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An Ecosystem Approach to Assessing the Effects of Forest Heterogeneity and Disturbance on Birds of the Northern Hardwood Forest in Michigan's Upper Peninsula.

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has been accepted towards fulfillment of the requirements for

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Major professor

Date 3/10/00

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AN ECOSYSTEM APPROACH TO ASSESSING THE EFFECTS OF FOREST HETEROGENEITY AND DISTURBANCE ON BIRDS OF THE NORTHERN HARDWOOD FOREST IN MICHIGAN'S UPPER PENINSULA

By

Maya A. Hamady

A DISSERTATION

Submitted to
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2000

ABSTRACT

AN ECOSYSTEM APPROACH TO ASSESSING THE EFFECTS OF FOREST HETEROGENEITY AND DISTURBANCE ON BIRDS OF THE NORTHERN HARDWOOD FOREST IN MICHIGAN'S UPPER PENINSULA

By

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Forested regions such as the Upper Peninsula of Michigan, are considered population sources for area sensitive forest birds which have disappeared from many human-dominated landscapes because of forest loss and fragmentation. Northern hardwood forest landscapes in the Upper Peninsula have been affected by past human activities and continue to be periodically logged. The possibility that anthropogenic activities would over time favor bird species that are tolerant of some levels of forest fragmentation, at the expense of area sensitive species, needs to be evaluated. I developed an ecosystem model for northern hardwood forest landscapes and explored relationships among bird species, and among bird densities, microhabitat variables and landscape level variables to identify criteria necessary to make such an evaluation.

I modeled heterogeneity of the northern hardwood forest at the landscape level in terms of historical change in land use and land type association. I considered period elapsed after last logging to affect vegetation structure at the locality of the bird census station. Habitat relationships among 10 bird species were derived from individual bird species associations with microhabitat variables. A forest fragmentation dimension was evident in habitat relationships among 3 shrub nesting bird species, black-throated blue warbler (*Dendroica cerulescens*), American redstart (*Setophaga ruticilla*) and chestnut-

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sided warbler (*Dendroica pensylvanica*). Forest fragmentation aspects however could not explain density disparities between the 2 conifer associated bird species, blackburnian warbler (*Dendroica fusca*) and black-throated green warbler (*Dendroica virens*). Historical change in land use affected the density of late maturity conifers and forest loss at landscape levels. Logging affected canopy cover and shrub layer development, effects that were local and highly dynamic. Logging was responsible for increased densities of all birds that nest in the shrub-sapling layer in managed forest landscapes but was also associated in some landscapes with a relative greater increase of edge tolerant bird species. Restratification of sampling units based on levels of forest cover within a radius of 1.6 km, length of forest edge within a radius of 500m from bird census station, shrub layer development and canopy opening elucidated what constitutes forest fragmentation effects in the northern hardwood ecosystem. This restratification permitted the quantification of conditions that were differently favorable to 2 edge species and one area sensitive species. The northern hardwood forest is a complex system that is both spatially heterogeneous and dynamic at different scales. Multiple factors modify or aggravate the effects of human activities on bird species that in turn respond differently to different dynamics in the system. Simple assessments of the effects of anthropogenic activities on bird species are inadequate for evaluating the long term maintenance of area sensitive species in the system. The inadequacies of treating the northern hardwood forest as a homogeneous system at equilibrium, and of disregarding differences among forest bird species, relative to their differential sensitivity to forest fragmentation, in current assessments of human activity effects are discussed.

ACKNOWLEDGMENTS

From its inception this research was bent on a tortuous path. I am indebted to my advisor Dr. Scott Winterstein for his efforts in resolving many crises along the way. Special thanks go to all my other graduate committee members, Drs. Henry Campa Stephen Stephenson, John Hart and Jonathan Haufler for their individual contributions to this research effort. I was inspired to present this work within an ecosystem context by my earlier exposure to landscape ecology perspectives that were being progressively promoted on the Hiawatha National Forest, and by opportunities to learn about the latest modeling and ecosystem theories presented in course work and by guest lecturers in Dr. Jianguo Liu's class 'Computer Simulation and Modeling'. This study was greatly facilitated by ecological classifications of land units undertaken by Dr. E. Padley on the West Unit of the Hiawatha and by J. Jordan on the Ottawa National Forest.

Funding and logistic support was provided by the Hiawatha National Forest through the Neotropical Migrant Bird funding initiative. Funding was also received from North Central Forest Experiment Station. In kind matching grants were received from Michigan State University. A College of Natural Resources grant of 5,000 $ was used to defray some additional costs. Logistic support and information were provided by many individuals on the Hiawatha National Forest, Ottawa Forest and Huron Mountain Club.

It was possible to collect extensive field data that were necessary for this research because of the dedication and enthusiasm of many field assistants: Mike Berg, Amy

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Proehl, Paul Thompson, Mark Parkinson, Jason Hoeksema, Mike Livingston, Kim Smith, Tony Duffiny, Mark Ledhebur, Christine Hill, Sue Tangora, Laurie Necaise, Julie Car, Tim Nuttle, Brad Kassuba and Robyn Oliver. Field work alongside this crew of young biologists was enjoyable and motivating. I am especially indebted to Amy Proehl, Paul Thompson, Mike Berg and Mike Livingston for preparatory work prior to field excursions and for training and supervision of field crews.

Many individuals on the Hiawatha National Forest and individuals on the Ottawa National Forest provided the necessary digital data, maps and aerial photos from which GIS coverage could be derived. Rich Minnis prepared some GIS coverage for this project. I am grateful to Andrea Schmidt, Abdoul Hayee, Jim Schopper and Beth Ursel for undertaking the tedious task of reviewing and correcting GIS maps. Lauri Keen's tedious tasks of initial manuscripting of aerial photos and later of cleaning GIS maps proved critical to the completion of this project.

This study would not have been undertaken if it wasn't for the support I received at a critical initial stage from Stan Benes my then supervisor on the Hiawatha National Forest. Stan's vision and maverick attitude towards embarking on difficult tasks to foster better understanding of the effects of forest management were crucial to study support and initiation. The support I received from colleagues on the biology staff, Kevin Doran, Steve Sjogren and Lawson Gerdes was uplifting and encouraging. Returning to graduate school after being employed for over a decade was excruciating. It was good to have a trusted friend like Tim Van Deelen whose own familiarity and experience with the administration of the Hiawatha National Forest and the Department of Fisheries and Wildlife eased my transition from work to graduate school.

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CHAPTER I

INTRODUCTION

ISSUES IN THE CONSERVATION OF FOREST BIRD SPECIES

1. A Need for a Holistic Approach.

As the number of imperiled species continues to spiral upward (LoveJoy 1979; Wilson 1988,1992; Collar and Andrew 1988 cited in Marcot and Murphy 1996, Ehrlich and Erlich 1981, Ehrlich and Wilson 1991, Soulé 1991, Gentry 1996), skepticism is growing about the effectiveness of managing biological diversity on a species by species basis (Hutto et al. 1987, Franklin 1993, Laroe 1993). The futility of saving species after the processes that sustain them have disintegrated also points to the need for more efficient conservation strategies. New efforts in species conservation consider structures, processes and functions existing in the natural world to be fundamental to the persistence of species diversity and to its evolution (Allen and Starr 1982; Mooney and Godron 1983; Delcourt et al. 1983; Wiens et al. 1986a, 1986b; Grumbine 1990,1994; Wilson 1992; Scott et al. 1993; Franklin 1993). In the holistic and ecosystem approaches that are being proposed (Risser 1985, Agee and Johnson 1988, Grumbine 1990, Pickett et al. 1992, Franklin 1993, Laroe 1993, Crow et al. 1994), there is strong recognition that individual species cannot be separated from their system, because complex relationships link species together and because species respond to the dynamics of the systems that encompass them. In a holistic approach, the appropriate questions that need to be

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that need to be asked and the phenomena that need to be explained for the conservation of species are relative to the behavior of the whole system (Allen and Star 1982, Naveh and Lieberman 1994).

The concept of an ecosystem as a combination of the whole organism-complex and the whole physical-complex forming the environment was first described by Tansley (1935). Tansley considered natural systems to be organized in a hierarchy; smaller ecosystems embedded in larger ones, overlapping and interacting with one another. A holistic approach likewise views the ecosystem as progressively subdividable into smaller units. Interacting units at fine temporal and spatial scales produce patterns that are recognizable at higher levels. Patterns and processes at higher levels in turn affect all lower units.

The conservation of species through ecosystem approaches is becoming feasible because recent advances in landscape ecology have provided a basis for establishing relationships between the ecology of organisms and patterns of patchiness in environmental conditions (Freemark et al.1992). Landscape ecology as a discipline has emerged from 2 different perspectives. One aspect of the discipline has focused on the study of land heterogeneity and the underlying structures and dynamics that cause it (Weinstein and Shugart 1983, Milne 1991). This facet of landscape ecology is based on the physical factors (e.g.climate, geomorphology) that operate at different scales. Vegetation patterns that develop under natural disturbance processes reflect the patterns of these hierarchical physical factors. This aspect of landscape ecology has provided the basis for ecological land classification schemes (Barnes et al. 1982). An ecological land classification stratifies a geographical area into a hierarchy of land units that comprises the spatial scal

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the spatial scales at which major environmental physical factors affect patterns of patchiness in vegetation (Bailey et al. 1978, Bailey 1985, Pregitzer 1981, Barnes et al. 1982).

Another more recent aspect of landscape ecology, which is still emerging, seeks to relate population dynamics (e.g. productivity and dispersal) to spatial patterns of land heterogeneity (Forman and Godron 1986, Dunning et al. 1992). The theoretical basis for ecological relationships between the biology of organisms and landscape patterns can have an evolutionary aspect (Wiens 1976, Riddle and Jones 1996). Life history characteristics of species such as habitat selection, generation time, life span and ability to disperse are adaptations to predictable disturbance events that generate patchiness in time and space (Wiens 1976, Hansen and Urban 1992, Samson 1992). Because they are likely to reflect evolutionary adaptations, relationships between population processes and spatial patterns of patchiness are a potential basis for species conservation (Pickett et al. 1992, Harper 1992).

2. Neotropical Birds in the Northern Hardwood Forest.

Multi-scale patchiness of the vegetation is highly evident in the Upper Great Lakes Region. The transition between the boreal forest to the north and the deciduous forest biome to the south creates a pattern of large scale patchiness that is associated with high bird species richness (Temple et al. 1979, Pastor and Brochart 1990). The northern hardwood forest is a major component of the vegetation cover. Within it, a finer scale of patchiness is evident as a mosaic of many different tree species and heterogeneous vegetation structure. This in turn is associated with 'a within forest type' high diversity in bird species (Noon et al. 1979). The large scale patchiness is a long-lasting effect of landforms left behind from retreating glacials some 10,000 years ago. The fine scale patches within the long lived northern hardwood forest, in contrast are due to small scale forest disturbances such as blow downs from severe storms (Frelich and Lorimer 1991). Small scale patches also result from small scale variations is soils, local topography and aspect that provide a diversity of local microsites for different plant species to grow. Because processes of forest maturation and of frequent small scale disturbance are continuous, the state of forest maturity in small scale patches is continually shifting. Bird species must also continually track microhabitats created by these small scale disturbances.

A large portion of the Great Lakes forest is second growth forest that was heavily cut at the end of the 19th and early 20th centuries (Cunningham and White 1941, Ahlgren and Ahlgren 1983). This second growth forest is largely managed for multiple use and is subjected to logging. The Upper Great Lakes forest however still comprises in several locations primary forest that is continuous over several square kilometers. Such a forest provides the opportunity to assess how multi-scaled forest patchiness resulting from differences in environmental conditions and from forest management induced disturbances affect the relative densities of bird species within the northern hardwood forest ecosystem.

The majority, over 75% of songbird species at the latitude of the Great Lakes region are neotropical migrant birds (Degraaf et al. 1992). Neotropical migrant bird species winter in the tropics and subtropics but migrate to breed in North America (Koford et al. 1994). They make up a large proportion of the vertebrate biodiversity in many North

American ecosystems (Finch 1991; Freemark et al. 1992, 1995; Block et al. 1995). A concern for these species in recent years stemmed from reports of declining populations and species loss evident in some human dominated landscapes (Robbins et al. 1989a; Askins et al. 1990). For many bird species, trends of declines and increases are not consistent but vary by geographical region and by time period (Peterjohn et al. 1995). Because of this variability, trends from specific localities cannot be extrapolated to the general (James and McCulloch 1995). Reports of declines of some bird species (Holmes and Sherry 1985, Robbins et al. 1989a, Askins et al. 1990, Hill and Hagen 1991, Terborgh 1989, 1992) have nevertheless triggered a great concern for their welfare. There is a general consensus that management of these species would be extremely complex and the ecological consequences severe, if these observed declines were long term and occurred over broad areas of species distributions' (Senner 1988, Finch 1991, National Fish and Wildlife Foundation 1994).

Limiting factors that have been outlined for neotropical migrant birds include tropical deforestation, deterioration of habitat along migratory routes due to rapid urban encroachment along coastlines, and habitat fragmentation. For the eastern deciduous forest biome, declines in some bird species were blamed on forest fragmentation. Forest fragmentation was represented by a pattern of forest patches imbedded in a nonforest matrix in early studies that have identified it to have a detrimental effect on forest interior bird species (Whitcomb B.F. et al. 1977, Whitcomb R.F. et al. 1981, Wilcove and Whitcomb 1983). Forest interior birds nest in the interior of forest in contrast to those that nest along an edge between openland and forest (Koford et al. 1994). Several independent arguments have been presented to support forest fragmentation as a limiting factor on the breeding grounds (Wilcove 1987,1988; Finch 1991). Among these are the high predation rates reported along forest edges (Gates and Gysel 1978; Wilcove 1985, 1987; Small and Hunter 1988; Yahner and Scott 1988) and high cowbird parasitism rates in agricultural landscapes (Ambuel and Temple 1982, 1983; Brittingham and Temple 1983). Forest interior bird species have disappeared from parks and forest reserves in many human-dominated landscapes (Lynch and Whitcomb 1978; Robbins 1979, 1989a; Wilcove and Whitcomb 1983; Ambuel and Temple 1983; Blake and Karr 1984; Askins et al. 1987; Terborgh 1989, 1992; Hill and Hagan 1991). Some forest interior bird species that require large forest areas are considered area-sensitive species (Koford et al. 1994). Area-sensitive species such as the black-throated blue warbler and Canada warbler (all scientific names are given in Table B1) have become restricted to large forest tracts in largely forested regions (Robbins et al. 1989b, Binford 1991).

The immensity of the task of conserving the diversity of neotropical migrant birds, and the huge administrative obstacles that would likely be faced, once these species started facing perils, provided the impetus for the formation of Partners in Flight (National Fish and Wildlife Foundation 1994, Martin and Finch 1995). Formed in 1990 to address the conservation needs of neotropical migrants, to educate and to coordinate conservation and research efforts, the organization has grown to include many government agencies and private organizations from the United States, Canada, Mexico and several countries in Central America. As a result of the Partners in Flight initiative, support for it from the U.S. Congress and public response to it, the conservation of these species is beginning to dominate many aspects of land management on public lands, including national parks, state parks, and federal and state forests (National Fish and Wildlife Foundation 1993).

A hierarchical organization for addressing species conservation needs has been proposed and followed by Partners in Flight. In this strategy, conservation issues and the species that need prioritization are identified at the highest geographical levels, such as at continental and national levels (Noss 1983, 1987, 1992; Probst and Crow 1991). Because forest fragmentation has been identified as an important issue in species conservation and has increased with increasing human domination of landscapes (Whitney and Somerlot 1985; Wilcove 1987, 1988; Wilcox and Murphy 1985; Faaborg et al. 1995), many conservation strategies have focused on forest interior bird species that are area-sensitive (National Fish and Wildlife Foundation 1993).

The percent of forest cover in the Upper Peninsula of Michigan and in general in the Upper Great Lakes today is not very different than it was prior to settlement by non-native Americans (McCann 1991). This is in contrast to the Lower Great Lakes area where agriculture and urbanization have resulted in forest loss and fragmentation. The highly forested northern Great Lakes region, stands out from a regional perspective to be most promising for the conservation of forest interior and area-sensitive bird species. The conservation of these species has also received public attention (Probst and Crow 1991, Crow et al.1994) in forest management of this region (Northern Wisconsin and the Upper Peninsula of Michigan).

Because of the expansive area it occupies, the northern hardwood forest is an ecologically important forest type in the Upper Peninsula of Michigan. It is an extension of the eastern deciduous forest (Braun 1950, Pastor and Mladenoff 1992). The northern hardwood fore

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highly area-hardwood forest bird communities comprise many of the same species found in the eastern deciduous forest, including many that have been identified as area-sensitive species such as the black-throated blue warbler, Canada warbler, and northern parula (Robbins et al. 1989b).

3. An Ecosystem Approach to Relate Bird Species Densities to Forest Heterogeneity.

The research reported herein, was motivated by the participation of the Hiawatha National Forest in the 'Neotropical Migrant Bird Initiative' set by Congress (1992) to advance 'neotropical migrant bird' conservation in national forests. I focused on the northern hardwood forest ecosystem as this is the forest type that harbors many bird species (e.g. ovenbird, black-throated blue warbler, northern parula and red-eyed vireo) that have been identified as forest interior and area-sensitive species (Robbins et al. 1989b). In a region that is still largely forested, the assembly of bird species that are forest interior and area-sensitive would be more complete. In such a system the different forest bird species are likely to greatly overlap in their habitat selection. If there is a gradient in the aspect of forest fragmentation, bird species that are most forest interior specialists could become affected by competitors that are less sensitive to habitat fragmentation at some point along that gradient. To prioritize the conservation of the most area-sensitive bird species at the level of a national forest, it is important to identify what factors contribute to fragmentation effects. It is important to test whether variables such as canopy opening, amount of forest edge and forest cover (i.e., variables that could be related to a forest fragmentation dimension) affect density differences between highly area-sensitive and the less area-sensitive bird species. The heterogeneity of the northern har

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northern hardwood forest would need to be assessed relative to these environmental factors that create these differences. In this undertaking two related hypotheses were made: the densities of forest bird species, and the relationship among forest interior and edge bird species differed along the range of heterogeneity encountered at the scale of a national forest.

A conceptual model was necessary to represent the hierarchy of strata into which the total heterogeneity of the northern hardwood forest would be divided. The model also serves to frame hypotheses about the importance of different factors on forest bird species in testable formats. A theoretical basis however was needed to give biological justification to the structure of the conceptual model. The ecologies of forest interior bird species are related to processes of small scale disturbance and succession in the northern hardwood forest. The pattern of small scale forest processes could be affected by many factors including geographical location and forest management. An emerging paradigm in ecology (Pickett et al. 1992) that considers disturbance to be an organizing force in natural communities was considered. This paradigm justified considering physical features of local geographic areas, past disturbance history, current land use, and disturbance caused by current management as main factors affecting variability in vegetation structure and composition and consequential bird responses. Bird densities are considered to reflect bird population responses to that heterogeneity. The conceptual model of the northern hardwood forest would serve to give a structure to that heterogeneity and to provide a vehicle to reduce that heterogeneity to spatial scales that are pertinent to the life histories of forest bird species. The model is an exploratory tool that would provide new perspectives for looking at relationships between habitat charateristics a

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charateristics and bird species densities and at habitat relationships among species. Newly uncovered relationships would in turn be used to refine a future model of the northern hardwood forest ecosystem. Such a refined model could be used to more effectively predict the effect of different management strategies in the northern hardwood forest on forest interior bird species. Justifications for variables, factors and spatial and temporal scales of sampling units incorporated in this initial model of the northern hardwood forest are discussed in the Methodology Section.

OBJECTIVES

An overall objective of this study was to test whether the northern hardwood forest varied sufficiently, along habitat variables which are related to a forest fragmentation dimension, to affect the densities of forest bird species in general, and to affect the relative densities of bird species that are known to be differently sensitive to forest fragmentation. Specific objectives of this study were to:

1) Develop a conceptual model to represent and stratify the heterogeneity of the northern hardwood forest at different spatial and temporal scales, based on past and current anthropogenic forest disturbance, and local geographical area.

2) Describe how factors incorporated in the model affect densities of 10 bird species in the northern hardwood forest. More specifically:

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i) Test the effects of historical divergence in land use, time elapsed after logging disturbance, and local geographical area on densities of 10 songbird species.

ii) Identify microhabitat elements affecting densities of 10 songbird species.

iii) Compare the availability of major microhabitat elements for each of 10 songbird species across different land use trajectories of the northern hardwood forest consisting of : primary forest, managed forest and settled forest and across time periods elapsed after logging.

iv) Compare the effects of landscape level factors (availability of habitat at the landscape level and amount of edge) to the effects of microhabitat availability on 4 forest bird species densities.

v) Test how interactions among landscape and microhabitat factors affect interspecific relationships of 3 bird species (black-throated blue warbler, American redstart, and chestnut-sided warbler) that each nest in the sapling layer but differ in their requirements of forest interior habitat.

3) Explain how forest disturbance processes, and land characteristics as might be described in an ecological land classification, can be used to integrate the conservation of forest interior bird species into forest management.

4) Evaluate the function of managed national forest relative to forest interspersed with agriculture and forest reserve areas with respect to providing habitat for a diversity of

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songbird species in general, and forest interior bird species in specific. Discuss aspects associated with forest fragmentation in the context of a largely forested region.

5) Evaluate the use of a holistic approach (e.g. multi species, hierarchy of different temporal and spatial scales, species interrelationships) to assess the effects of anthropogenic impacts on bird species.

