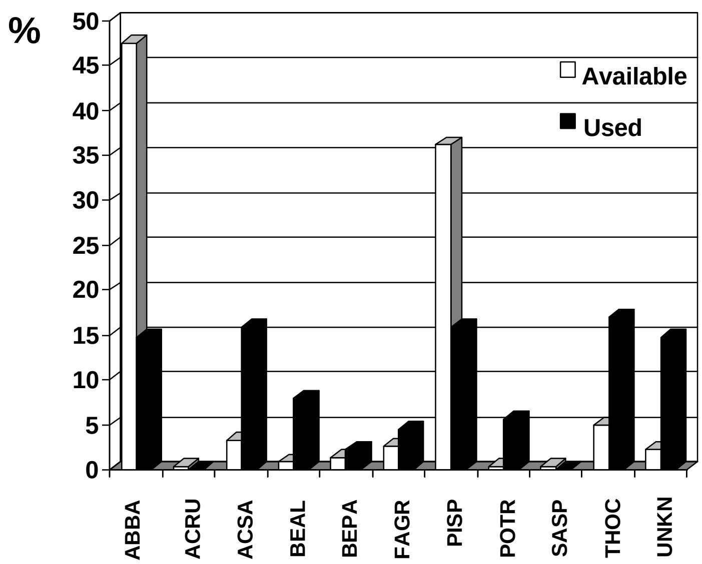

Figure 4: Relative availability of snags (and live firs and spruces) and their use for foraging by Pileated Woodpeckers in winter and spring. See Appendix 1 for the meaning of species codes.

Ovenbird

As expected, this species was more frequent in the moderately-harvested landscape (74.2%) than in the intensively-harvested landscape (56.8%). It was also more abundant in the moderately-harvested landscape (1.49 vs. 1.08 individuals/station). This largely reflects the greater proportion of stations in mature forest (canopy height >12 m, >40% canopy closure) in the moderately-harvested landscape (57.1% vs. 39.7%; G-test, P=0.0008). However, it should be noted that in both landscapes, roughly 30% of Ovenbird detections were made in young (canopy height: 4-12 m) or open (30-40% canopy closure) stands.

Reproductive Success

Pileated Woodpecker

Although we did not search specifically for Pileated Woodpecker nests, we recorded the fate of three nesting attempts in the intensively-harvested landscape between 1997 and 1999. Interestingly, two of these nesting attempts were made in different cavities within the same tree within an uncut hardwood stand. The other nest was found at the edge of a selection cut. Of the three nesting attempts we monitored, only one was apparently successful (presence of large nestlings in the cavity) - in the uncut stand. Both nest trees found were excavated in live but declining American Beech (*Fagus grandifolia*).

Ovenbird

From 1997 to 1999, we found 52 Ovenbird nests and we monitored a total of 132 territories (Bourque and Villard 2000). Nest predation was the main cause of nest failure during this period (Bourque 1999). According to tooth marks left on plasticine eggs in artificial nests, mammals were responsible for 80 to 84% of cases of predation in 1998 and 1999. The main mammalian nest predators were murid rodents (mice and voles), Black Bear (*Ursus americanus*), Eastern Chipmunk (*Tamias striatus*), and Red Squirrel (*Tamiasciurus hudsonicus*) (Carignan and Villard, submitted).

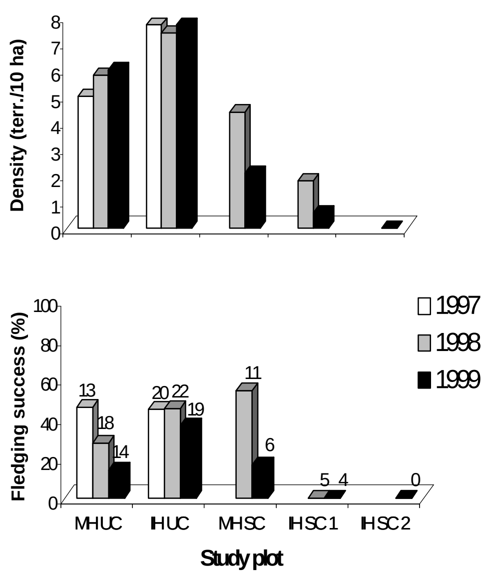

Figure 5: Ovenbird density and fledging success per territory in 25-ha study plots within the intensively-harvested (IH) and moderately-harvested (MH) landscapes shown on Fig. 3.

When pooling data from all three years, neither daily nest mortality nor fledging success per territory differed significantly between the intensively-harvested and moderately-harvested landscapes (fledging success: IH: 37.1%, n=70; MH=32.3%, n=62; G-test, P=0.56). However, there was a clear effect of stand-level treatment. With the exception of one plot and year, Ovenbird density was extremely low in selection cuts and so were pairing and fledging success (Fig. 5). A loglinear model indicated a significant effect of local treatment (selection cut vs. uncut) but no effect of landscape type. When pooling all territories monitored in 1998 and 1999 in selection cuts and uncut plots, only 23% of the estimated number of Ovenbirds fledged during this period were born in selection cuts (see Bourque and Villard 2000 for details).

Landscape permeability to movements

A total of 84 Ovenbirds were translocated in 1998 and 1999 (Gobeil and Villard, in prep.). Landscape permeability to Ovenbird movements was significantly related to the proportion of mature woodland, which in turn varied among forest landscape types. In the control landscape, 80.0% of translocated males had returned to their territory within 48 hours, compared to 62.1% in the harvested landscape and 53.3% in the agricultural landscape. However, when comparing the probability of return between each fragmented landscape and the control, neither the effect of landscape type nor the proportion of mature woodland was not significant for the harvested landscape vs. control comparison, whereas its effect was significant for the agricultural landscape vs. control comparison. Results from the survival analysis were identical: the speed of return was significantly lower in the agricultural landscape than in the control, whereas this was not the case for the harvested landscape. These results strongly suggest that the permeability of forest landscapes fragmented by agriculture to Ovenbird movements (1) is lower than that of harvested landscapes and naturally-patchy landscapes and that (2) this result either reflects the lower proportion of mature woodland in the agricultural landscape (i.e., below a species-specific threshold), or an intrinsic characteristic of agricultural landscapes making them less permeable to Ovenbird movements.

SUMMARY

Not surprisingly, our point count data indicate that the intensively-harvested landscape supports lower populations of our indicator of mature, closed-canopy forest, the Ovenbird. However, the reproductive success of this species did not vary significantly with harvesting intensity at the landscape scale. At the local scale, Ovenbirds maintained substantially lower densities in selection cuts than in uncut plots and their reproductive success was significantly lower in the former.

Pileated Woodpeckers were as frequent in both landscapes, suggesting that this large bird can make up for the loss of mature stands if enough large trees or snags are left in cutblocks and residual stands. However, our sample size of nests was insufficient to assess the probability of

persistence of this woodpecker species in intensively-harvested landscapes. Furthermore, the apparent rarity of suitable foraging substrates at intensively-harvested sites indicates that this species may not be tolerant to harvesting, but simply more conspicuous in intensively-harvested landscapes.

Based on our results from Ovenbird translocations, moderate forest harvesting (i.e. leaving ca. 65% of mature forest) does not appear to significantly reduce the permeability of the landscape for mature forest specialists such as the Ovenbird.

Our results indicate that both of our indicator species can tolerate the intensive silviculture currently practiced in New Brunswick, providing that their nesting and foraging requirements are met. However, we could not determine whether Pileated Woodpecker populations could reproduce successfully in such landscapes. Further research will be necessary to determine the degree of silvicultural intensity beyond which these species are no longer able to maintain viable populations.