6) Examine how a holistic approach to assessing human interference with forest processes differs from comparing bird densities before and after a specific disturbance.

STUDY AREA

1. General Description of the Upper Peninsula

Ten study sites, located in the central and western Upper Peninsula of Michigan (Figure 1), spanned an area between 42° 50' and 46°52' N latitudes and between 86° 5' and 89° 50' W longitudes. The climate in the Upper Peninsula of Michigan is dominated by the northern location of the Upper Peninsula and by the proximity to Lake Superior and Lake Michigan. It is characterized as continental humid. The Upper Peninsula is located in an active weather zone (Frelich and Lorimer 1991). Some of the most severe thunderstorms occur in the summer when polar air masses collide with sub tropical air masses. Summers are cool and short and winters are cold with average July temperatures varying from 19° C to 19.8° C and average January temperatures of -7.5°C to -10.9° C (Frelich and Lorimer 1991, Albert et al. 1986). Annual precipitation

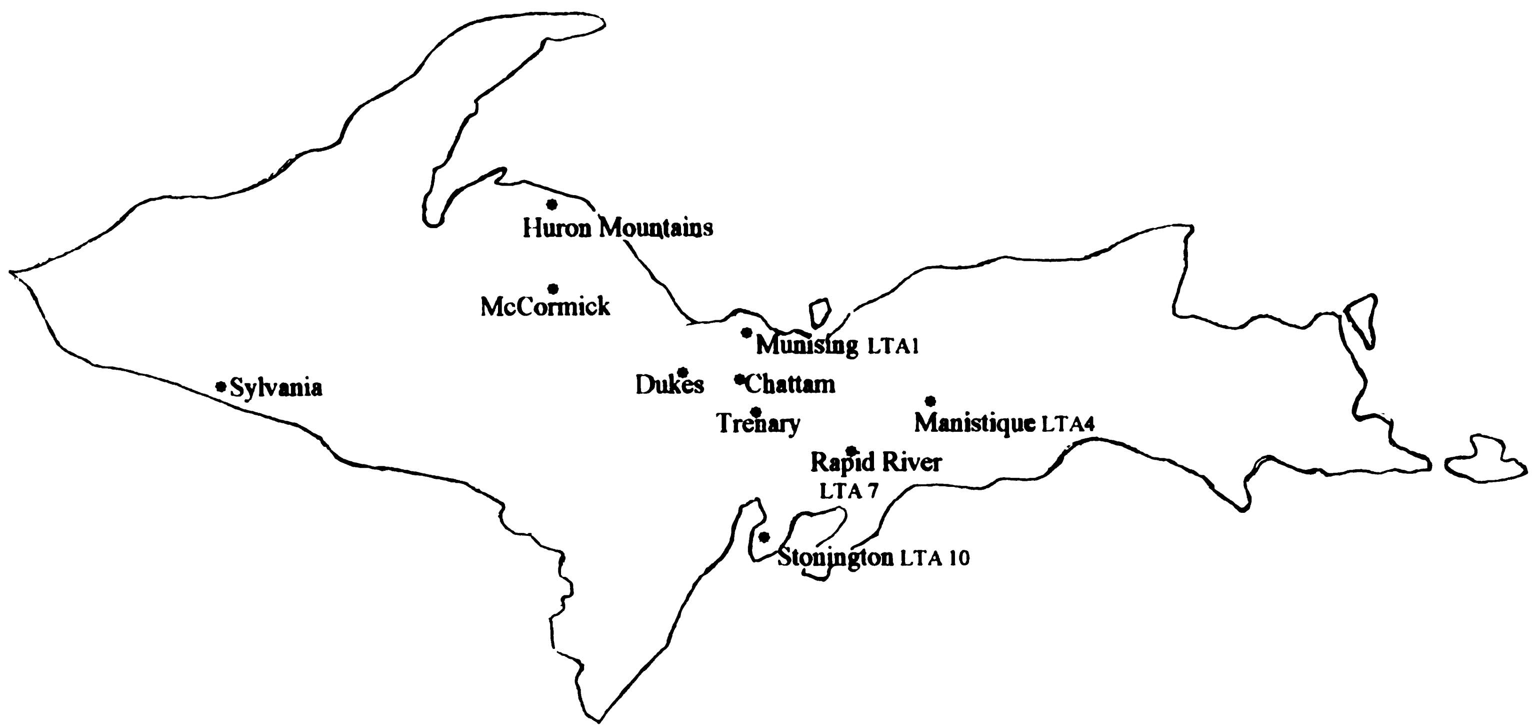

Figure 1. Location of 10 landscapes in the Upper Peninsula of Michigan in which bird censusing and vegetation sampling were conducted 1992-1994.

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averages 80-90 cm and is evenly distributed throughout the year. The entire Upper Peninsula was glaciated. Glaciers began retreating some 16,000 years ago but the Upper Peninsula did not become ice free until 10,000 years ago.

Physiography is largely determined by features left by the retreating glacials: end moraines, outwash plains, till plains, lake plains, kettle lakes, kames and eskers. Soils were formed by erosion and weathering processes acting on glacial materials. Local climate is determined by proximity to either Lake Superior or to Lake Michigan. The vegetation of the Upper Peninsula falls under the hemlock-white pine -northern hardwoods region described by Braun (1950). The Upper Peninsula occurs in a zone of transition between the boreal forest occurring to the north and the deciduous forest biome more to the south (Braun 1950, Pastor and Brochart 1990). Boreal tree species, black spruce, white spruce, balsam fir, large-toothed aspen, trembling aspen, balsam poplar, white birch and jack pine mix with eastern deciduous forest species sugar maple, beech, basswood, yellow birch, red maple, American elm, white ash, hemlock, white pine and yellow birch. The sequence of tree species establishment following the retreat of glacial ice has been described by Davis et al. (1995). Sugar maple, a dominant species in the present day ecosystem did not get established in the Upper Peninsula until about 6,000 years ago; black spruce established some 10,000 years ago.

Northern hardwood forest[1] ([1]) occurs over a large range from shallow soils over bedrock to poorly drained soils. Graham (1941) and Braun (1950) have described in detail the variability of the northern hardwood forest in the Upper Peninsula of Michigan.

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[1]- Footnotes are given by chapter beginning on page 163.

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Most typically this forest developed on fine-grained loamy soils that are well drained (Tubbs 1977). The component species differ in shade tolerance and moisture requirements and establishment ecology. Tree species composition varies based on soil texture and content of organic material, topography, and disturbance history (Brubaker 1975, Tubbs 1977). Secondary northern hardwood forest is predominantly sugar maple in all variations of the type (Tubbs 1977, Tubbs and Goodman 1983). The high diversity of tree species and the ecotone of boreal and deciduous forest result in a characteristically high bird species diversity; among the highest in North America (Temple et al. 1979).

A large portion of the Upper Peninsula is in public ownership, mostly state and national forest. Large tracts are also commercial forest. Human settlements occur in dispersed small towns and clustered agrarian communities. Agriculture consists mostly of pasture and hay production. Although the Upper Peninsula remains largely forested, the present day forest is very different from the original forest that existed some 100 years ago (McCann 1991). Much of the present forest is second growth and differs in the extensiveness of forest types and in the relative tree species composition. The relative importance of tree species within forest types has changed. The vegetation patchiness, the interspersion of different forest types and the extensiveness of a particular forest type depend on the constituent land forms, topography and soils, local climate and historic disturbance. In some areas a particular forest type would stretch for kilometers, in others the interspersion would occur at intricately small area scales (Braun 1950). The regionalization of landscapes of the Upper Peninsula (Albert et al. 1986) have delineated different sections and subsections of the Upper Peninsula that differ ecologically because of differen

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of differences in local climate and physiography. Land type associations (LTAs) [2], smaller units in a hierarchy of spatial scales organizing ecological heterogeneity based on physical factors and potential vegetation (Appendix A; Table A1), have also been delineated on national forest lands (Appendix A; Table A2).

2. Description of the 10 Study Areas

Ten study areas were selected to replicate 3 different land use categories that had diverged historically since the turn of the century. In general, a study area corresponded to a different land type association (LTA). Percent composition of different land cover types for each of the 10 areas is given in Table 1. The Huron Mountains, McCormick Wilderness Area and Sylvania Recreational Area, represented 3 different land type associations replicating primary forest. Both the Huron Mountains and the McCormick Wilderness Area fall in the Superior Upland Subsection of the white pine -hemlock-northern hardwoods region described by Braun (1950) and in the Michigamme Highlands in the regionalization of Michigan landscapes (Albert et al. 1986). The Huron Mountains study area was located within a 7,285 ha forest preserve area (Simpson et al. 1990). The Huron Mountains border the south shore of Lake Superior in Marquette County. The McCormick Wilderness Area is part of the Ottawa National Forest and is located south of the Huron Mountains in Marquette and Baraga Counties. The study area was located within a designated natural area in the McCormick Wilderness Area. This area is approximately 1550 ha within a 7000 ha tract (Pregitzer and Barnes 1984). Areas along Lake Superior are under heavy lake effect but this effect declines precipitously inland. The annual extreme minimum varies from -23° C along the lake to

Table 1. Percent composition of land cover types in 10 study areas.

	TOTFORCO[5]	THWDNHW[6]	TOTCON[7]	TOTLMCON[8]	TOTOPEN[9]
Huron Mts					

Table 1. Percent composition of land cover types in 10 study areas.

		TOTFORCO[5]	THWDNHW[6]	TOTCON[7]	TOTLMCON[8]	TOTOPEN[9]
Huron Mts	x[3]	92	24.35	63.71	54.63	7.97
n[1]=3	se[4]	0.3	2.3	0.69	4.19	0.27
McCormick Wilderness Area	x	95.81	85.51	10.31	6.11	4.18
n=2	se	1.44	13.24	1.13	1.95	1.43
Sylvania Recreational Area	x	88.91	22.33	64.39	54.99	11.09
n=2	se	4.07	0.47	4.81	7.63	4.07
Dukes Experimental Forest	x	90.99	55.25	35.73	3.45	9.01
n=2	se	0.87	2.008	0.9	0.4	0.87
Munising Moraine LTA[2]-1	x	93.22	78.96	13.35	4.43	7.069
n=7	se	1.88	3.1	2.38	2.21	1.41
Manistique LTA=4	x	80.01	49.69	20.61	3.61	19.77
n=8	se	1.41	5.35	3.29	0.78	1.61
Rapid River LTA=7A	x	80.18	42.88	29.47	2.38	17.23
n=6	se	3.08	4.84	2.54	0.689	1.97
Chattam	x	48.49	23.08	24.73	0	51.5
n=2	se	4.29	6.75	3.36		5.25

Table 1. *(continued)*

	TOTFORCO[5]	THWDNHW[6]	TOTCON[7]	TOTLMCON[8]	TOTOPEN[9]
[illegible]	[illegible]	[illegible]	[illegible]	0	35.25

Table 1. *(continued)*

		TOTFORCO[5]	THWDNHW[6]	TOTCON[7]	TOTLMCON[8]	TOTOPEN[9]
Trenary	x	64.57	13.07	42.54	0	35.25
n=4	se	3.44	3.95	5.43		3.4
Stonington	x	64.12	12.34	36.27	0.81	35.86
n=3	se	2.25	1.86	5.69	0.47	2.26

[1]n = number of 1 mile of non overlapping 1 mile circles.
[2]LTA = land type association.
[3]x = mean.
[4]se = standard error of the mean.
[5]TOTFORCO = total forest cover within 1 mile.
[6]THWDNHW = total hardwood dominated northern hardwoods.
[7]TOTCON = total conifer contains all conifer forest types.
[8]TOTLMCON = late maturity conifers hemlock and hemlock–white pine.
[9]TOTOPEN = total openland within 1 mile.

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-35° C inland (Albert et al. 1986). The higher elevations relative to other regions of the Upper Peninsula, are due to the underlying preCambrian bedrock. Much of these areas are shallow to bedrock and bedrock is exposed in locations. Deeper mineral soils support hardwood dominated northern hardwoods while shallow soils on ridges support white and red pine, red oak and aspen. Swampy depressions support conifer forest, hemlock, red maple, balsam fir and black ash. Although land type associations had not been delineated for the Huron Mountains and the McCormick Wilderness Area, delineations of geomorphological features (Farrand and Bell 1982) and detailed descriptions of local climate (Simpson et al. 1990, Pregitzer and Barnes 1984) were sufficient to at least recognize that these 2 areas would be in different land type associations within the same subsection (E. Padley, U.S. Forest Service, Milwaukee, Wis; J. Jordan, Ottawa National Forest, MI; pers. comm).

A 3rd primary forest area, Sylvania Recreation Area is part of the Ottawa National Forest and is located in Gogebic County (Figure 1). The area is characterized by a swale and ridge topography. The dominant landform is a rolling, sandy and loamy terminal moraine. Depressions are occupied by lakes and bogs. The low relief, pitted ice contact topography and heavy drift cover are in contrast to both the McCormick and Huron Mountains. Sylvania Recreation Area has been classified under LTA-2 in the land type association delineations of the Ottawa National Forest (J. Jordan, Ottawa National Forest, MI; pers. comm) .

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Three land type associations within the West Unit of the Hiawatha National Forest in which the northern hardwood forest comprises a major forest type were selected to replicate managed forest. The Munising moraines (LTA-1 in Appendix Table A1), a ridge-swale complex on the Rapid River Ranger District (LTA-7A) and a lake-pitted northern hardwood area on the Manistique Ranger District (LTA-4) were included to represent areas of northern hardwood forest within the core of the national forest. The Munising Moraine (LTA-1) is located along the southern shore of Lake Superior in Alger County (Table A1). It falls under the Luce District-Grand Marais subdistrict in the regionalization of Michigan (Albert et al. 1986). The local climate is heavily affected by Lake Superior with heavy snowfall in the winter. Soils consist mostly of well developed upland sands and loamy sands of morainal origin. The natural vegetation consists of relatively continuous northern hardwood forest. The Manistique LTA-4 is the Steuben Segment of the Newberry Moraine. Loamy sands of morainal origin support northern hardwood forest. Depressions are occupied by lakes. The ridge-swale complex of LTA -7A formed by the retreating glacial Lake Algonquin. The upland areas supports northern hardwood forest and the lowlands support a mixture of lowland conifers. The greater part of the northern hardwood forest in all 3 land type associations is intensively managed for timber.

Areas that comprised several square miles around the settlements of Chattham in Alger County, Trenary in Alger and Delta counties and on the Stonington Peninsula (Table A2) in Delta County were included to represent settled forest landscapes. The climate on the Stonington Peninsula is dominated by lacustrine influence. Severe thunderstoms are not as frequent nor as intense because temperatures are moderated by lake effects T

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lake effects. Thin soils that originally supported northern hardwood forest are at present mostly in pasture. Poorly drained soils support lowland conifers. Both the Chattam and the Trenary study areas occur in the Dickinson district in the regionalization of Michigan landscapes (Albert et al, 1986). The landscape comprises poorly drained sandy outwash. Land use includes agriculture, mostly pasture. Both areas occur in the interior of the Upper Peninsula. Air mass instability storms are more common here in the absence of the moderating effects of lakes. Average annual minimum temperature is -29° C (Albert et al. 1986).

The 10th study area consisted of a large unlogged (old growth) northern hardwood area and adjacent logged areas within Dukes Experimental Forest. This study area lies in the Hermansville subdistrict in the Dickinson District (Albert et al. 1986) described above.

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METHODOLOGY

BUILDING AN ECOSYSTEM MODEL

1. Spatial Scales Pertinent to Assessing the Effects of Forest Heterogeneity on Songbird Species.

With advances in landscape ecology, the importance of using relevant spatial and temporal scales to describe ecological processes is increasingly receiving attention (Wiens 1981, Wiens et al. 1986a, Meentemeyer and Box 1987, Wiens 1989, Golley 1989, Turner 1989, Allen and Hoekstra 1990, Dunning et al. 1992, Ruggiero et al. 1994). Wiens (1976, 1981) and Kotliar and Wiens (1990) discussed how different organisms perceive the environment at different spatial resolutions, and how different ecological processes occur at multi scales that differ from anthropocentric scales. Ongoing discussions about scale suggest that the effects of environmental variables on forest bird species could be predicted with more precision in the future, if these effects are studied at spatial scales that are pertinent to the ecologies of forest birds.

Density relationships among forest bird species that might differ in their sensitivity to forest fragmentation, would be best revealed at spatial and temporal scales at which habitat selection and competitive interactions among bird species occur[1]. There are indications from bird census comparisons and from field studies that bird species select habitat at different spatial scales (Wiens and Rotenberry 1981, Anderson 1981, Gutzwiller and Anderso

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and Anderson 1987). Macrohabitat variables such as size of habitat and distance from edge, patterns of horizontal and vertical heterogeneity are correlated with bird community structure and geographical distribution of species (Wiens and Rotenberry 1981, Anderson 1981). Microhabitat variables that quantify vegetation structure and species composition, are best correlated with habitat selection by individual species within a habitat type (Holmes and Robinson 1981). Habitat variables measured in small areas reveal differences between occupied sites vs unoccupied sites for individual species, as well as habitat selection among different species within a habitat (Anderson and Shugart 1974).

Most forest songbird species have small nesting territories in the range of a fraction of a hectare[2] (many Parulidae species) to a few hectares. It is now well established that bird species perceive patchiness of vegetation structure and composition at fine spatial scales (James 1971, Anderson and Shugart 1974, Rotenberry and Wiens 1980)[3]. Habitat selection of songbird species has been measured by sampling vegetation structure and composition in small plots (0.04-0.08 ha) within nesting territories[4] (James 1971, Anderson and Shugart 1974, Whitmore 1977, Noon et al. 1980). Habitat relationships among bird species have also been established from such fine scale environmental measurements (James 1971, Anderson and Shugart 1974, Whitmore 1977, Rotenberry and Wiens 1980)[5].

The recognition that environmental factors at several spatial scales affect bird community structure and composition (Wiens and Rotenberry 1981, Anderson 1981, Askins et al. 1987, Robbins et al. 1989b) has led to the consideration of a landscape concept to refer to a mosaic of habitat patches in which a particular type of a habitat patch is embedded (Dunning et al. 1992, Freemark et al. 1995). The landscape [6] concept has been used as a

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been used as a theoretical basis for linking population processes of bird species to land characteristics. From an organism perspective, no absolute size is given to a landscape because the size of a habitat patch is specific to the organism. Dunning et al. (1992) considered a landscape to occupy a spatial scale that is intermediate between the scale of a species' home range and that of its regional distribution. Landscapes differ as population sources of a species and thus in their ability to supply individuals that would occupy suitable habitat sites when these become vacant. Landscape characteristics affect immigration and dispersal rates by the degree of environmental resistance they present to dispersing individuals. Population source or sink theory (Pulliam 1988, Donovan et al.1995) links landscape characteristics to population productivity. The concept of metapopulation theory considers a population to be composed of subpopulations that interchange individuals (Opdam 1991). The abundance of a bird species measured at point locations thus can be affected by landscape characteristics that control the rate of interchange of individuals among subpopulations (immigration into area) and species productivity [7] in a larger area surrounding the census point (Askins and Filbrick 1987, Dunning et al. 1992, Freemark et al. 1992, 1995).

For the majority of songbird species however, little is known about the spatial and temporal scales at which populations exchange individuals because of the many population and environmental variables involved. Organism related variables can include the inherent capability of the species to disperse, and numerous population processes that affect yearly fluctuations and population saturation. Land characteristics that could affect resistance to dispersal and population productivity could include structural characteristics, availability, and spatial configuration of patches at the smallest scale that bird species respond to (patch that would illicit a response by the bird species to settle into a territory); the spatial configuration of small scale patchiness at larger spatial scales (the relationship of small scale patchiness with higher level patchiness); characteristics of the physical structure (landform complexes, soil complexes) at different spatial scales that affect patchiness, and spatial and temporal scales of disturbance processes (natural or human-induced) that affect patchiness at different spatial scales (Kotliar and Wiens 1990) .

There are increasing attempts and calls in bird ecology to relate bird population characteristics and processes to landscape characteristics in spite of the complex ways in which population and land characteristics could interact (Freemark et al. 1995, Petit et al. 1995, Donovan et al.1995). The effects of landscape characteristics on songbird species have mostly been revealed from empirical studies undertaken in landscapes in which loss of forest cover was extensive (Ambuel and Temple 1983, Askins et al.1987, Freemark and Merriam 1986). This aspect is largely due to the recentness of the landscape concept, and the increasing concern with habitat fragmentation as a threat to species persistence (Wilcox and Murphy 1985). Several studies however have included a wide range of regional forest cover that extends into landscapes in which forest loss has been extreme (Lynch and Whigham 1984, Robbins et al. 1989b). Landscape level effects were often represented by forest cover measured within a range of 1-3 km from the point at which, or from the habitat patch in which, bird abundance was estimated (Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989b). Relationships of bird species abundances to landscape characteristics, and to territory level characteristics (vegetation structure) were considered linear and additive; represented by stepwise multiple regression and multiple correlation models.

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Variation in landscape level characteristics however could result in variability in bird species composition and in the relative abundance of species in different landscapes. Several studies have shown that a difference in the assemblage of bird species (species composition and the relative abundance of species) affect the habitat utilization and resource overlap among bird species (MacArthur 1958; Cody 1974,1978,1981). Variability in patchiness at the landscape level could cause variability in the species response to (and therefore the species abundance in) similar small scale habitat in different landscapes. A more general model of the effects of northern hardwood forest heterogeneity on forest bird species, would be one that considers interactive effects of characteristics of small scale habitat (spatial scale representing the territory level) and landscape characteristics. Such a model would explicitly recognize that variability exists at different spatial scales. Relationships between the relative abundance of forest bird species and landscape characteristics for northern hardwood forest landscapes in the Upper Peninsula are however not known. The interactive model is therefore presented as a postulate in need of testing.

That forest fragmentation (many human- induced changes have forest fragmentation aspects) has affected forest bird species abundance has been well documented in landscapes in which loss of forest cover has been extreme (Lynch and Whitcomb 1978, Whitcomb et al. 1981, Freemark and Merriam 1986, Ambuel and Temple 1983, Askins et al.1987). Comparative studies that considered a range of regional forest cover[8] in which forest fragmentation is at advanced stages have shown that area sensitive bird species are replaced by habitat generalist birds in fragmented landscapes. The apparent area sensitivity of some forest bird species (those species only found in extensive forest) is like

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forest) is likely to be the result of competitive exclusion from species that are less sensitive to forest fragmentation and to forest loss. This postulate is based on a large body of literature that has described habitat occupancy by a species to be a process mediated by numerous species interactions in contrast to the premise that habitat occupancy by a species is a simple response to habitat conditions (Cody 1974, Morse 1976, Cody 1978, 1981).

The ability of ecologically similar bird species to coexist has been attributed to the presence of coexistence mechanisms. Cody (1974) recognized some of these mechanisms as segregation by geographical area, by altitude, between habitat and within habitat. Until recently the limited spatial extent of single studies precluded the need to describe heterogeneity in a hierarchy of spatial scales. The ability of many ecologically similar songbird species to coexist within the northern hardwood forest (e.g. many species of warblers of the family Parulidae; many even within the same genus *Dendroica*) has been attributed to a high vertical and horizontal heterogeneity in the forest. This heterogeneity is in turn related to small scale variations in topography, aspect, soils and frequent small scale disturbances that continually reset forest maturation processes and provide many different niches to different bird species. In this single scale perspective[9], the northern hardwood forest would be viewed as made up of units the size of bird territories (in the range of a fraction of a hectare to several hectares) and occupancy of these units by individual species to be solely determined by availability of the necessary vegetation components.

In reality however the effects of northern hardwood forest heterogeneity at higher scales could modify bird species response to small scale heterogeneity. In managed forest where the r

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where the range of variability in forest cover among landscapes is narrow, it is not known if area sensitive forest bird species are differently affected in different landscapes. Should the variability of landscape characteristics be large enough to impact the relative abundance of bird species in the larger landscape, then habitat occupancy of the microhabitat sites could be affected. A spatial scale at the level of the patches that a species would establish a territory in is the spatial scale at which habitat occupancy can be assessed with the least amount of noise. Habitat overlap between 2 species (that are potentially competitors) also needs to be measured at this level (under constant landscape conditions) because this is the spatial scale at which the effects of one species replacing another (competitive exclusion) can be observed[10]. Based on the frequency of small scale disturbances in the northern hardwood forest and the small territory size of the bird species considered, spatial scales in the range of 0.5 to several hectares would be most appropriate to investigate the effects of vegetation structure on habitat occupancy and on interactions among bird species (Wiens 1989).

Basic biological information concerning spatial scales at which population processes of individual species occur (e.g. immigration into area, species productivity) are lacking. Details about differences in the structure of bird communities (bird species composition and their relative dominance) in different landscapes are also lacking. A spatial scale of (1.6 km) was herein used to examine the effects of landscape scale variables on bird densities based on the fact that it is within a range of spatial scales for which correlations between bird abundance and landscape level variables were found to be statistically significant for a majority of forest bird species (Lynch and Whigham 1984, Askins et al. 1987, Robbins et al. 1989b)[11]. The relationship between bird species abu

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abundance and landscape level characteristics at these scales have only been emperically derived, and have not been determined from actual examinations of species dispersal patterns and productivities. The statistical significance of relationships between bird abundance and landscape level variables at these spatial scales, for a majority of forest bird species (Robbins et al. 1989b), suggests however that these scales must be relevant to at least some aspects of forest bird species ecologies, their life histories and population processes.

2. Sources of Forest Heterogeneity in the Northern Hardwood Forest and Their Impacts at Scales Relevant to Forest Bird Species.

Structure of forest heterogeneity.

Landforms left behind from retreating glacials in the quaternary provided the physical setting in which local ecosystems developed. Landforms differ in their soil composition, slope, aspect and position in the landscape. Because they vary in their physical structure and topography, and to some extent influence local climate, landforms affect the development of vegetative communities and the rate at which succession and forest disturbance occur (Swanson et al. 1988). The patterns of distribution of the northern hardwood forest and its association with other forest types in the presettlement forest of the Upper Peninsula is predominantly influenced by the pattern of glacial landforms (Brubaker 1975, White and Mladenoff 1994). Large scale disturbance such as fire and hurricanes have been hypothesized to be disturbance factors in pine forest and in the more western extension of the northern hardwood forest (Graham 1941, Heinselman 1973, Canham and Loucks 1984). For the northern hardwood forest in the Upper

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Peninsula and more easterly, small scale disturbance in the form of tree blow down is the most common form of disturbance (Nichols 1935; Lorimer 1977; Borman and Likens 1979a, 1979b; Runkle 1982; Frelich and Lorimer 1991). The variability of the northern hardwood forest in structure and tree species composition across its broad geographic range as well as within the Upper Peninsula has been described by Braun (1950). The landform is also likely to affect the structure and species composition of the vegetation at a more local extent. The current state of the northern hardwood forest however is also the result of human influences that have altered it from its mostly primaeval condition before clearcutting began in the late 1800's. Under current forest management (under all ownerships) a greater portion of the northern hardwood forest is periodically logged. Large scale heterogeneity within the present northern hardwood forest is the result of the overlaying of largely human-induced and recent multiple land disturbance events on heterogeneity that had been laid down by very large scale geological events.

It is not possible to assess directly the amount of variability that the northern hardwood forest of the Upper Peninsula presents in terms of available habitat for individual bird species at the microhabitat level, or in terms of forest fragmentation aspects at a landscape level. This information however is required to test if forest bird species could be impacted by forest fragmentation related variables[12] within the range of variability presented in the northern hardwood forest of the Upper Peninsula. An alternative to direct assessment of songbird based variables and spatial scales, is an indirect methodology that considers a hierarchical structure in the partitioning of the heterogeneity of the northern hardwood forest. A first step in this methodology is to develop a conceptual model that would break down the total variability of the northern hardwood at the spatial extent of the

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the Upper Peninsula, into the hierarchy of spatial and temporal scales that are related to major environmental and human induced factors that have created this heterogeneity. In this hierarchy, dominant environmental or human induced factors of higher levels would be assumed to affect units at lower levels imbricated within them. A second step is to consider the scale at which habitat occupancy of the bird species can be examined (at the territory level) at the appropriate level in the hierarchy. This would be justified if there is a basis for expecting factors of heterogeneity (at higher levels in the hierarchy) to affect habitat structure at the territory level, and to modify characteristics at the 1.6 km radius scale. Although the model would be based on known factors of heterogeneity, there is no way of knowing apriori how higher levels of heterogeneity affect individual bird species, their habitats at a territory level, and within a 1.6 km radius landscape level. Its utility needs to be evaluated with respect to how well it explains heterogeneity in bird abundance and in habitat structures they require at the appropriate scales. The test of the model also lies in how well it uncovers relationships between human induced disturbance, ecosystem processes and bird species ecologies.

A hierarchical ecosystem concept was taken by considering the northern hardwood forest (within the range of the Upper Peninsula) as one large ecosystem that is divisible into smaller interacting ecosystems. The structure of the model was based on a hierarchy of spatial and temporal scales that correspond to climatic and geological factors, known anthropogenic disturbance factors, current land use and forest management practices. The structure of the model provided the higher stratification design for sampling bird densities and habitat at the territory level and at the 1.6 km radius landscape level. The structural components of the model and the among strata comparisons that this structure makes possible are presented in Figure 2. Table 2 lists the major factors causing variability among units at each level.

Historical events that added a human induced factor to forest heterogeneity

Large scale clearcutting that occurred over much of the Upper Great Lakes region in the interval between the 1880's until the 1930's marked a historical change in the course in which the existing forest was unfolding. The disturbance level that was created by this event was unprecedented since the Upper Great forest began establishing 10,000 years before, after the retreat of glacial ice (Ahlgren and Ahlgren 1983, Frelich and Lorimer 1991). Land use changes that followed clearcutting brought anthropocentric control over much of this region's forest (Ahlgren and Ahlgren 1983, Simpson et al.1990, Mladenoff et al.1993, White and Mladenoff 1994). In the aftermath of clearcutting, extensive areas (and consolidated areas) on which a secondary forest was developing were incorporated into national forests (Hiawatha National Forest and Ottawa National Forest in the Upper Peninsula). On lands where topography and soils permitted agriculture, early homesteads and farms replaced the original forest. Large areas (several square kilometers) that had escaped clearcutting are today protected from logging in natural areas and forest preserves.

Forest clearcutting, because of its catastrophic scale, altered many ecological processes of different spatial and temporal scales that were ongoing in the preexisting forest. The structure of the secondary forest was changed from that in the primary forest. In the secondary forest that developed following clearcutting, slow growing, and long-lived tree species, white cedar, white pine, and hemlock were reduced from their former

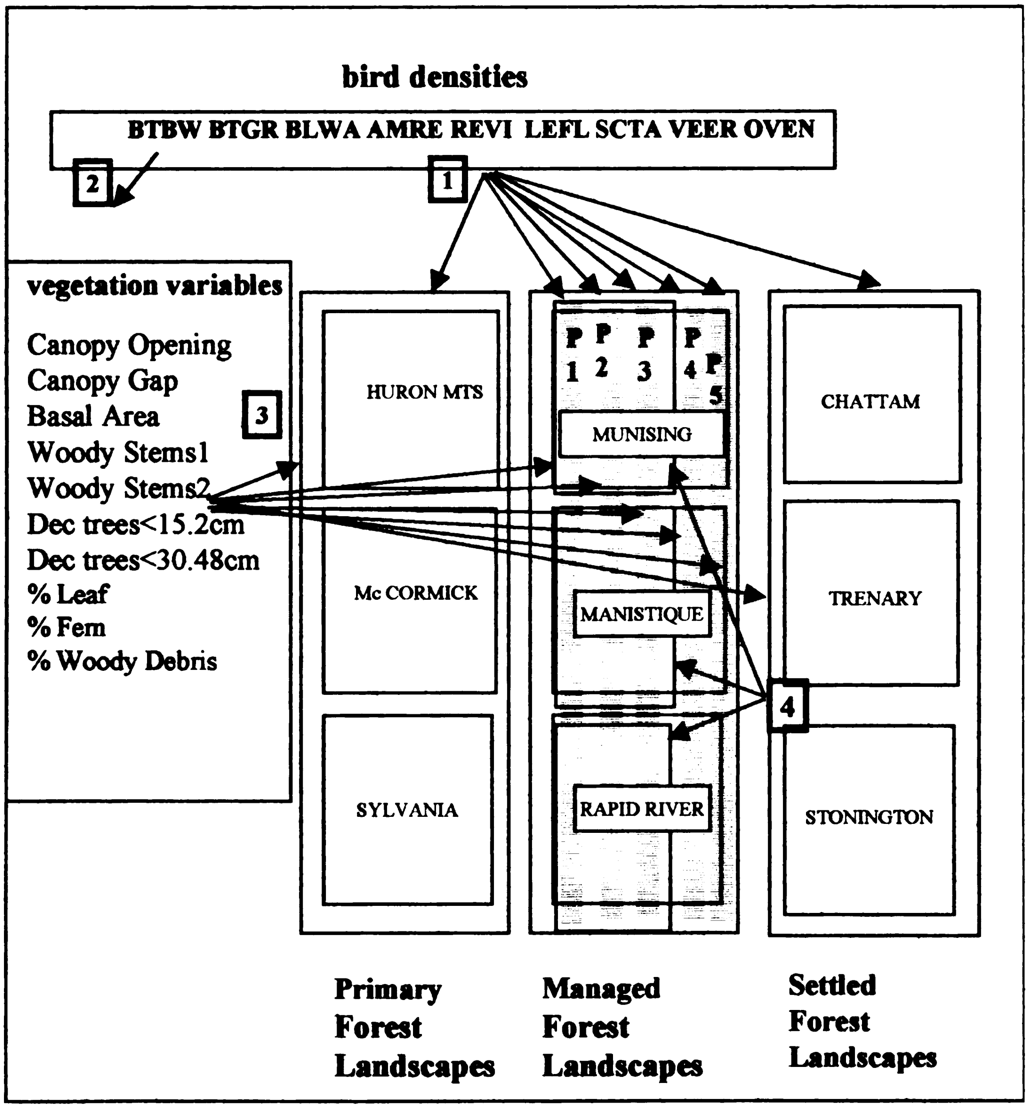

Figure 2. Main features of conceptual model and study design showing stratifications based on historical divergence, land use, land type associations, and time elapsed after logging; and comparisons of bird densities and vegetation variables among strata.

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Figure 2. (Continued)

Legend

Bird Species
AMRE American redstart
BLWA Blackburnian warbler
BTBW Black-throated blue warbler
BTGW Black-throated green warbler
LEFL Least flycatcher
OVEN Ovenbird
REVI Red-eyed vireo
SCTA Scarlet tanager
VEER Veery

Time elapsed after Logging disturbance strata
P1 Logged 1-5 years ago
P2 Logged 6-12 years ago
P3 Logged >12 years ago
P4 Second growth forest not yet entered into recent Logging cycle
P5 Older-growth forest

Analytical Steps
1. Bird density is compared among landscapes and logging periods in managed forest
2. Bird density is related to vegetation variables by regression analysis
3. Vegetation variables that are statistically significant in 2 are compared among land use (primary forest, settled forest) and logging periods in managed forest
4. Within managed forest, bird density and significant vegetation variables are compared in a 2-way comparison across time elapsed after logging and across landuse strata

→ refers to strata comparisons in a specific analysis

Table 2 *How different sources of variability in the northern hardwood forest were incorporated into the study design*

Level of Comparison	Main Source of Variability	How Treated in Study

Table 2. How different sources of variability in the northern hardwood forest were incorporated into the study design.

Level of Comparison	Main Source of Variability	How Treated in Study
1- Between different forest trajectories primary forest, managed forest and settled forest.	1) Past catastrophic disturbance + land use and management since last disturbance.	A stratification based on forest trajectory was designed into study.
2) Among landscapes (land type associations) within a forest trajectory.		
A - Among landscapes within primary forest trajectories: Huron Mountains, McCormick and Sylvania.	1) Differences in ecological factors operating at the landscape level.	A stratification by landscape was incorporated into study design.
B - Between landscapes within managed forest: Munising moraines (LTA1), Manistique moraines (LTA4) and Rapid River beach ridges and dunes (LTA7).	1) Differences in ecological conditions between landtype associations.	A stratification by landscape was incorporated into study design.
	2) A possible effect is that different timber managers write different silvicultural prescriptions.	Sources of variability 1 and 2 cannot be separated for logged forest.
	3) Differences in interactions between ecological conditions at the landtype association and silviculture prescriptions.	
C - Between landscapes within settled forest.	1) Differences in ecological conditions at the landtype association level.	A stratification by landscape was incorporated into study design.

Table 2 (continued)

Level of Comparison	Main Source of Variability	How Treated in St

Table 2. (continued)

Level of Comparison	Main Source of Variability	How Treated in Study
C- Between landscapes within settled forest.	2) Cumulative effects of differences in land management at scales below the landtype association .	This effect is to some degree randomized by consideration of many sites within a landtype association.
3- Among different northern hardwood forest sites within one landscape.		
A - Between sites within a primary forest landscape.	1) Stochastic disturbance events at different scales that create patchiness (in primary forest the time elapsed since last disturbance is not known).	Comparisons at this level were not considered. The effects were randomized for a higher level comparison.
	2) Site differences (topography, soil drainage).	This small scale variation is randomized by randomly placed bird census stations.
B-Between sites within one managed forest landscape.	1) Time elapsed since last logged.	A stratification for time elapsed since disturbance by logging was designed into study.
	2) Differences in initial state of site.	Second growth forest and older-growth forest were separated by a stratification.
	3) Random variability	Most of what is managed forest today had been clearcut within a short span of

Table 2 (continued)

Level of Comparison	Main Source of Variability	How Treated in Study

Table 2. (continued)

Level of Comparison	Main Source of Variability	How Treated in Study
C -Between sites within 1 settled forest landscape.	1) Patchiness within a site and among sites could be affected by land ownership patterns. 2) Initial state of site at time of incorporation into national forest or becoming private land.	Comparisons at this level were not considered. The effects of sources 1 and 2 were randomized by including many sites to replicate conditions for a higher level comparison.
4 -Among proximate bird census stations	1) Local variation in topography, drainage, and soils and small scale disturbance (natural and human induced) affecting local variation in presence and size of canopy gaps, and variation in tree species.	This represents variation in vegetation structure (measured at the bird census station) which affects microhabitat selection of bird species.

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extent both as forest types or as components within forest types (Mladenoff et al. 1993, White and Mladenoff 1994, Mladenoff and Stearns 1993, Crow 1995, Davis et al. 1995, Mladenoff 1995). Thus for bird species associated with a conifer component, habitat availability at the territory level, and habitat continuity at landscape levels, would have been impacted by such changes in tree species composition.

With the interspersion of human settlements and agricultural areas, and management of early successional forest, forest cover was also reduced in some landscapes. In addition human related activities introduced edge into areas that were devoid of it, in the form of induced interspersion of forest openings, early successional timber types that are periodically clearcut, pine plantations, roads and logging trails (Krummel et al. 1987, Robinson 1988). Because land use has had a dominant influence on the spatial configuration of forest cover at landscape scales and on forest composition and structure at finer scales, land use would be expected to account for a large amount of forest heterogeneity[13].

Hierarchy of physical and climatic factors affecting heterogeneity.

Regardless of anthropogenic influence, an underlying heterogeneity exists in the forest that can be attributed to multiple scales of physical and climatic factors (Allen and Star 1982, Turner 1987, Milne 1991). This multiple scaled heterogeneity forms the basis of an ecological classification system that has been adopted by the U.S. Forest Service (and recently by many other land management agencies) to classify land into a hierarchy of land units. Ecological classification systems are based on relationships between heterogeneity at large scales (regional climate) and heterogeneity at progressively smaller

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scales (landform, local climate; forest types) that are imbricated within larger units. Ecological classification systems reflect natural hierarchies of temporal and spatial dimensions of ecosystem processes unique to specified geographical locations. As such they can only deal with potential vegetation cover and do not incorporate well the patchiness imposed by human induced disturbance.

At the level of the national forest, the largest unit in the hierarchy of units is the land type association. The spatial extent of a land type association is in the range of hundreds to thousands of hectares (Table A1). The delineation of land units at the level of land type association emphasizes the effects of local climate and geomorphology. Different forest types are comprised within a land type association. Different microhabitats in turn are incorporated within each forest type. The configuration of the northern hardwood forest with respect to other forest types differs in different land type associations. Processes of forest maturation and disturbance, their intensity, frequency and the patchiness they produce are likely to also differ in the different land type associations since these are determined by higher level environmental factors. The difference in the configuration of the northern hardwood forest, in microhabitat conditions, and in modifications imposed by human induced disturbance that songbirds encounter in the different land type associations could be of a magnitude large enough to affect individual species densities, productivity, and the relative abundance of bird species.

Incorporating human-induced and environmental heterogeneity into model

In the Upper Peninsula, land use categories of primary forest, managed forest and settled forest can be delineated by large patches that cover several square kilometers. This results fro

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results from the perhaps relatively unique situation[14] (compared to a majority of eastern deciduous forest regions), in which large contiguous areas had been incorporated under national forest management, large tracts of remnant primary forest exist, and human settlements and agriculture are mostly concentrated where topography and soil productivity can support agriculture. Land use categories of primary forest, managed forest and settled forest were incorporated into the northern hardwood ecosystem model (Table 2, Figure 2) at the highest level in the hierarchy of factors affecting northern hardwood forest heterogeneity in the Upper Peninsula[15]. Each land use category was replicated by 3 different land type associations[16] (Fig. 2).

All 3 land type associations replicating the land use category of primary forest (Huron Mountains, Sylvania Recreation Area and McCormick Wilderness Area) are forest reserves. In primary forest not subjected to logging, most small scale forest disturbances such as tree fall result from natural processes[17]. The frequency and spatial extent of small scale disturbance are likely to be influenced by local topography, soil and climate but the actual events within a specified area and time period are stochastic. The emerging pattern of these small scale disturbances are likely to be reflected in differences in vegetation structure measured at small scales among the 3 primary forest areas. The objective of including different land type associations was to capture a broader range of the variability existing in the northern hardwood forest. The model was not designed to elaborate on the specifics of the different areas. Such an objective is better relegated to an ecological land classification or to the development of specific management objectives for these areas. Comparisons of bird densities and of microhabitats among the 3 land type associations however would test model assumptions concerning the effects of land type associations in ge

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general on bird species densities and their habitats. These comparisons would address whether the land type association level should be considered as a level of stratification for bird conservation or for further bird research (Table 2).