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 (DNRE 1995). Meanwhile, shade-tolerant hardwoods are quickly turned into extensive selection cuts, patch cuts, or so-called “partial cuts”. On Fraser Papers’ forest lands, partial cuts remove 30% of the basal area approximately every 20 years (Fraser Papers Inc. 1995). These selection cuts are performed using feller-bunchers, which create strips 18-22 m apart. Our results indicate that the latter silvicultural treatment reduces the density and reproductive success of the Ovenbird. 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.

Although this study does not provide definitive answers, our results suggest a number of precautionary measures that should 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. The long-term availability of such blocks will require a reduction in the areas planted with conifers, so that natural regeneration is allowed to take place.

2. Selection cutting practices should be altered to ensure the persistence of species requiring open understory conditions, such as the Ovenbird. Maintaining uncut blocks (see number 1), extending intervals between harvests, and cutting more widely-spaced strips should reduce the observed negative impacts.

3. Selection cutting should allow for the protection of large-diameter trees at all times, so that the life-history requirements of species such as the Pileated Woodpecker are met. Some of the large trees protected should represent suitable foraging substrates (e.g. Sugar Maple).

4. Maintaining a minimum of ca. 60% of mature forest in forest management units should ensure efficient movements by forest birds and, thus, the continuous occupation of suitable habitat.

REFERENCES

Bibby, C.J., Burgess, N.D., and Hill, D.A. 1992. Bird census techniques. Academic Press, San Diego, USA.

Bourque, J. 1999. Coupe progressive et exploitation forestière à l'échelle du paysage: influence relative sur la productivité de deux passereaux forstiers. M.Sc. thesis, Département de biologie, Université de Moncton, Moncton, New Brunswick.

Bourque, J., and Villard, M.-A. 2000. Relative effect of stand and landscape-level harvesting on the reproductive success of two Neotropical migrant bird species in northwestern New Brunswick. Conservation Biology 14: in press (accepted 30 March 2000).

Bull, E.L., and Jackson, J.A. 1995. Pileated Woodpecker, *Dryocopus pileatus*. In Birds of North America No.148. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, D.C., USA.

DNRE. 1995. Management of forest habitat in New Brunswick. Forest Habitat Program, Fish and Wildlife Branch, Department of Natural Resources and Energy, Fredericton, NB.

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. Ecological Monographs.

Fraser Papers Inc. 1995. New Brunswick Timberlands, 1995-1999 Forest Resources Management Plan. Edmundston, AB. Pp. 31-33.

Gunn, J.S., Desrochers, A., Villard, M.-A., Bourque, J., and Ibarzabal, J. 2000. Playback of Black-capped Chickadee mobbing calls as a method to estimate reproductive success of forest birds. J. of Field Ornithol. 71: in press (accepted 21 June 1999).

Holling, C.S. 1988. Temperate forest insect outbreaks, tropical deforestation, and migratory birds. Mem. Ent. Soc. Can. 146: 21-32.

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).

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. In Ecology and Conservation of Neotropical Migrant Landbirds. Edited by J.M. Hagan III and D.W. Johnston. Smithsonian Institution Press, Washington, DC. Pp. 431-442.

Van Horn, M.A., and Donovan, T.M. 1994. Ovenbird (*Seiurus aurocapillus*). In 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, D.C., USA.

Villard, M.-A. 1999. Effects of landscape structure on distribution, abundance, and reproduction of forest songbirds. Project Report 1999-21. Sustainable Forest Management Network. Edmonton, Alberta.

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 1: Meaning of tree species codes used in Figure 4.

ABBA	*Abies balsamea*	Balsam Fir
ACRU	*Acer rubrum*	Red Maple
ACSA	*Acer saccharum*	Sugar Maple
BEAL	*Betula alleghaniensis*	Yellow Birch
BEPA	*Betula papyrifera*	Paper Birch
FAGR	*Fagus grandifolia*	American Beech
PISP	*Picea* sp.	Spruce (red, white or black)
POTR	*Populus tremuloides*	Trembling Aspen
SASP	*Salix* sp.	Unknown willow species
THOC	*Thuja occidentalis*	Eastern White Cedar
UNKN		Unknown species