Managed forest was also replicated by 3 different land type associations (Munising Moraine, Manistique section of the Newberry Moraine, and an interior sand ridge -swale complex in the Rapid River District). Although the spatial configuration of forest types is affected by topography, slope, aspect and soils, in managed forest it is also modified by forest practices such as management for early successional forest and pine plantations. In national forest, logging is a predominant forest disturbance factor for much of the northern hardwood areas. Management guidelines for northern hardwood forest in the Great Lakes Region specify a selective cut every 8-10 years (Ohmann 1979, Tubbs 1977), a cycle of 12-15 years is given in the Hiawatha National Forest Management Plan (1986). The structure of a northern hardwood forest after logging is related to a large extent on the time elapsed since that disturbance, and on ecological conditions. Periodic selective cutting in northern hardwood forest interferes with forest maturation and disturbance processes. Stochastic events such as severe storms and tornadoes would still occur but their effects could be confounded, influenced or overshadowed by logging disturbance. Another source of variability within the northern hardwood forest under national forest management can be attributed to the initial patchiness of the northern hardwood forest when it was entered under national forest management. Although the majority of the area of the northern hardwood forest had been clearcut around the turn of this century (Cunningham and White 1941), some areas were not completely logged and these areas currently represent older growth within the national forest. Other areas that had been c

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clearcut had not yet been entered into the logging cycle. The pattern of small scale patchiness is likely to differ based on the time elapsed after logging[18]. To account for this variability, the northern hardwood forest within managed forest was stratified into 5 classes representing forest that was logged 1-5, 6-12, and >12 years ago, second growth forest not logged since the initial cut at the turn of the century, and older-growth forest[19] in areas which had not been completely clearcut and therefore contain at least some features of the original forest (e.g. lack of white pine or hemlock stumps, presence of large sugar maple and hemlock trees).

The landscapes on the fringes of the National Forest where human settlement intersperse forest lands are subjected to both natural and anthropogenic disturbance (e.g. logging, road building). Because of the multitude of ownerships, no systematic form of human-related disturbance can be identified at the landscape scale. Within these landscapes the northern hardwood forest was not stratified any further. Similar to the situation in the primary forest category, replication would recognize differences between these areas on the basis of local environmental conditions and randomize their effects. .

3. Selection of Bird Species to Include in the Model and Representation of their Habitat

The forest bird community is multidimensional in that it is composed of many different species that would respond differently to changes in the forest. To examine a contrast in bird species response to different ecosystem processes, it was necessary to simultaneously consider a number of bird species that share the northern hardwood forest, but differ in their individual ecologies. Ten bird species were selected for study: ovenbird, black-throated blue warbler, American redstart, chestnut-sided warbler, blackburnian warbler

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warbler, black-throated green warbler, least flycatcher, red-eyed vireo, veery and scarlet tanager (scientific names are given in Table B1). These bird species are generally associated with the northern hardwood forest (Brewer et al. 1991). As a group they require different vegetational components: the black-throated blue and American redstart nest in the shrub layer, the scarlet tanager nests at mid-canopy level, the ovenbird and veery on the ground, and the red-eyed vireo at various heights in the subcanopy and canopy. The blackburnian and black-throated green warblers are associated with a coniferous forest component. These species differ with respect to their area sensitivity and to the degree to which they are habitat specialists associated with deciduous and deciduous-coniferous interface. Many have been linked to large tracts of forest (Bond 1957, Ambuel and Temple 1983, Lynch and Whigham 1984, Robbins et al.1989b). Area sensitive species were purposely included to allow examination of some forest landscape level effects such as the reduction of forest cover, and the increased amount of forest edge. These aspects have been associated in general with forest fragmentation but have not been addressed within largely forested regions (Ambuel and Temple 1982, 1983; Freemark and Merriam 1986).

It was also desirable to have species with geographical ranges that extend well beyond the geographical area spanned by the study sites. A difference in the locations of study areas with respect to the geographical distribution of a species would affect densities of a species among different study units. Consideration of geographical distribution was important to remove a possible confounding effect of geographical distribution with the response of the species to habitat conditions caused by forest disturbance. Current distributions of a number of these species, the blackburnian, black-throated green and the black-throa

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black-throated blue warbler, correspond to the geographical range of the northern hardwood-hemlock forest. This correspondence could indicate a closer link between the ecologies of these species and the northern hardwood forest ecosystem. The black-throated blue warbler and the American redstart were included because of similarities and contrasts of their individual ecologies. The distributional range of the black-throated blue warbler has shrunk in southern Michigan, a change that has been attributed to loss of extensive forest (Binford 1991). The American redstart however is well distributed across Michigan and eastern North America (Peterson 1980, Reinoehl 1991). The American redstart is more tolerant of forest edges and might benefit from them. Both species nest in the lower understory vegetation and likely respond positively to disturbance that stimulates dense undergrowth. They were included because of the possibility that their relative distribution within the range of variability of the northern hardwood forest might reveal how forest changes might differently affect ecologically overlapping species.

4. Sampling Units and their Groupings

The basic sampling units considered were point locations at which bird censusing and vegetation sampling were undertaken. Variables representing characteristics of the landscape within a 1.6 km were also determined for these point sampling units. A total of 321 points were located in the northern hardwood forest following the stratification considered in the ecosystem model (Figure 2, Table 2). The distribution of sampling units into the various strata considered in the model is given in Table 3. An initial stratification of 321 sampling units into model strata permitted comparisons among categories of land use, land type association, and the various states of the northern hardwood forest after

Table 3. ***Distribution of sampling points (bird census stations) in strata based on historial divergence in lanc period and land type associations***

Table 3. Distribution of sampling points (bird census stations) in strata based on historial divergence in land use forest disturbance period and land type associations.

	Managed Forest Landscapes			
	Munising n[1]=67	Manistique n=69	Rapid River n=78	Dukes Experimental Forest n=17
Logged 1-5 yrs ago	12	16	14	2
Logged 6-12 yrs ago	12	14	22	7
Logged >12 yrs ago	11	24	21	2
Unlogged 2nd growth	18	4	20	0
Older growth	14	11	0	6
	Primary Forest Landscapes n=46			
	Huron Mountains	McCormick	Sylvania	
	14	15	17	
	Settled Forest Landscapes n=42			
	Chattam	Trenary	Stonington	
	10	16	16	

[1]n = number of sampling units (bird census stations).

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disturbance by logging, with respect to vegetation characteristics of small area patches and bird densities. Sampling units were also poststratified into new groups that were based on specific ranges of values for vegetation characteristics (i.e. density of woody stems and canopy opening) measured at the bird census stations and landscape level characteristics (i.e. % forest cover, length of forest edge). Such poststratification permitted the comparison of differences in the density patterns among the black-throated blue warbler, American redstart and chestnut-sided warbler along a forest fragmentation dimension at spatial scales that are relevant to their interactions.

5. Linking Habitat Selection at the Microhabitat Level to Ecosystem Processes

Vegetation structure and composition are both multidimensional, composed of many interrelated components. The importance of vegetation structure to birds has been well established in the current ornithological and wildlife management literature (James 1971, Noon et al.1979, Robbins et al. 1989b). Ecosystem processes and human related disturbance can be linked to bird species ecologies by assessing how they affect habitat features at the spatial scales bird species respond to. It was important to identify vegetation features that each bird species would most likely respond to and to test how these features differed among the different levels of stratification incorporated in the ecosystem model (Figure 2). Vegetation variables were selected to describe forest canopy, tree species composition and structure, shrub layer and ground layer structures[20]. Bird densities were related to vegetation variables through regression analysis. Figure 2 shows how the density of each individual bird species, and each vegetation variable impo

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important to that bird species would be compared across the different strata of variation in the northern hardwood forest.

6. Incorporating Landscape Scale Effects on Bird Species

There is increasing theoretical basis linking population dynamics of bird species to habitat continuity at the landscape level (Pulliam 1988, Kotliar and Wiens 1990, Opdam 1991, Freemark et al. 1992, 1995). Many human related activities reduce habitat continuity, a process that has been referred to as habitat fragmentation. At this time vagueness still surrounds concepts of what constitutes fragmentation, its quantification, and its progressive nature as a process (see Godron and Forman 1983, Haila 1986, Freemark and Merriam 1986, Krummel et al. 1987, Kotliar and Wiens 1990, Hansen and Urban 1992, Harris and Silva-Lopez 1992, Franklin 1993, Freemark et al. 1995, Faaborg et al.1995). Edge has been associated with many biotic processes such as increased predation, brood parasitism by the brown-headed cowbird and interactions with habitat generalist species. Perhaps it is because most studies have addressed forest fragmentation at its end stages, that predation and brood parasitism have received more attention (Brittingham and Temple 1983, Wilcove 1985, Yahner and Scott 1988, Small and Hunter 1988, Donovan et al. 1995, Pearson et al. 1996). One study however, Rosenburg and Raphael (1986) found that in the recently disturbed primary forest of Northern California, some bird species completely avoided edges while others utilized them. This indicates that species of a bird community previously undisturbed by human interference have different tolerance to edge. At advanced stages of forest fragmentation, the most area sensitive species would be expected to have completely dropped out. It is in largely forested region

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regions, where the assembly of area-sensitive forest birds is more complete, that a true assessment of the relative sensitivity of different forest bird species to edge can be made. The possibility that the introduction of edge by human activities into largely contiguous forest areas would provide suitable habitat for edge-interior bird species at the expense of highly specialized, area- sensitive forest bird species, was the justification for exploring the effects of increased edge in the northern hardwood forest. The theoretical indication that habitat continuity and edge affect bird species warranted exploring the nature of these landscape level effects. This exploration might lead to a better conceptualization of the process of habitat fragmentation in a highly forested region.

Landscape level effects were incorporated by considering forest edge[21] within 500m-radius areas, and total canopy cover and northern hardwood forest within a 1.6 km radius circular areas centered at bird census stations. Thus to each bird census station corresponded variables that quantified the environment at different scales. Figure 3 depicts the spatial relationship between the area scale at which vegetation structure was quantified and area scales at which landscape level aspects were quantified.

7. Integrating Microhabitat and Landscape Level Effects

Bird species could respond to landscape level conditions (areas within 500m and 1.6 km radius), and to microhabitat conditions which were measured at the locality of the bird census station. Sampling units (bird census stations) were poststratified into new strata defined by ranges of values for the selected microhabitat and landscape level variables. Figure 4 represents the poststratification of sampling units initially grouped by land use category, forest landscape and period elapsed since logging, into strata .

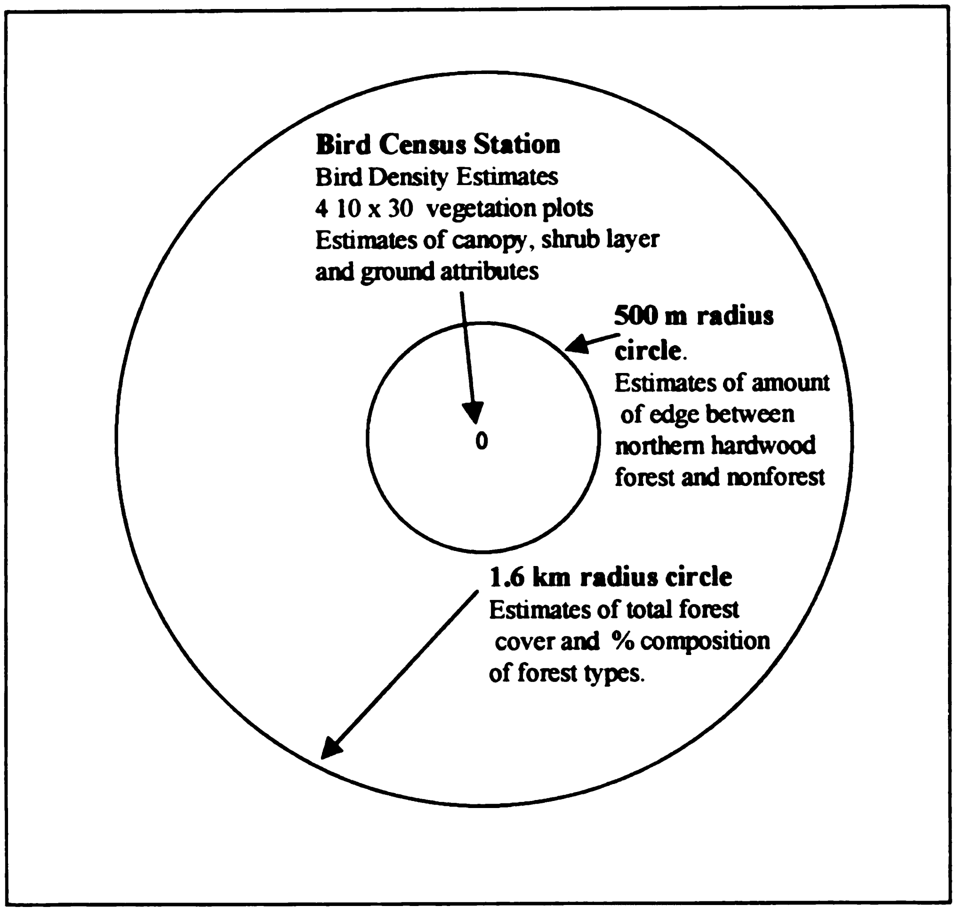
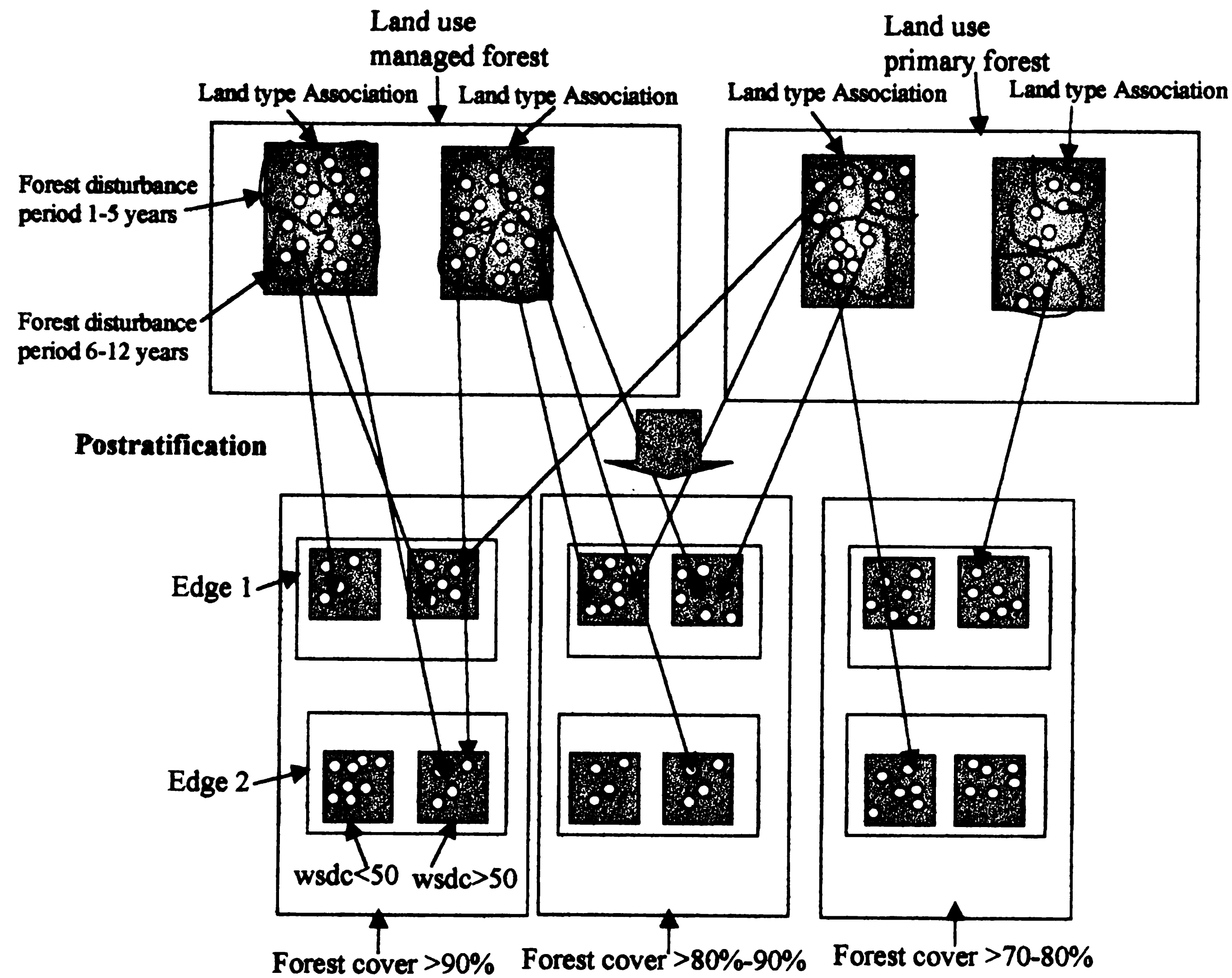


Figure 3. Spatial scales considered in measuring environmental variables associated with a bird census station.

Figure 4. Schematic representation of poststratification of sampling units from a classification based on land use, land type association, and forest disturbance period to a classification based on levels of % forest cover at the landscape scale, amount of edge within 500m radius and number of deciduous woody stems in the vicinity of the bird census station. This poststratification was used on vegetation data and forest cover data collected in 1992-1994 in the Upper Peninsula of Michigan.



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Land type Association
Land use
primary forest
Land type Association
Land type Association
Forest disturbance
period 1-5 years
Forest disturbance
period 6-12 years
Postratification
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Forest cover >80%-90%
Forest cover >70-80%

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representing a range of microhabitat conditions and a range of landscape level variables. The poststratification of sampling units based on their characteristics of vegetation at small scales (measured around the bird census station) and on their characteristics of forest cover and amount of forest edge (measured at 1.6 km radius and 500m radius from bird census stations) is equivalent to reducing the heterogeneity of the forest to spatial scales and in terms of variables that are relevant to bird population processes. Poststratification of the sampling units based on a number of variables that relate to fragmentation effects at the 2 spatial scales (vicinity of territory and within 1.6 km radius) permit the viewing of the heterogeneity of the forest along a forest fragmentation dimension. Variables that can be related to fragmentation include number of large canopy gaps and % canopy opening measured around the bird census station[22], and length of forest edge, % forest cover, % coniferous forest, % deciduous forest measured at 1.6 km radius landscape level. If the effects of forest fragmentation at the vicinity of the territory and those in a broader landscape were linear and additive then multiple regression could be used to show how bird density is affected by fragmentation aspects at the 2 scales. Bird ecology studies however of competitive interactions and coexistence mechanisms point to the need to explore the interactions among variables measured at the 2 scales since it is likely that the effect of fragmentation at the larger scale would affect community structure. If there is a difference in the relative abundance of bird species in different landscapes, bird census stations from different landscapes would be exposed to different bird species population abundance from the broader landscape even if they had similar characteristics at the breeding territory level. Thus the sampling units would need to be grouped based on values of fragmentation related variables at the 2 scales. Both the range of values of the frag

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fragmentation variables and the total number of sampling units placed a limit on how fine of a gradation to consider for each variable and therefore on the number of new strata. Two- way analysis of variance was used to elucidate the interactions between fragmentation related variables in the vicinity of the territory and those in the larger area. In effect, with the 3- way and 4- way analyses of variance that were performed using variables from the 2 scales[23], the total range of variability of the forest captured in the model was reassessed in terms of fragmentation related variables at new spatial scales. Because the whole range of northern hardwood forest was considered in these poststratifications, the original association of sampling units with land use and landtype association was lost[24].

FIELD METHODS

1-Selection of Study Units

Selection of Primary Forest, Managed Forest and Settled Forest Landscapes.

The gathering of field data was undertaken from May-August in each of 1992, 1993 and 1994. An endeavor to locate all possibly suitable study sites was attempted in 1992. The land type association was the largest land unit, within the hierarchy of spatial scales considered in the model that needed to be selected. The focus of the study on northern hardwood forest ecosystems required that this forest type be a dominant forest cover type within the selected land type associations representing a category of land use. In the settled forest category, where some forest cover was lost to agricultural use, it was required that the northern hardwood forest would have historically been a dominant cover type. This requirement was easily met because of the preponderance of northern h

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hardwood forest. The selection of land type associations in the land use category of primary forest was dictated by the availability of large tracts of primary forest that comprised northern hardwood forest. The Huron Mountains, McCormick Wilderness Area and Sylvania were selected since these were among the few remaining primary forest landscapes in the Upper Great Lakes region. Delineations and descriptions of land type associations on the West Unit of the Hiawatha were used to select land type associations comprising northern hardwood forest in managed forest and in settled forest (Table A1). The suitability of hardwood forest soils for agriculture accounted for the patchiness of the northern hardwood forest in settled forest landscapes.

Locating northern nardwood forest sites in primary forest, managed forest and settled forest landscapes.

Locations of northern hardwood forest within a land type association were identified from U.S. Forest Service data bases (CDS), from aerial photos and from land cover maps resulting from an ecological classification of the land base. Forest cover typing in managed forest was available from compartment maps, and from a pilot GIS project for parts of the Hiawatha National Forest. Forest cover maps for the Huron Mountains and for the McCormick Wilderness Area were produced during past studies in those 2 areas that involved an ecological land classification (Pregitzer and Barnes 1984; Simpson et al. 1989). These vegetation cover maps were available from the Ottawa National Forest and from the Huron Mountain Club respectively.

The forest types and their delineations in managed forest are the result of many decades of silvicultural exams that had emphasized assessments of forest resources. There are diff

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are differences in the forest typing produced by silvicultural examinations and that resulting from ecological studies. The recognized forest types resulting from silvicultural examinations emphasize finer differences in commercial tree species to reflect a difference in the suitability of different areas for timber management. An ecological study in contrast emphasizes subtle differences in tree species composition when these reflect ecological differences such as those due to soil variations, slope and aspect; variations that often are recognized by ground flora (Pregitzer and Barnes 1982, 1984). Forest typing in ecological studies included finer divisions of nonforest cover types and noncommercial tree species associations, than those recognized by U.S. Forest Service forest types. Differences between forest cover types recognized in forest cover maps of the McCormick and the Huron Mountains, and those recognized in forest cover maps of managed forest (compartment maps), also reflect differences in the patchiness of hemlock and white pine between primary forest and secondary growth forest. Table C1 matches the forest types of both systems.

In primary forest landscapes, forest cover types along a gradient of hemlock - northern hardwoods include the cover types of hemlock, hemlock dominated hemlock-northern hardwoods, hardwood dominated hemlock-northern hardwoods and sugar maple-hardwoods. For the McCormick Wilderness Area, that range was further divided into finer differences based on ground vegetation. Although in the presettlement forest, natural forest succession of northern hardwoods was to hemlock, I did not include forest cover typed as "hemlock" in my sampling. Because of time and budget limitations, the main focus was on the managed northern hardwood forest. Primary forest landscapes and settled forest landscapes were included only to put the managed forest in the perspective of less and

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of less and more disturbed forest. For this purpose, considering northern hardwood forest areas that are hardwood dominated hemlock-northern hardwood, a type prevalent in primary forest landscapes would suffice to extend the managed forest towards the less disturbed forest end. All types that could be included in the broader categories of hardwood dominated hemlock-northern hardwoods, and sugar maple-hardwoods, in the cover maps compiled by Simpson et al. (1989) for the Huron Mountains, and by Pregitzer and Barnes (1984) for the McCormick Wilderness Area, defined the availability of suitable sites. No cover type map was available for Sylvania at the time of the study. Aerial photos (1992 leafoff, infrared scale 1: 15,840) were used to delineate areas that were hemlock-northern hardwood forest dominated by hardwoods. Areas of heavy eastern hemlock or eastern hemlock-white pine cover were avoided since these were considered to be the equivalent of hemlock or hemlock-white pine forest types (U.S. Forest Service types 04 and 05).

In all primary forest landscapes, accessibility due to lack of roads had to be considered in the selection of suitable sites. Only those northern hardwood areas that could be accessed within 1 hour of travel whether on foot or by motor vehicle were included. In the Huron Mountains few areas of hardwood dominated, hemlock-northern hardwood forest could be reached within an hour's travel.

All lands on national forest lands that exclude wilderness and recreation areas are broken down into management units called stands which are comprised within larger land units called compartments. As a management unit, a stand is not exactly congruent to any well defined ecological factor[25]. This is in contrast to ecological classification systems in which the ecological factors that differentiate between land units at a particular level are a

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defined (USDA Forest Service-National Hierarchical Framework of Ecological Units)[26]. An ecological classification of land units presents a consistent basis of ecological heterogeneity, and the pattern of lower units occurrence is repeatable within a higher unit[27].

The U.S. Forest Service data base "CDS" was used to locate northern hardwood forest in the 5 categories of time elapsed after disturbance within the 3 different land type associations in managed forest. In the data base, management units are identified by compartment and stand number. Descriptive information on a stand in general consists of forest type, age-class, silvicultural treatment, year of silvicultural treatment, basal area, average diameter of trees, survey year, and for some stands the year of origin[28]. Northern hardwood forest types are included in the range of U.S. Forest Service forest types 81-89 (all forest cover types used on the Hiawatha National Forest are given in Table C1). Within each of the selected managed forest landscapes, a first cut for suitable locations was all the forest types in the range 81- 89 in U.S. Forest Service classification.

In managed forest, the northern hardwood forest was further stratified based on when it had been last disturbed by logging. More complete information in the recent computerized database (CDS) was available for forest management activities undertaken within the previous 15 years (from the beginning of field sampling in 1992). For the 3 categories of forest logged 1-5 years ago, logged 6-12 years ago and logged >12-15 years ago, the number of locations in each of the 3 land type associations used to replicate managed forest was well defined[29].

In the data base there was a category of northern hardwood forest areas for which there was no record of logging. This category actually represented different conditions:

areas that were logged prior to 15 years ago (from the beginning of field sampling in 1992), unlogged second growth, and older growth areas[30]. Mean average diameter at breast height (DBH) and stand origin (when it was available) were used as a guide to locate second growth northern hardwood forest, and older growth forest. Information from old compartment folders was used to further identify areas that were logged prior to 1979, and eliminate these from unlogged second growth, and potentially older growth forest. Because of the rarity of old-growth forest outside of research natural areas and wilderness areas, the knowledge of U.S. Forest Service personnel was also relied upon to suggest forest areas showing old-growth characteristics. Size of trees, an uneven canopy, and canopy gaps, lack of tree stumps, and tree species composition[31], as revealed by field checks further refined the separation of older growth from second growth forest.

Because the placement of timber sales across the forest is not random, the location of northern hardwood forest patches in the different classes of time elapsed since logging 1-5, 6-12 and >12-15 years would not be random. In many instances logging also did not involve the whole stand unit. Patches that were logged were identified from timber sale contractor files and from field checks. A large enough area is required to be representative of forest interior conditions and of conditions of northern hardwood forest in the different stages of time elapsed after disturbance. Recommendations by Morrison et al. (1981) that a 20 ha area is the smallest area that could be considered continuous habitat were followed in the selection of suitable northern hardwood forest locations

In settled forest landscapes the northern hardwood forest had become patchy and distinct from the surrounding matrix. Potential suitable patches of 20 ha or larger were rare but easily located from aerial photos. After giving consideration to the shape of the patch and getting permission from private land owners few patches were available. In some land type associations (Stonington), all available patches were used for the placement of points in settled forest landscapes.

2- Locating Bird Census Stations

The model structure specified 21 strata of northern hardwood forest needed to be sampled which included 3 land type associations in each of primary forest and settled forest, and 5 strata of forest disturbance in each of 3 land type associations within managed forest (Figure 2)[32]. A larger number of sampling units would be required to test for differences in bird densities and vegetation variables among strata of the northern hardwood forest than among strata representing different forest types [33]. In a previous bird study, a number of sampling units in the range of 10-15 was sufficient to show differences between habitat occupied by each of 10 bird species and random points in the northern hardwood forest (Hamady 1983). In the absence of specific apriori data, this latter study was used as a rough approximation of the number of bird census stations that would be required to test for differences in bird species mean densities and vegetation variable means among northern hardwood forest strata (among land type associations and forest disturbance periods). Because bird density and vegetation variables were sampled at a spatial scale close to the territory level, each bird census station was an independent sampling unit and not a replicate of bird density or vegetation conditions of a larger area. It was important not to sample the same individual birds from 2 adjacent bird census stations. Because the bird census methodology used (Distance Sampling) estimated the number of birds from their singing and calling, a minimum distance of 150m was required be

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required between bird census stations so that birds could not be heard from 2 adjacent ones. Thus although theoretically the sampling space would be the number of territories that can be fitted within the space available, technically the maximum number of samples possible would be the number of 150m radius areas than can be fitted into the space available. In order to evaluate habitat conditions in the interior of the forest another constraint on the placement of bird census stations was that they be placed at a minimum of a 100 m from any forest edge. The distance between adjacent stations greatly exceeded the minimum of 150m because of irregular shape and avoidance of edge, which further reduced the number of possible samples.

The number of bird census stations that can possibly be fitted within a strata of northern hardwood forest was determined to a large extent by the total area in that stratum that was 100m away from a forest edge. A completely random design for placing bird census stations would subdivide the area available in each category of northern hardwood forest into units that had a 150m radius and then would select 15 points at random. For most strata of time elapsed after logging within a land type association, the number of locations available were less than the number of bird census stations required (Table B3). Thus a random selection of points would result in several bird census stations being placed in one location of a category of forest. The methodology of locating points within the strata of northern hardwood was modified from a completely random design in order to accommodate logistic constraints. Several bird census stations were located in one patch depending on the size of the patch. The successive order of locations to be considered for placement of bird census stations was determined from a randomly ordered list of available locations prepared for each class of time elapsed after logging. For

northern hardwood forest logged <15 years ago, this list was well defined. New locations were not considered if the required number of bird census stations had already been assigned. For other less well defined classes (unlogged second-growth forest and older growth), new entries were placed on the list if the locations already on it were not found, following a field check, to be representative of the class of forest disturbance period. The actual number of bird census stations placed in a location depended on the size of the patch and the length and spatial distribution of forest edges that needed to be avoided. A total of 321 bird census stations were placed in a total of 78 patches.[34]

Layouts of bird census stations were drawn on U.S. Forest Service compartment maps when available, or on aerial photos prior to field location. Fifteen different individuals were involved in locating bird census stations on the ground. This reduced the potential for bias in the placement of bird census stations. Edges avoided were those created by roads that are maintained as system roads (Table C2), by management created openings, clearcut stands where the forest canopy had not recovered, stands with canopy openings >50%, streams, and lakes. Edges around canopy gaps that were the result of tree blow down, or logging were not considered. Logging skid trails and 2-track roads within the stand that are not maintained after a logging operation were not considered in the quantification of edges. Their effects on canopy opening was evaluated in the quantification of canopy gaps.

3- Bird Census Methods

Distance sampling (Buckland et al. 1993) was used to estimate densities of bird species. In distance sampling, distances are measured from randomly placed points to

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objects. Distance sampling uses these measured distances to make unbiased estimates of density, given that certain assumptions are met. Underlying the theory of distance sampling is a detection function $g(y) = \text{prob}\{\text{detection}|\text{distance } y\}$. Bird census points were considered the point transects in distance sampling. Distances were estimated from these randomly placed points to singing or calling birds. Detectability of birds decreases as a function of distance from the census point. Distance sampling fits curves of known functions to the distances. The theory allows for the estimation of bird densities without requiring that all individuals be detected or that the size of the sample area be defined. These 2 aspects of distance sampling are advantageous in multispecies studies when detectability differs among species.

The objective of estimating bird densities was to assess how birds respond to microhabitat and landscape differences in different forest trajectories. Many factors can affect bird species censusing and introduce noise into the data (Ralph and Scott 1981). It was crucial therefore to reduce the amount of variability in bird density estimates that is due to other sources than the intended comparisons. The methodology followed was that recommended for point sampling. A number of measures were taken to reduce undesired effects that include observer bias, weather, sampling bias and time of day. Each bird census station was censused 4 times during a field season. A few bird census stations were censused only 3 times because of a combination of logistic problems and bad census conditions. Censuses were scheduled at intervals of 10 days beginning the first week in June. Censuses began at 630 AM Daylight Saving Time and ended by 10 AM Daylight Saving Time. Different observers censused the same plot during the course of the field season. No censuses were taken on windy and rainy mornings. Censusing was terminated if the wi

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The field methodology for point transects in distance sampling is equivalent to the variable circular plot method (Reynolds et al. 1980). Training of observers was identified as critical to the proper use of the variable circular-plot method (Kepler and Scott 1981) and to reduce among observer differences. Training of observers was a major task in accomplishing the field work. All personnel involved in censusing began learning the identification of bird songs and calls beginning several months prior to the respective field season. Unexperienced censusers were trained for a period of a month prior to censusing independently. Observers were trained in a group situation where the opportunity to compare field data was possible. Six field personnel were involved in censusing birds during the 1992 field season. Of those 6, 3 individuals were experienced birders with several years of bird censusing experience. Nine and 8 individuals were involved in the census in 1993 and 1994 respectively. More than half of the individuals involved in censusing were experienced censusers. Training centered on proper identification of bird species songs and calls and on estimating the distances to birds heard or observed. Checks on observer skills were maintained throughout the census season by having 2 or 3 observers periodically census the same points together[35]. More effort was spent on species that were harder to locate aurally and on the species prioritized in this study.

Statistical inference in distance sampling is based on the validity of certain assumptions that impose requirements on field methodology. An important requirement is that birds at or very near the census point be detected with a probability of 1. Birds should also be detected at their initial location, prior to any movement in response to the observer. A third requirement is that distances from the census point to the bird should be measur

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measured accurately. Personnel training discussed above was crucial to meet these requirements. In addition censusers were required to wait 2 minutes after arrival at the bird census station to allow birds to settle back and stop responding to the observer's movements. To aid in the estimation of distances to detected birds, flags were tied at known distances from the bird census station.

4- Sampling of Microhabitat Variables

Variables describing microhabitat structure and composition (Table B3) were measured at the bird census station. Four 10 x 30 m plots were setup, aligned along the 4 cardinal directions from the bird census station (Figure B1). Tree species, diameter at breast height and height were recorded for all trees within the North and South 10 x 30 m plots. Several tree heights were measured using a clinometer and visual estimates were recorded for the rest of the trees in the vegetation plots. The number of woody stems <0.5" (1cm) and >0.5- 2" (>1cm-3cm) was counted at breast height in 12 5 x 2 m plots within the 4 10 x 30 m plots. Canopy cover was recorded by 2 measures, percent canopy cover and number of canopy gaps in 4 canopy gap size classes. The quantification of canopy cover followed a modification of the Canfield method (Canfield 1941). Percent canopy cover was obtained by stretching a measuring tape along the 30 m length of the vegetation plot, and recording the stretches of tape above which the canopy was open or closed. This involved visually projecting points in the canopy onto the tape at the position where the canopy changed from open to closed and from closed to open (Figure B2A). The edges of each canopy gap within the vegetation plots were visually projected onto the forest floor. The area of a canopy gap was estimated based on its width and length

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(Figure B2). Four classes were considered: >10-25m2, >25-50m2, > 50-100m2, and >100-<150m2. When the canopy was so open that gaps could not be defined the canopy was recorded to be >50% open. Training of personnel involved the estimation of the size class of canopy openings.

5- Developing Geographical Information System (GIS) Coverage for Study Areas

Geographical information system (GIS) coverage was constructed during the years 1995-1998 for each study area. The first objective of a GIS coverage was to quantify the area of the different cover types within a 1.6 km radius of a bird census station. The second objective was to quantify the length of edge between specified cover types, and between cover types and roads, in areas within 500 m from bird census stations.

Digital coverage for forest cover types, was available for part of the public land within the boundaries of the Hiawatha National forest. The roads, water bodies and water courses layers were available for most USGS quadrangles covering the study areas. Access to these data was available through the US Forest Service (Hiawatha and Ottawa National forests). Geographical digital data were created from the initial stage of manuscription of cover types for lands that did not have an already available coverage. Table C3 lists all the 7.5 minute quadrangles which covered study sites, and the sources of land cover types of the corresponding spatial data.

Map manuscripting of forest cover available from the Hiawatha National Forest was based on infrared, ortho-photos for 7.5 minute USGS quadrangles (scale 1:24000). Aerial photography covering the Upper Peninsula was taken in 1992 during leaf-off. The manuscripting of land cover on public lands began in 1992. Much of the manuscripting was c

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was contracted out by the Hiawatha National Forest. Manuscripts of cover types were verified on site by U.S. Forest Service personnel using the same photos, infra red photos (1992 infrared, leaf-off, scale 1:15,840), compartment maps, field checks and other data bases.

During the period between 1992 to 1996, digital coverage became available for only a portion of the public land. Spatial data had to be created starting from the manuscripting stage, for all public lands that had not yet been covered and for all private lands. The same procedure was followed to create these coverages as was used by the U.S. Forest Service, when ortho photos of USGS quadrangles were available. Ortho photos were available for lands within and adjacent to the boundaries of the Hiawatha National Forest and for Sylvania Recreation Area but were lacking for the Huron mountains and for the McCormick area.

Coverages were created for the McCormick Wilderness Area and the Huron Mountains from available forest cover maps. New cover maps were created that also included land lying just outside the boundaries of these areas, and to retype cover designations in a way that it could more easily be tied back to U.S. Forest Service typing. The new cover manuscripts were based on the original cover maps and on black and white photos obtained from the Michigan DNR (1986; scale: 1/15,840). For the McCormick Wilderness Area, the relative dominance of tree species in the different local ecosystems, given in Pregitzer and Barnes (1984) were used, to match cover types with U.S. Forest Service types. The cover type map compiled by Simpson et al. (1989) for the Huron Mountain Club recognized types along the successional gradient of northern hardwoods as 'hardwoods', 'hardwood dominated hemlock-northern hardwoods', 'hemlock dominated hemloc

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hemlock-northern hardwoods' and 2 types of hemlock. Table C1 lists all cover types recognized in the classification of different study areas and the corresponding classification prepared for landscape-level comparisons.

For the Sylvania Recreation Area, delineation of cover types was accomplished by using 1992 ortho photos of 7.5 minute USGS quadrangles (scale: 1/24000; infrared leaf off) that covered the area. A distinction was made between hardwood areas, hardwood-hemlock and pure hemlock areas. Figure C1 is a schematic representation of the relative position of forest types, in managed and primary northern hardwood forest, along the gradient of forest succession from hardwood to hemlock. Much of the hemlock component in the original forest was lost when the forest was clearcut at the turn of the century. The U.S. Forest Service typing of northern hardwood forest, as was previously discussed, does not separate the second growth forest that has retained some component of hemlock from that which has completely lost it. The presence of a coniferous component however as likely to be important for some bird species. It was therefore important to separate northern hardwood forest that had a coniferous component from forest that did not. An additional type 819-hemlock was added to U.S. Forest Service typing of forest cover to achieve this separation. In U.S. Forest Service typing, patches of hemlock are often recognized as separate cover types within the matrix. The data base shows patches as small as 1 ha, as separate hemlock stands. Because the delineation of hemlock patches was not consistent, the existing cover typing could not alone be relied upon to insure that the presence of hemlock was delineated. This separation could only be achieved on a qualitative basis. In the USFS stand data base (CDS) the presence of hemlock is only noted qualitatively. Quantification of the actual amount of hemlock could theoretically be obtained from silvicultural examinations but these data are not computerized. A coniferous component could also be recognized from aerial photos taken with leaf-off; this separation was possible for private lands not covered in the USFS database. Digitizing of maps of areas not covered by an already available GIS was accomplished by various individuals using the program Arc/Info. Public and private land coverages and adjacent coverages were 'edge-joined' if the study area overlapped 2 different coverages.

Attribute data were entered that identified each polygon in the coverage. For private lands the land cover type of a polygon was noted at the manuscripting stage. When the polygon represented national forest land, the identification it was given corresponded to the compartment and stand numbers that it represented. The land cover type then could be obtained from U.S. Forest Service data bases. Areas of polygons within 1.6 km-radius circles centered on the location of bird census stations can be identified by the capability of Arc/Info (ESRI-Environmental Systems Research Institute 1993) to generate a buffer zone around a geographic feature. These 1.6-km radius circle clips overlaid over the original coverage, created new coverages with new polygon relationships (Figure C2). The initial design of spatial data analysis however called for a 1.6-km radius, for each bird census station. Many technical difficulties were encountered after 1.6-km radius clips were obtained. Because digital information was obtained from the U.S. Forest Service while the agency was still putting together this GIS system, there were many instances of incomplete digital data discovered within the 1.6 km circle clips. Compartment maps provide maps of forest cover types. Circle clips that contained polygons that were not well defined in the digital coverage were redrawn on compartment maps and the areas of the different polygons measured with a planimeter. For bird census points that were only a distance of 150 m from one another, 1.6 km circles around these points overlapped extensively. When a visual inspection of the area outside of the area of overlap showed no difference in forest cover pattern, the large effort it would take to remeasure portions of missing polygons justified consideration of one circle for adjacent points. The difference in percent cover of different cover types would be of a magnitude that it would not affect the classification of bird census stations with respect to landscape variables.

Roads, trails, water courses and water bodies were separate coverages provided to the U.S. Forest Service by the U.S. Geological Survey. Base maps for these features were available for most quadrangles covering study areas. In the road coverage, roads and structures were classified into types following U.S. Forest Service specification. These are given in Table C2. All road types that were maintained, from primary to dirt roads were considered in the calculation of edge. Because the amount of edge within a 500 m of a bird census station was of interest, clips of 500 m circles were created in which edges were quantified.

STATISTICAL TECHNIQUES

1. Estimation of Bird Densities

The program Distance for point transects (Distance, Version 2.1; Laake et al. 1994) was used to estimate bird densities from bird distance data. Analyses of distance sampling data were repeated for each of 10 bird species to obtain a density estimate for each species at individual bird census stations. Distance sampling (Buckland et al. 1993) estimates bird density from observed bird distances by modeling a detection function. Several models and adjustments to these models were initially tried for fitting a detection function to distance data. The model with the best fit was selected by comparing alternative model fits with the Akaike's Information Criterion (AIC). Details of sample size (number of time the species was encountered), model selected, cutoff points and intervals applied in the estimation of each species density are given in Table D1. In addition to bird density, I defined encounter rate to be the % of total bird census stations at which a species was encountered. Density and encounter rate (Table D2) were used to describe the relative patterns of distribution and abundance among species.

2. Assessing the Effects of Historical Divergence in Land Use, Recent Logging Disturbance and Land Type Association on Bird Species Densities.

Mean density of each of the 10 bird species herein considered was calculated for the 2 strata of landuse primary forest and settled forest, and for 5 strata of forest disturbance within managed forest (Figures 5-8, Table D3). Univariate ANOVA (MGLH; SYSTAT 5, 1992) was used to test for statistical significance among the 7 means. The overall F test indicated the statistical significance of the overall difference among all strata (Table D4). Mean density and variance of each species was also calculated for managed forest landscapes. Anova in the procedure Test in MGLH (SYSTAT 5, 1992) was used to test hypotheses of no difference in the mean density of individual bird species between: primary forest landscapes and managed forest landscapes; between managed forest landscapes and settled forest landscapes; and between primary forest landscapes and settled forest landscapes (Table D5). The statistical significance between means of bird

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density of the strata older growth forest within managed forest landscapes, and northern hardwood forest in primary forest landscapes was tested. A number of apriori tests, applied to contrast density of a bird species among specific model strata, were also planned once habitat availability patterns in northern hardwood forest were identified (Table D6). These habitat availability patterns were revealed by comparisons of habitat variables among model strata and are presented in a following section[36]. In the absence of a logical basis for apriori planned contrasts, the procedure Bonferroni in MGLH was used as a Anova post test to determine the statistical significance of differences in bird density means between all possible pairs of forest disturbance periods and historical divergence in landuse strata (Table D7).

Mean bird density for each species was estimated for each land type association within the land use strata primary forest and settled forest and for each forest disturbance period stratum in managed forest. Univariate ANOVA (Manova in MGLH; SYSTAT 5, 1992) was used to test for the effect of land type association on bird densities (Table D8). Bird density means were compared among the 3 replicate land type associations, Huron Mountains, McCormick and Sylvania within primary forest landscapes (Table D9); among the replicate land type associations, Munising, Manistique and Rapid River for each of the 5 forest disturbance periods in managed forest landscapes[37] (Table D 10); and among the 3 replicate land type associations, Chattam, Trenary and Stonington within settled forest (Table D11).

Within the managed forest, recent logging disturbance was represented by 3 periods of forest disturbance that spanned 15 years preceding the herein reported collection of bird and vegetation data. A Two-way ANOVA (MGLH; SYSTAT 5, 1992) was used to test for the effects of the interaction between land type association and forest disturbance period on mean densities of the black-throated blue warbler, American redstart and chestnut-sided warbler (Table 5). Two-way ANOVA (MGLH; SYSTAT 5, 1992) considered the 3 land type associations of Munising, Manistique, and Rapid River within managed forest landscapes and the 3 forest disturbance periods, logged 1-5 years ago, logged 6-12 years ago, and logged >12 years ago (Figure 13).

3. Habitat Relationships Among Bird Species.

Univariate regression[38] (MGLH; Systat version 5, 1992) was used to identify habitat variables that affected densities of the 10 bird species (Table 4). The data set used in these regressions included all habitat variables and densities sampled at 321 bird census stations. Variables which had a statistically significant regression coefficient in the regressions of bird density on habitat variables, in regressions involving the black-throated blue warbler, American redstart, chestnut-sided warbler, blackburnian warbler and black-throated green warbler were considered in further ANOVA tests of means. These variables included % canopy opening (CANOPEN), number of canopy gaps of size >100m2 (GAP>100), shrub layer development measured as number of deciduous woody stems <0.5" (WSDC<0.5), number of conifer trees (TOTCON), and number of late maturity conifer trees (LMCON). Means of these habitat variables (TOTCON, LMCON, CANOPEN, GAP>100, WSDC<0.5) were calculated for each of the 5 strata of forest disturbance period within managed forest, and for each of the 2 land use strata of primary forest and settled forest (Figures 9-12; Tables D13, D20). Univariate ANOVA was used to test habitat variable means among various strata of northern hardwood forest. These comparisons elucidated the effects of forest management and environmental variables on these habitat variables (Table D12). Testing the means of habitat variables between managed forest and primary forest, between managed forest and settled forest, and between primary forest and settled forest elucidated how different land uses had affected habitat variables[39]. Comparisons also tested means of habitat variables between managed forest that is under active management (logged<12 years ago) and other strata within managed forest. Univariate ANOVA (MGLH; Systat 5, 1992) was also used to test means of habitat variables among land type associations within each forest disturbance period category in managed forest, and within primary forest and settled forest respectively (Tables D14 and D15).

To delineate the habitat selected by the black-throated blue warbler, American redstart and chestnut-sided warbler, bird census stations at which the density of the respective species was $\geq$ 80 birds/km2 were considered representative of the habitat selected by the species[40]. Univariate ANOVA (MGLH; Systat 5, 1992) was used to compare the means of microhabitat variables among the 3 species across the whole range of the northern hardwood forest sampled (Table D23) and within individual strata of forest disturbance period (Table D24).

Univariate ANOVA was also used to test for habitat variable differences among the blackburnian and the black-throated green warbler. Because of the low density of the blackburnian warbler, habitat variable means for this species and the black-throated green warbler were habitat variable averages of bird census stations at which the respective species was at or above a density of 30 birds/km2[41]. Differences between the 2 species were examined with respect to the total range of northern hardwood forest that was sampled, as well as within specific ranges of forest conditions: managed forest excluding older growth, in older growth forest within managed forest landscapes and in primary forest landscapes (Tables D16, D18).

4. Effects of Interactions of Habitat Fragmentation Related Aspects of Forest with Habitat Availability on Bird Species.

Approximations of total forest cover, and land cover types for the different land type associations were calculated by averaging land cover types for within 1.6 km radius circles centered in the different land type associations (Table 1). The range of forest cover within 1.6 km FC1MIL in the settled forest landscapes stratum was below 70%. A general absence of the black-throated blue warbler and the blackburnian in settled forest landscapes precluded testing for effects of fragmentation within this stratum. Sampling units from settled forest landscapes were as a result dropped from further analyses involving the effects of forest fragmentation related aspects on densities of blackburnian warbler and black-throated blue warbler. Bird census stations aggregated from primary forest landscapes and managed forest landscapes were stratified into 3 groups with respect to forest cover within a 1.6 km radius FC1MIL, into 2 groups with respect to length of forest edge within a 500m- radius EDGE, and into 2 groups with respect to shrub layer development WSDC<0.5. The resultant data set comprised 181 bird census stations from managed forest landscapes and primary forest landscapes. The cutoff point of 2000m, was selected for the variable EDGE to create 2 groups <2000m and >2000m; the median for 181 bird census stations for which edge data were available was 1888m. FC1MIL ranged from 70% to >90% in the aggregation of bird census stations from managed forest and primary forest landscapes. Bird census stations were stratified into 3 groups of FC1MIL >90%, FC1MIL >80%-<90%, and FC1MIL <80%->70%. The number of bird census stations, as well as land type association and forest disturbance period strata represented in each of the 12 groups resulting from this 3 variable classification are given in Table D28.

Densities of the black-throated blue warbler, American redstart and a derived variable BTARCS (Table D30) were compared among the 12 groups of bird census stations formed in the stratification based on FC1MIL, EDGE and WSDC<0.5. The variable BTARCS was derived from the difference between the density of the black-throated blue warbler BTBW and the combined densities of the American redstart AMRE and the chestnut-sided warbler CSWA. Univariate ANOVA (Manova in MGLH Systat 5,1992) was used to test the statistical significance of the effects FC1MIL, EDGE, WSDC<0.5 and to test for effects of various interactions among these variables, on BTBW, AMRE, and BTARCS (Table D29).

The effects of interactions among FC1MIL, EDGE and WSDC<0.5 were further investigated by a series of Anovas. Within each FC1MIL group, separate Anovas were used to test the effects of EDGE and of WSDC<0.5 on densities of BTBW and AMRE and on BTARCS. In considering EDGE and WSDC<0.5 separately, the effect of the variable not considered (WSDC<0.5 in the first case and EDGE in the second case) was randomized (Figure 15, Table 8). The effects of interactions between WS<0.5 and EDGE were also assessed within each of the 3 groups of FC1MIL.

To identify landscape and microhabitat aspects in highly forested landscapes (>80% forest cover) that favored the more edge tolerant American redstart and chestnut-sided warbler, ANOVA was used to test the effects of 2 additional variables, amount of northern hardwood forest within a 1.6 km radius NHWD1MIL, and % canopy opening CANOPEN, and their interactions with EDGE and WSDC<0.5. This analysis excluded the group of bird census stations for which FC1MIL in the 3-way stratification was >70%-80%. This new 4-way stratification produced 16 different bird census station groups based on 2 levels of NHWD1MIL, 2 levels of CANOPEN, 2 levels of EDGE and 2 levels WSDC<0.5. For EDGE and WSDC<0.5 the cutoff points were as previously established in the 3-way stratification. Under natural disturbance regimes (in primary forest landscapes) CANOPEN ranged from 0 to 18%; in northern hardwood forest subjected to logging, canopy opening ranged from 18% to 26%, 1-5 years after logging. A cutoff point of 20% canopy opening was selected for CANOPEN. This value of canopy opening exceeded the average of naturally occurring disturbance but was within the range of recently logged forest. Within the data set considered, a natural break in the data set at roughly 30% occurred in the continuum of percent of northern hardwood forest within a 1.6 km radius (NHWD1MIL). A cutoff point of 30% was established to reflect the actual occurring difference among the land type associations included in this study.

CHAPTER 3

RESULTS

1. Densities and Encounter Rates of Bird Species Across the Northern Hardwood Forest.

Across all combined strata of the northern hardwood forest, the 2 least common bird species of the 10 herein considered, the blackburnian warbler and the chestnut-sided warbler, were encountered in respectively 19% and 24% of all bird census stations visited (Table D2). All other 8 bird species were common with encounter rates > 40%. The red-eyed vireo, ovenbird, least flycatcher, and black-throated green warbler had high densities (Tables D2, D3) and high encounter rates >75% (Table D2). The black-throated blue warbler and the American redstart were about equally encountered at respectively 49% and 44% of bird census stations. The veery and scarlet tanager were common (encounter rate>40 %) but occurred at low densities of <15 birds / km2.

2. Association of Bird Species with Small Scale Vegetation Characteristics

Densities of all 10 bird species had significant regression coefficients on several vegetation variables that described characteristics of shrub, canopy, tree and shrub layers. Basal area, canopy opening, deciduous and coniferous woody stems (representing shrub layer development), and the presence of coniferous tree species affected densities of the most number of species (Table 4). Seven of the 10 bird species were significantly related to basal area. Densities of the American redstart, chestnut-sided warbler, and veery were

Table 4. Probability values of regressions of densities of bird species on vegetation characteristics sampled within 1200m2 at locations of 321 bird census stations in northern hardwood forest of the Upper Peninsula of Michigan.

Vegetation variable	Black-burnian w.	Black-throated green w.	Black-throated blue w.	American redstart	Chestnut-sided w.	Ovenbird	Red-eyed vireo	Scarlet tanager	Veery	Least Flycatcher
<u>Canopy Layer</u>										
% Open canopy	ns	0.01(-)	ns	<0.001	<0.001	<0.000(-)	ns	ns	0.017	ns
Basal Area	0.004	0.005	ns	<0.001(-)	<0.001(-)	0.005	ns	ns	0.014(-)	0.025
Gap 10m2	ns	ns	0.001	ns	ns	ns	ns	0.015	ns	ns
Gap 50m2	ns	0.053(-)	ns	ns	ns	ns	ns	ns	ns	ns
Gap 100m2	ns	0.051(-)	ns	ns	ns	0.051(-)	ns	ns	ns	ns
Gap >100m2	ns	0.014(-)	ns	0.006	<0.001	0.043(-)	ns(-)	ns	0.017	ns
>50% open	ns	ns	ns(-)	0.004	<0.001	ns	ns	ns	ns	ns
<u>Shrub Layer</u>										
Dec stem <0.5"	ns	<0.001(-)	<0.0001	<0.0001	0.002	0.001(-)	ns	0.002	<0.001	ns
Dec stem >0.5"	ns	0.004(-)	0.041	<0.0001	0.027	ns	ns	ns	<0.001	ns
Con stem <0.5"	ns	0.015	ns	0.04	ns	ns	ns	ns	0.004(-)	0.049(-)
Con stem >0.5"	0.001	ns	ns	0.035	ns	ns	ns	ns	0.040(-)	0.062(-)
<u>Tree Layer</u>										
Dec tree <6"	0.036(-)	ns		0.030	ns	<0.0001	ns	ns	ns	ns
Dec tree <12"	<0.001(-)	ns	ns	0.004	ns	ns	ns	ns	ns	ns
Dec tree 14-16"	ns	ns	0.005	0.025(-)	ns	ns	ns	ns	ns	ns
Dec tree >18-22"	ns	ns	0.028	<0.0001(-)	0.024(-)	ns	0.014	ns		ns
Dec tree >22"	ns	ns	ns	<0.005(-)	<0.015(-)	ns	<0.0001		ns	0.040(-)
Y. birch	0.003	ns	ns	ns	ns	ns	0.03(-)	ns	ns	ns
B. cherry-P. birch	ns	ns	ns	ns	ns	0.027	ns	ns	0.027(-)	ns
Con tree <6"	<0.001	ns	ns	ns	ns	ns	0.010(-)	ns	ns	ns(-)
Con tree <12"	<0.001	<0.004	0.022(-)		ns	ns	ns		0.023(-)	0.006(-)
Con tree 14"	<0.001	<0.001	0.033(-)	ns	ns	0.007(-)	0.03(-)	ns	0.011(-)	ns

Table 4. (continued)

Vegetation variable	Black-burnian w.	Black-throated green w.	Black-throated blue w.	American redstart	Chestnut-sided w.	Ovenbird	Red-eyed vireo	Scarlet tanager	Veery	Least Flycatcher
Tree Layer (cont'd)										
B. fir–W. spruce	0.048	ns	ns	ns	ns	ns	ns		ns	ns
Hemlock <12"	<0.001	<0.001	0.029(–)	ns	ns	0.042(–)	ns	ns	0.017(–)	0.017(–)
Pine >12"	<0.001	<0.001	ns	ns	ns	0.059(–)	ns	ns	ns	ns
W. cedar	ns	<0.001	ns	ns	ns	ns(–)	0.046(–)	ns	ns(–)	ns
Snags >10"	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Number of tree sp.	<0.001	<0.001	ns	ns	ns	ns	0.038(–)	ns	0.018(–)	0.025(–)
Ground Layer										
% Forb	ns	0.002(–)	0.006(–)	ns	ns	0.004	ns	ns	ns	0.002
% Fern	ns	ns	0.044(–)	ns	ns	ns	ns	ns	ns	ns
% Moss	0.056	0.001	ns	ns	0.013(–)	ns	ns	ns	0.035(–)	0.008(–)
Leaf	ns	0.001	0.016	0.052	<0.001(–)	ns	ns	ns	0.035(–)	ns
Grass	ns	<0.007(–)	ns	0.052	0.04	ns	0.024	ns	ns	ns
Seedling	0.034(–)	ns	ns	ns	0.04	0.044	0.031	0.036	ns	0.022(–)
Shrub	ns	0.01(–)	<0.0001	ns	<0.001	ns	ns	ns	<0.0001	ns
Con. shrub	ns	0.051	0.004	ns	ns	ns	ns		ns	ns
Low dec. tree	ns	0.016(–)	ns	ns	0.001	ns	ns	ns	0.006	ns
Low con. tree	ns	ns	ns	ns	ns	ns	0.042(–)	ns	ns	ns
Lar. woody debris	ns	0.03	ns	ns	ns	<0.0001(–)	ns	ns	ns	ns

[1](–) = negative regression coefficient.
[2]ns = not significant at 1% level of significance.

negatively related to basal area and positively related to % canopy opening. The blackburnian warbler, black-throated green warbler and ovenbird were positively associated with basal area; the ovenbird and the black-throated green warbler were negatively associated with % canopy opening and number of large canopy gaps. Densities of the blackburnian warbler, black-throated blue warbler, scarlet tanager, least flycatcher and red-eyed vireo however were unaffected by the range of variability in % canopy opening and number of canopy gaps that was sampled.

Densities of 5 of the 10 bird species, the black-throated blue warbler, American redstart, chestnut-sided warbler, scarlet tanager, and veery were positively associated with deciduous woody stems (Table 4). The black-throated green warbler and ovenbird were negatively associated with deciduous woody stems ($p<0.001$). Only densities of the blackburnian warbler, red-eyed vireo and least flycatcher were not affected by the development of the shrub layer.

Most species showed either a strong association with either deciduous or coniferous trees. The black-throated green warbler and the blackburnian warbler were highly associated with large coniferous trees. The black-throated blue warbler, ovenbird, red-eyed vireo, veery and least flycatcher were negatively associated with a coniferous tree component. Only the American redstart and the least flycatcher did not show any strong affinities to either deciduous or coniferous trees. Both species were however negatively associated with large deciduous trees.

3. Vegetation Differences Among Northern Hardwood Forest Landscapes at Different Spatial Scales

Landscape level differences

Forest cover within 1.6 km radius circles centered in settled forest landscapes ranged from 40 to 60 %, compared to forest cover of > 70% to >90% in managed and primary forest respectively (Table 1). Loss of forest cover between primary forest landscapes and managed forest landscapes was gradual and the 2 land use categories overlapped in this respect. Forest cover declined sharply in settled forest landscapes relative to managed forest. Other differences among landscapes included differences in the percentage of total land cover that is in late successional upland conifer forest (hemlock and hemlock-white pine) and in northern hardwood forest (Table 1). All managed forest and settled forest landscapes had lower levels of late maturity conifer forest types than did primary forest landscapes. Percent composition of late successional conifers and hardwood dominated northern hardwood forest however also varied among primary forest landscapes (Table 1). Land type associations replicating a land use also differed with respect to percent total forest cover that is northern hardwood forest.

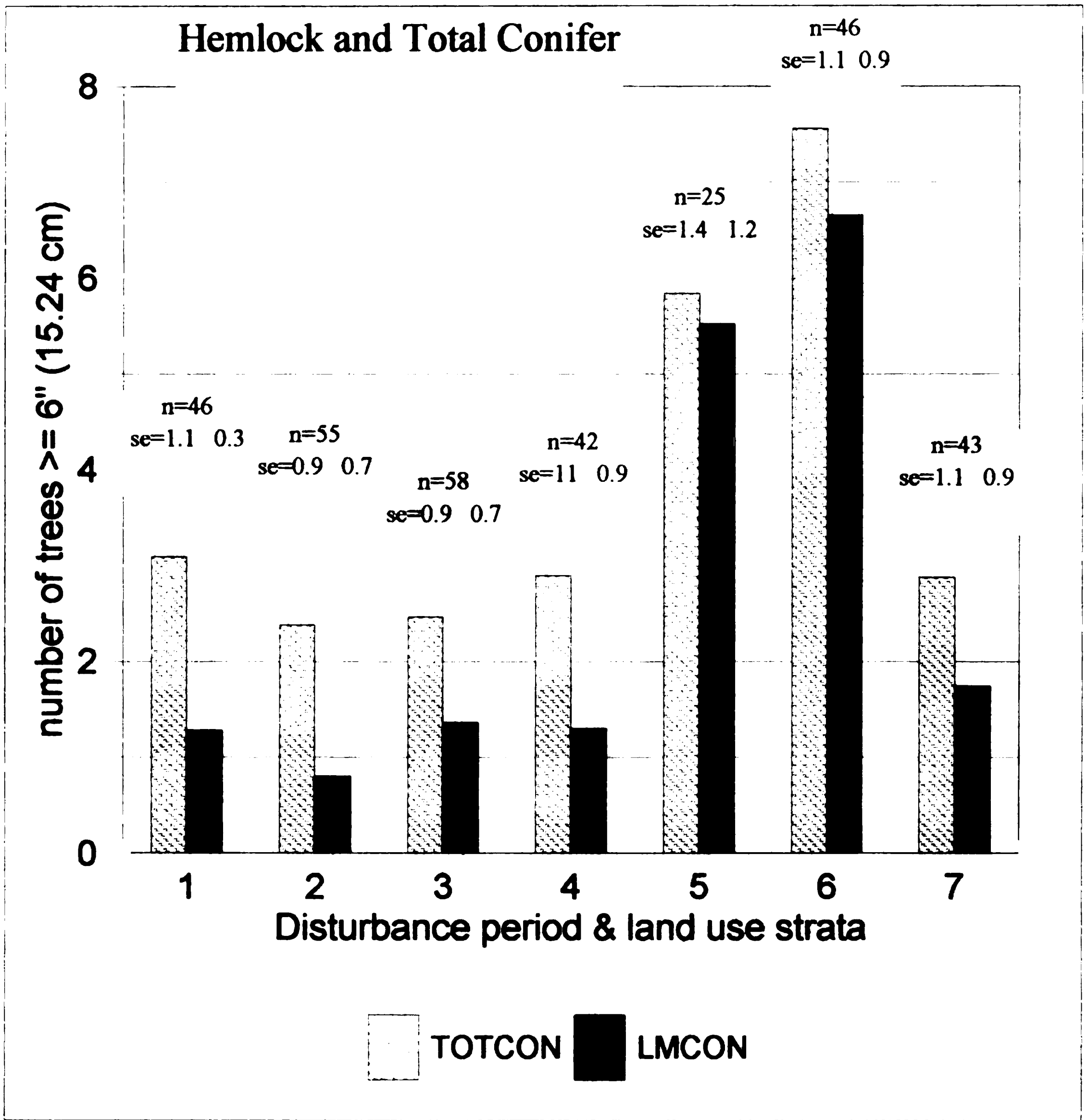
Small scale differences in the conifer tree component among northern hardwood forest strata

Small scale vegetation characteristics differed among different land type associations and different land uses. Both the number of total coniferous trees, TOTCON (includes all conifers red and white pine, hemlock, cedar, balsam fir and white spruce), and the number of late forest maturity conifers (hemlock and white pine) were significantly different among the 3 land uses primary forest, managed forest and settled forest (Table

D3). TOTCON and LMCON were significantly higher in primary forest than in either managed forest or settled forest landscapes (Tables D3, D4). Managed forest landscapes however did not differ with respect to TOTCON and LMCON from settled forest landscapes. TOTCON and LMCON did not significantly differ among different land type associations within the land use categories primary forest or settled forest. Within managed forest, neither TOTCON nor LMCON varied among land type associations replicating a forest disturbance period (Tables D5, D6). LMCON was significantly higher in the older growth forest category than in the combined 4 other strata of forest disturbance period (Figure 5; Table D3). TOTCON and LMCON however did not differ between the older growth category within managed forest and primary forest landscapes (Figure 5, Table D3).

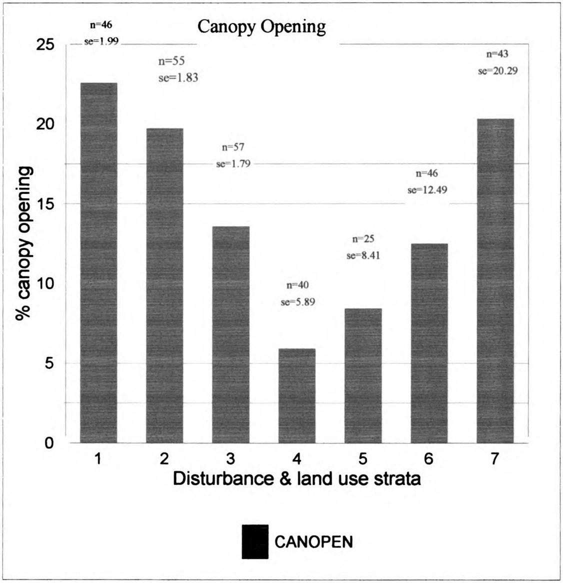
Canopy characteristics among strata of northern hardwood forest

Canopy characteristics represented by % canopy opening (CANOPEN), and canopy gaps of different size classes (GAP50, GAP100, and GAP>100) did not vary among primary forest landscapes (Tables D7, D8). Within managed forest however, significant differences among means of CANOPEN, GAP50, GAP100 and GAP>100 were common among landscapes replicating forest disturbance period strata (Tables D7, D8). In managed forest, canopy characteristics reflect the time elapsed after logging (Figures 6, 7). Percent canopy opening is highest in managed forest that had been logged less than 12 years prior to sampling (Fig. 6; Tables D9, D10). Mean canopy opening within 12 years following logging is significantly higher than means of canopy opening in primary forest and in settled forest (Table D10). It is also significantly higher than means of



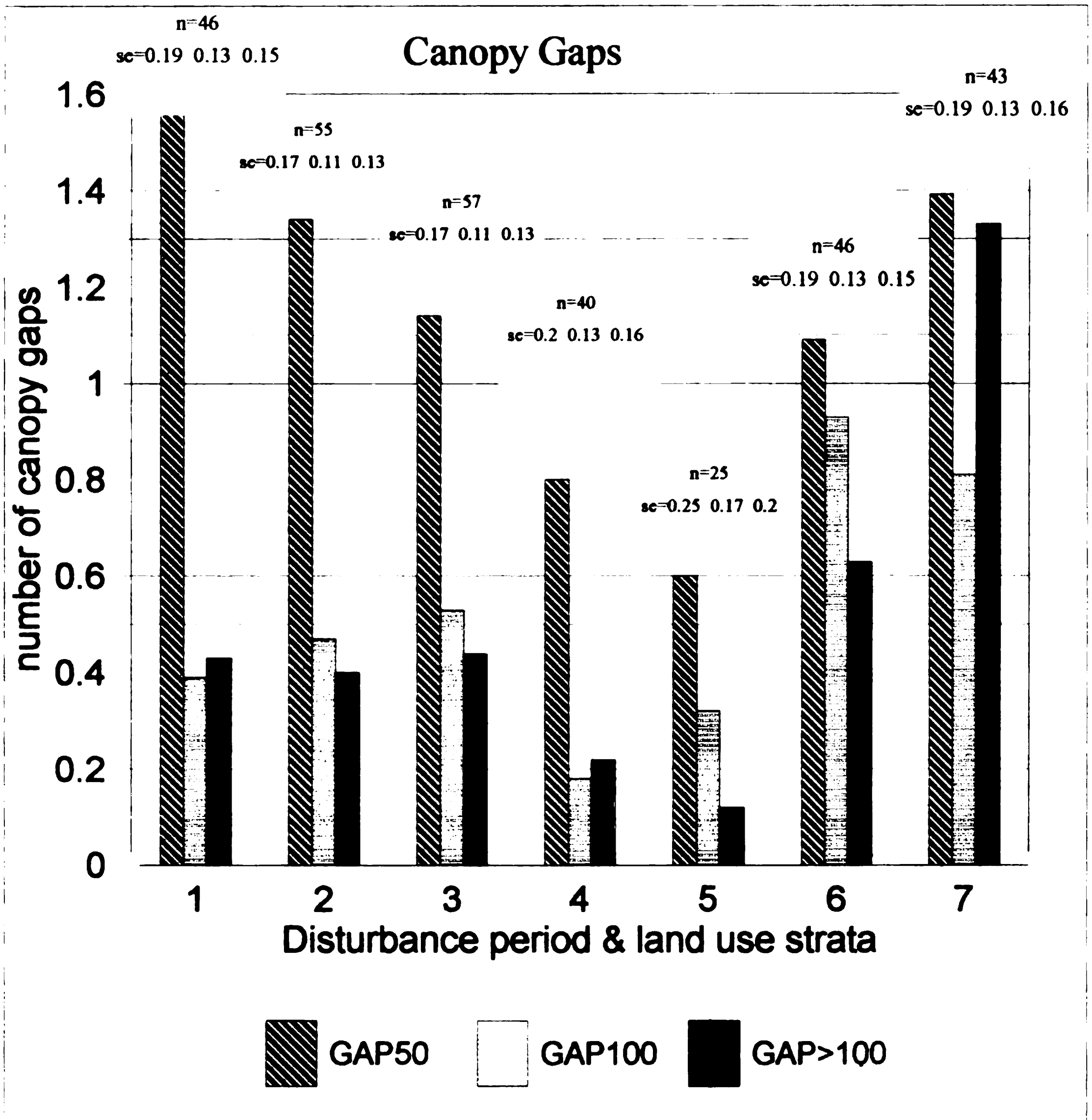
Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 5. Means of total number of conifer trees (TOTCON) and of late maturity conifers (LMCON) counted in 1200 m^2 vegetation plots at bird census stations in northern hardwood forest strata of forest disturbance period and land use.



Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 6. Means % canopy opening measured within 1200 m^2 vegetation plots in different northern hardwood forest strata representing forest disturbance period and land use.



Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

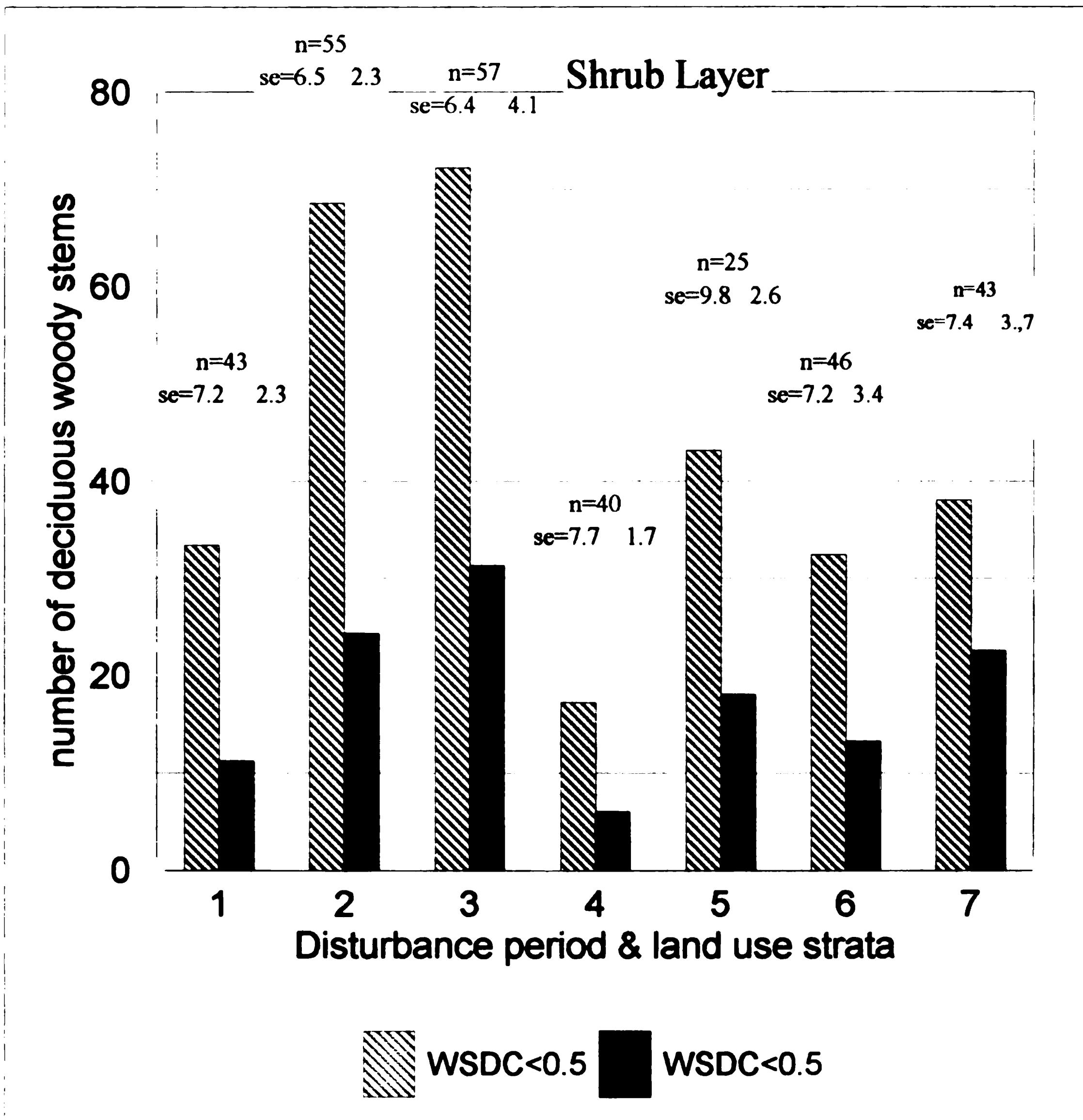
Figure 7. Mean number of forest canopy gaps of different sizes sampled with 1200 m^2 vegetation plots in different northern hardwood forest strata representing forest disturbance period and land use.

canopy opening in unlogged second growth and older growth strata in managed forest (Table D9, Table D10).

Within managed forest, mean number of gaps of size classes >25- 50m2, >50-100m2, and >100-<150m2 were all higher within 12 years after logging than in the strata of unlogged second growth forest or older growth forest (Fig. 7; Tables D9, D10). Thus within managed forest the effect of logging was an increase in the mean number of gaps of all 3 size classes. Differences in % canopy opening between strata of managed forest logged <12 years ago and primary forest, and between strata of managed forest logged <12 years ago and settled forest, were largely due to an increase in the mean number of canopy gaps of size class 50m2, GAP50 (Tables D10, D9). Mean number of gaps of the 2 size classes 100m2 and >100m2, GAP100 and GAP>100 respectively, were not significantly different between primary forest and managed forest logged <12 years ago (Table D10). Mean number of canopy gaps of size class >100m2 was significantly greater in settled forest than it was in managed forest logged <12 years ago.

Shrub layer differences among northern hardwood forest strata

Shrub layer development represented by deciduous woody stems <0.5" (1.26cm), WSDC<0.5, in general showed significant differences among different landscapes replicating a northern hardwood forest category (Table D7). Primary forest landscapes differed significantly with respect to mean number of woody stems <0.5" (p=0.023). Within managed forest, mean WSDC<0.5 differed among landscapes replicating the same forest disturbance period category (Table D7). In managed forest the mean number of woody stems increased 6-12 years after logging (Fig. 8). It was lowest in unlogged



Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 8. Means of woody stems <0.5" (1.26 cm) WSDC<0.5 and woody stems >0.5" WSDC>0.5 sampled within 12 2x5m vegetation plots located at bird census stations of different northern hardwood forest strata of forest disturbance period and landuse.

second growth forest reflecting the low % canopy opening (Figure 6). Mean WSDC<0.5 in the strata of managed forest logged <12 years ago was significantly higher than it was in either primary forest, settled forest or in the older growth forest within managed forest (Table D10).

Dynamics of canopy opening and shrub layer development within 15 years following logging across different managed forest land type associations

Dynamics of canopy characteristics and shrub layer development within 15 years following logging differed among the 3 land type associations replicating managed forest. These differences were revealed from patterns that means of % canopy opening, number of gaps in the different size classes, and number of woody stems <0.5" (1.26 cm) exhibited across forest disturbance periods in the different landscapes (Figures 9,10,11). CANOPEN, WSDC<0.5 and GAP>100 differed among the 3 different land type associations Munising, Manistique and Rapid River (Table 5, Table 6). A statistically significant interaction at the 1% level between land type association and period elapsed after logging indicates that dynamics of shrub layer development differ among landscapes. (Figures 9,10,11).

4. Density Patterns of 10 Bird Species Across Northern Hardwood Forest Strata

Density patterns across land use categories

The density of each of the 10 bird species differed significantly among strata of land use and time elapsed after disturbance (Tables D11, D12). The density pattern that a species exhibited across strata of northern hardwood forest heterogeneity, its association

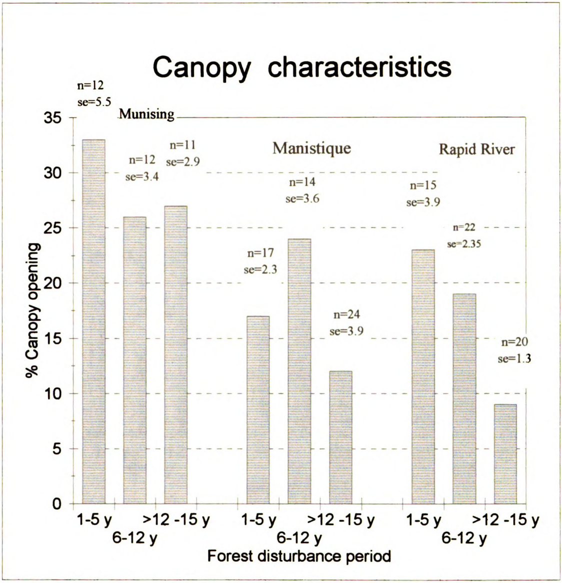


Figure 9. Mean % canopy opening sampled within 1200 m^2 vegetation plots in strata of northern hardwood forest representing 3 forest disturbance periods 1-5 years after logging, 6-12 years after logging, >12 -15 years after logging, in 3 land type associations replicating the land use strata of managed forest.

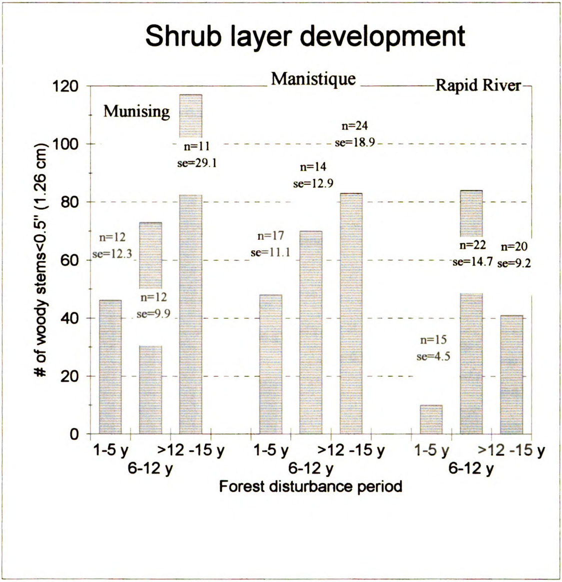


Figure 10. Mean number of woody stems<0.5" (1.26 cm) sampled within 1200 m^2 vegetation plots in strata of northern hardwood forest representing 3 forest disturbance periods 1-5 years after logging, 6-12 years after logging, >12 -15 years after logging, in 3 land type associations replicating the land use strata of managed forest.

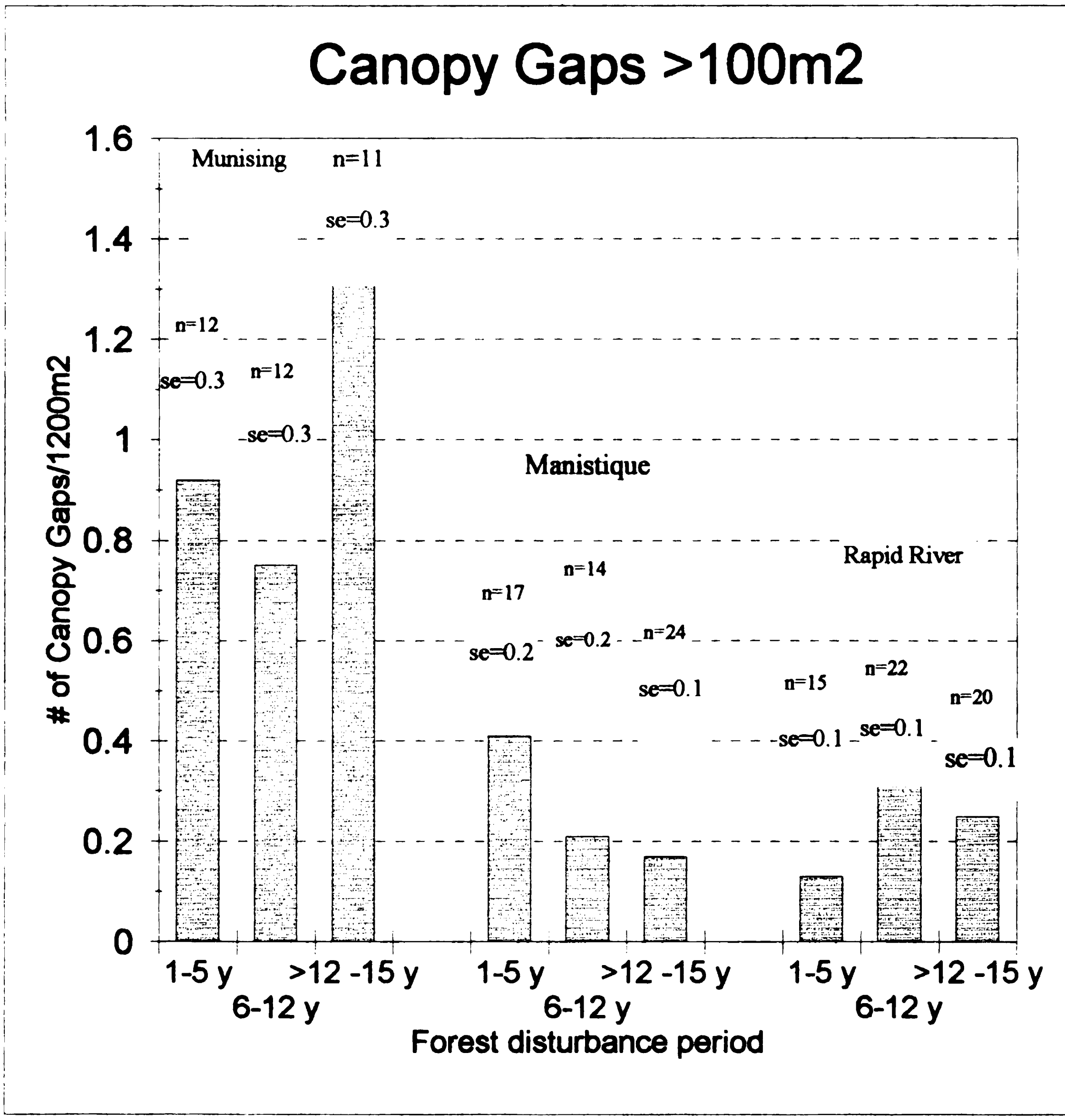


Figure 11. Mean number of canopy gaps>100m2 sampled within 1200 m^2 vegetation plots in strata of northern hardwood forest representing 3 forest disturbance periods 1-5 years after logging, 6-12 years after logging, >12 -15 years after logging, in 3 land type associations replicating the land use strata of managed forest.

Table 5. P values of 2 way ANOVAs undertaken to compare the effects of land type association, period elapsed after logging, and interaction of land type association X period elapsed after logging on means of CANOPEN, WSDC<0.5, GAP>100. Vegetation variables were sampled 1992-1994 in the Upper Peninsula of Michigan.

	CANOPEN[1]	WSDC<0.5[2]	GAP>100[3]
Land type association	<0.001	0.031	0.38
Period elapsed after logging	<0.008	0.001	<0.001
Land type association X Period elapsed after logging	0.208	0.058	0.112

[1]CANOPEN = % canopy opening.
[2]WSDC<0.5 = number of woody stems <0.5".
[3]GAP >100 = number of canopy gaps >100m2.

Table 6. Bonferroni adjusted P values of post test pairwise comparisons of CANOPEN, WSDC<0.5, and GAP>100 (during the 15 years following logging) among 3 land type associations. Vegetation variables were sampled in 1992-1994 in the Upper Peninsula of Michigan.

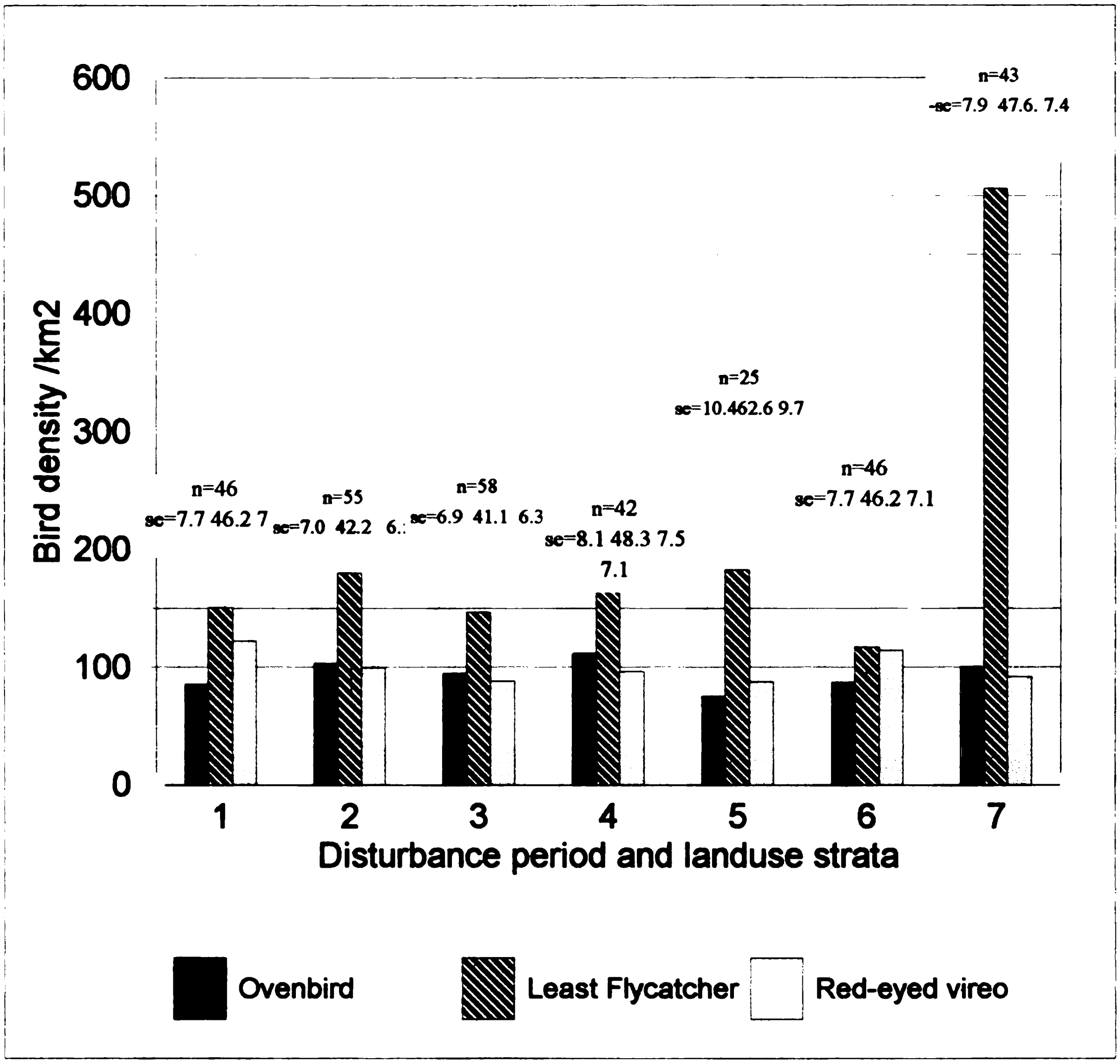
	CANOPEN	WSDC<0.5	GAP>100
Munising vs Manistique	0.001	1.00	<0.001
Manistique vs Rapid River	1.00	0.201	1.00
Munising vs Rapid River	0.001	0.037	<0.001

[1]CANOPEN = % open canopy.
[2]WSDC<0.5 = number of woody stems <0.5".
[3]GAP>100 = number of canopy gaps >100m2.

with microhabitat variables, and the pattern of vegetation characteristics across northern hardwood forest strata, suggested which underlying factors and their spatial scales affected densities of the different species. Bird species response varied from an increase in density to a near absence across land use strata from primary forest to settled forest landscapes.

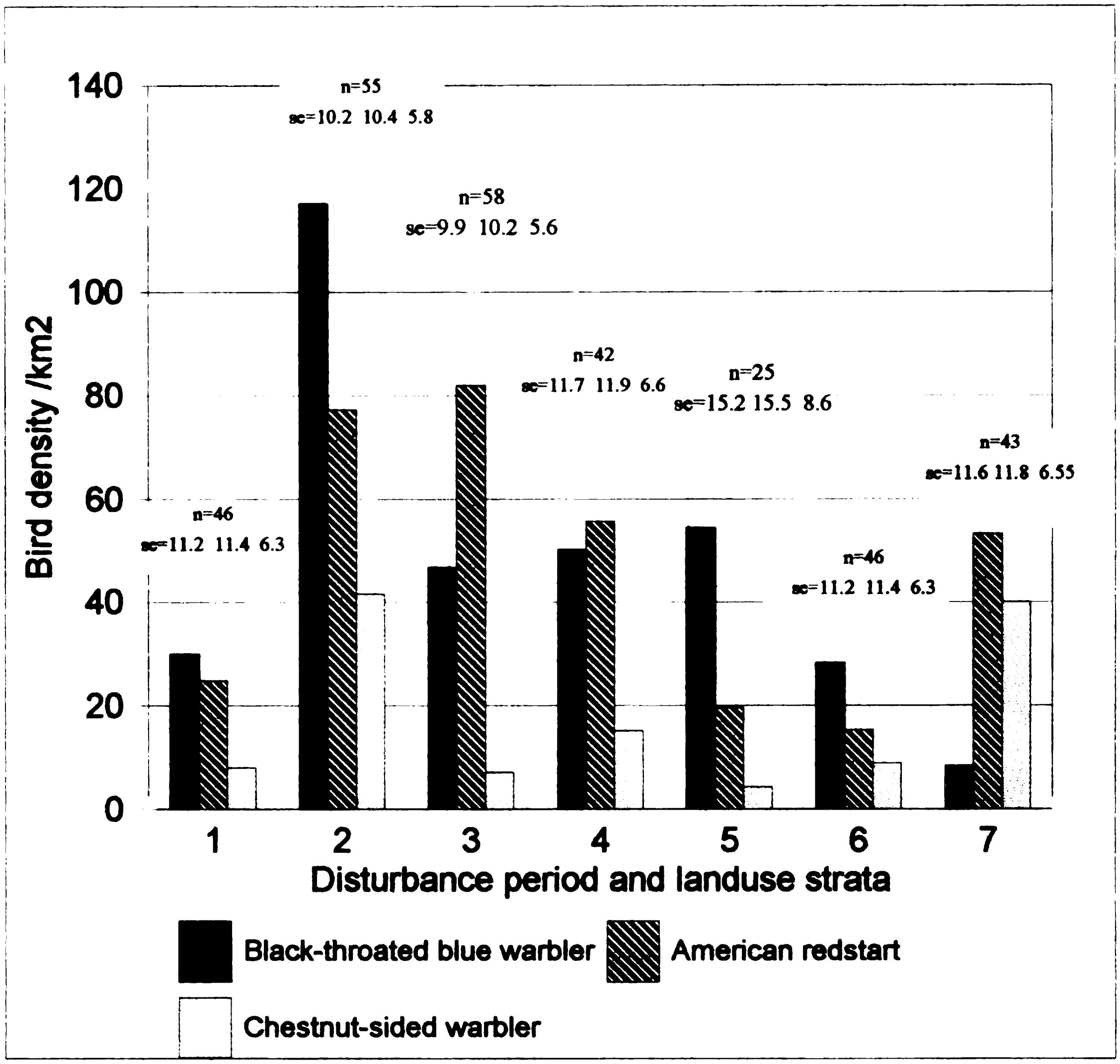
Density of the ovenbird did not differ among land use categories ($p>0.3$, Table D13, Figure 1). Three species, the least-flycatcher (Fig. 12), the chestnut-sided warbler (Fig 13), and the veery (Fig. 14) increased in settled forest landscapes (Table D13). The American redstart (Fig.13) density did not differ between managed forest and settled forest landscapes ($p=0.996$, Table D13). Densities of the red-eyed vireo (Fig.12), black-throated blue warbler(Fig. 13), scarlet tanager (Fig. 14), blackburnian warbler and black-throated green warbler (Fig. 15) were lowest in settled forest landscapes (Table D13) which suggested that these 5 species would be the most likely species to be sensitive to forest loss or fragmentation.

Density patterns of the 10 bird species among primary forest, managed forest and settled forest landscapes also served to demonstrate habitat relationships among bird species and to ordinate them along a disturbance intensity gradient. Blackburnian warbler density declined sharply between primary forest landscapes and managed forest landscapes ($p=0.003$) but to a much lesser degree than between managed forest and settled forest landscapes ($p=0.157$) (Fig. 15, Table D13) . In contrast, densities of the black-throated green warbler and scarlet tanager declined only between managed forest landscapes and settled forest landscapes ($p=0.002$ for each species, Table D13). Densities of the veery (Fig.14) and the American redstart (Fig. 13) increased significantly between



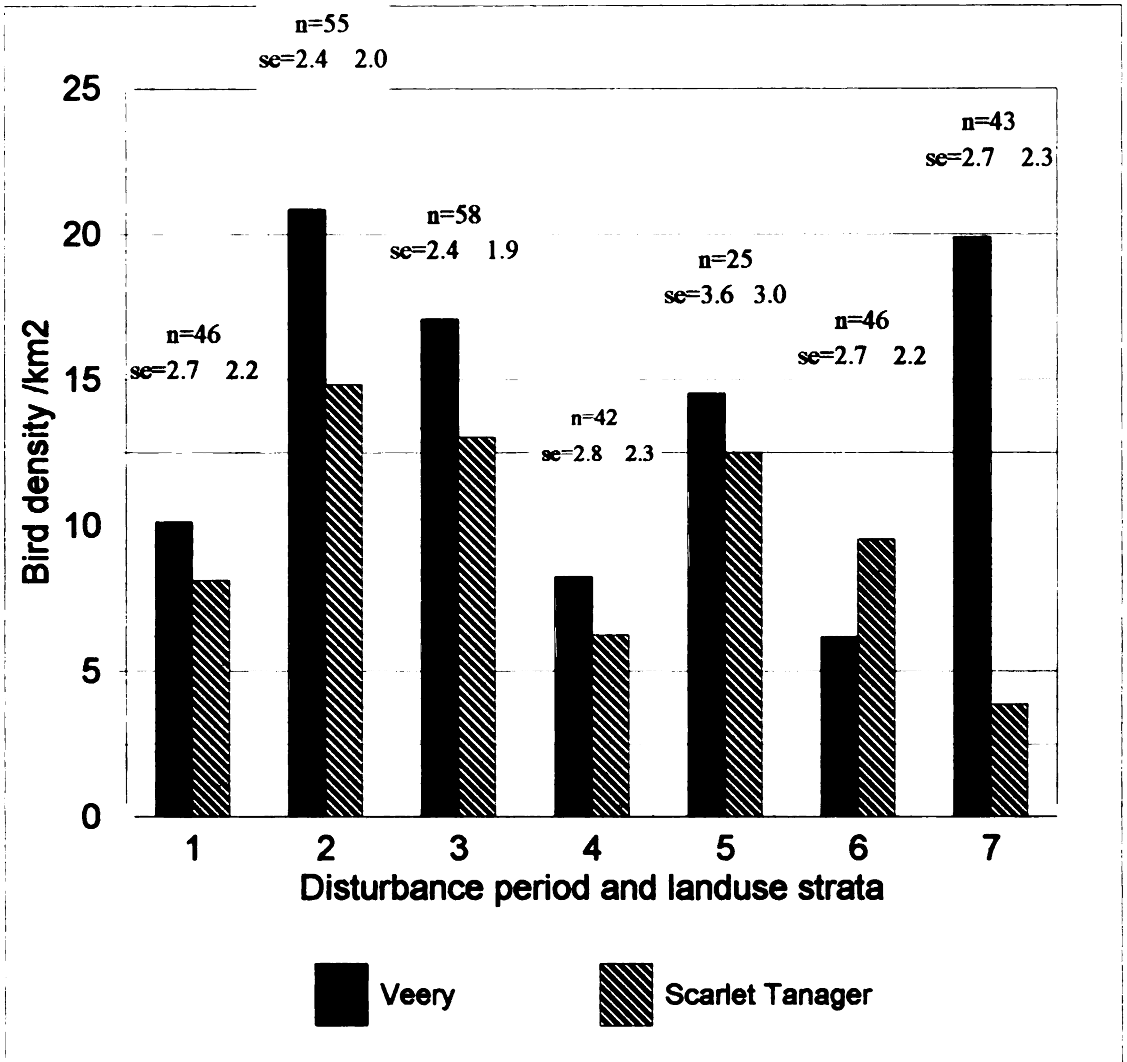
Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 12. Mean densities of ovenbird, least flycatcher and red-eyed vireo in northern hardwood forest strata of forest disturbance period and land use.



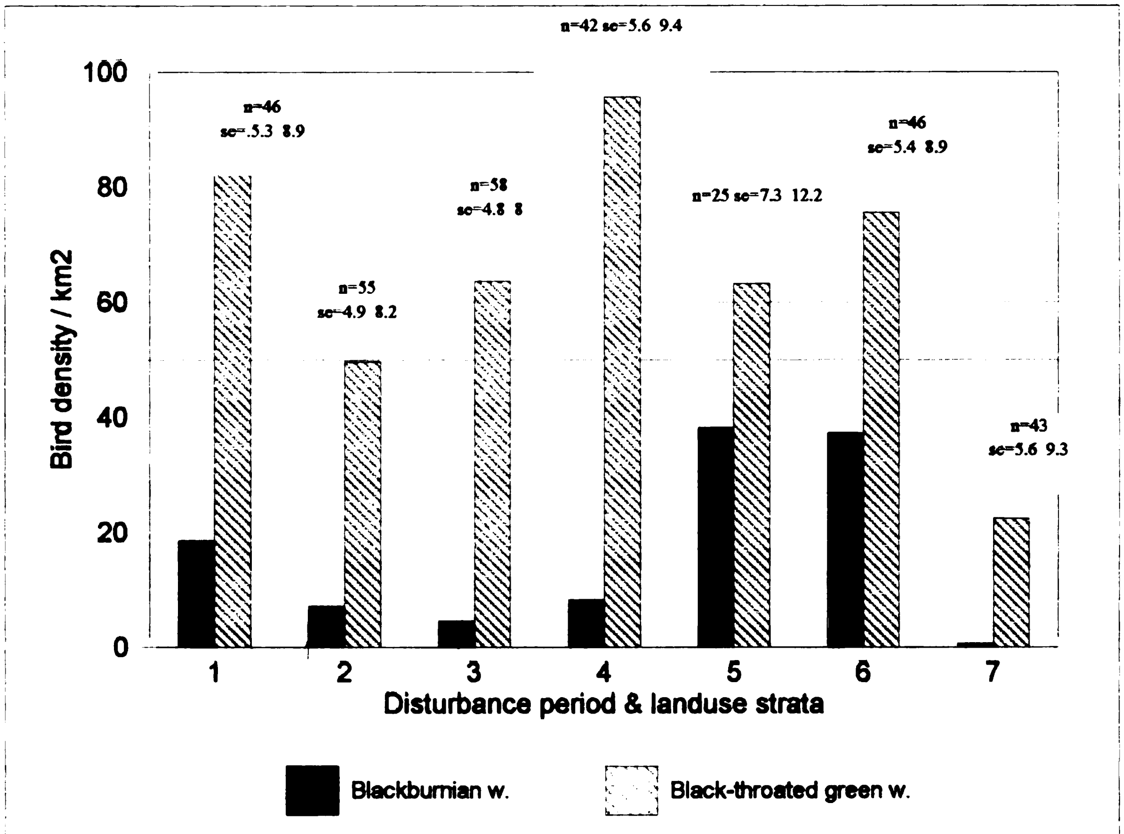
Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 13. Mean densities of black-throated blue warbler (BTBW), American redstart (AMRE) and chestnut-sided warbler in northern hardwood forest strata of forest disturbance period and land use.



Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 14. Mean densities of the veery (VEER) and scarlet tanager (SCTA) in northern hardwood forest strata of forest disturbance period and land use.



Legend: Forest disturbance and landuse strata of northern hardwood forest:
1.Managed forest logged 1-5 years ago; 2.Managed forest logged 6-12 years ago; 3.Managed forest logged >12 -15 years ago; 4.Managed forest unlogged second growth; 5.Managed forest older growth forest; 6.Primary forest; 7.Settled forest.

Figure 15. Mean densities of blackburnian warbler (BBWA) and black-throated green warbler in northern hardwood forest strata of forest disturbance period and land use. F

primary forest landscapes and managed forest landscapes (p=0.03, p=0.006 respectively; Table D13), but did not significantly differ between managed forest landscapes and settled forest landscapes. Although common in primary and managed forest landscapes, the least flycatcher sharply increased in settled forest landscapes (p=<0.001; Table D13). The chestnut-sided warbler (Fig. 13), was uncommon in primary and managed forest landscapes but increased sharply in settled forest landscapes (Table D13).

In general bird species showed a linear decline or increase along the range from primary forest landscapes to settled forest landscapes. The black-throated blue warbler (Fig. 13) was the only species that showed a significantly higher density in managed forest than in either primary forest landscapes or settled forest landscapes. Density of the black-throated blue warbler increased significantly between primary forest landscapes and managed forest landscapes (Table D13), and declined significantly between managed forest landscapes and settled forest landscapes (p=0.001). The density of the black-throated blue warbler was low in both primary forest and settled forest landscapes. The 2 land use strata did not differ (p=0.36, Table D13). [In actuality the black-throated blue warbler differed significantly between primary forest landscapes and settled forest landscapes when the 2 land use categories were compared in an Anova that included only these 2 categories. The least square means for the black-throated blue warbler was 28.28 birds/km2 (se = 4.85) in primary forest and 8.4 birds/km2 (se=5.017) in settled forest (F=8.162; df=1 and 87; p=0.005). The high increase in black-throated blue warbler density with logging in managed forest resulted in the difference between primary forest and settled forest to become insignificant relative to total variance in the ANOVA that also included all strata within the managed forest landscape.]

Overall the density patterns of all 10 bird species was as follows. Blackburnian warbler density declined sharply from primary forest to managed forest and continued a slight decline in settled forest landscapes. The red-eyed vireo, common throughout, declined gradually from primary forest landscapes to settled forest landscapes. The black-throated green warbler common in all landscape categories maintained similar densities over primary forest landscapes and managed forest landscapes but then declined sharply in settled forest landscapes. The scarlet tanager maintained similar low densities (relative to other bird species) across primary and managed forest landscapes but declined sharply in settled forest landscapes. The black-throated blue warbler density peaked in managed forest relative to both primary forest landscapes and settled forest landscapes. The ovenbird maintained high densities in all landscape categories. The American redstart was uncommon in primary forest but maintained similar densities in managed and settled landscapes. The veery which occurred at low densities throughout, had similar higher densities in settled forest landscapes and managed forest landscapes relative to its significantly lower density in primary forest. The chestnut-sided warbler was uncommon in both primary forest and managed forest landscapes but increased sharply in settled forest landscapes.

Density patterns of conifer associated bird species

Densities of the blackburnian warbler did not differ between the land use stratum of primary forest and the older-growth stratum of forest disturbance period within managed forest landscapes ($p=0.583$; Tables D14, D15). Within managed forest, blackburnian warbler mean density in the older growth stratum was significantly greater than the mean of its densities in the 4 other strata of forest disturbance period (p=0.01; Table D14). The pattern of blackburnian warbler densities in the 7 northern hardwood forest strata herein considered (Fig. 15, Table D14) closely matched the pattern of means of total number of conifer trees (TOTCON) and of number of late maturity conifer trees (LMCON) in these strata (Fig 5; Table D3). A regression of means of blackburnian density on means of late maturity conifers, LMCON, in the 7 categories of land use and forest disturbance periods explained >80% of the total variability in blackburnian warbler density ($p=0.005$, $r^2 = 0.82$).

The precipitous declines that blackburnian warbler density exhibited between primary forest landscapes and managed forest (p=0.003, Table D13) and between primary forest and settled forest landscapes suggested that a shift from primary forest to second-growth was the major factor affecting it. More exactly, blackburnian density declines reflect a loss of the coniferous tree component that had occurred as second growth northern hardwood forest replaced primary forest. In addition to representing second growth forest conditions, however settled forest also presents a decline in forest cover and in late maturity conifer forest cover at a landscape scale (Table 1) . Because of the confounding of 3 factors, loss of conifer tree component with the northern hardwood forest, loss of forest cover at the landscape level, and loss of late maturity conifer forest types at a landscape level, it is not possible to attribute the almost absence of blackburnian warbler from settled forest landscapes to any one specific factor. The fact however that the density decline between managed forest and settled forest was not statistically significant at the 1% level (p=0.157; Table D13) indicated that loss of the coniferous tree component that came about with the growth of the second growth forest was the more immediate limiting factor[1].

The density pattern that the black-throated green warbler exhibited across land use and forest disturbance period strata differed from the blackburnian's in that a significant decline occurred between managed forest and settled forest (Table D13). In contrast to the blackburnian warbler density pattern, the greater availability of late maturity conifer and total number of conifer trees in the older growth stratum (Fig. 5, Table D3) within managed forest, did not result in a greater density of black-throated green warbler relative to other forest disturbance strata (Fig. 15; Table D15). Regressions of means of black-throated green warbler density on means of total conifer trees, TOTCON, and means of late maturity conifers, LMCON, in the 7 categories of land use and forest disturbance periods were not statistically significant ($p=0.69$ and 0.84, respectively). For the black-throated green warbler, a density decline between managed forest and settled forest (Tables D11, D13) is more likely to be due to a loss of forest cover at a landscape scale.

In general neither blackburnian warbler nor black-throated green warbler mean densities differed significantly among land type associations that replicated a land use (Tables D16, D17), or among land type associations within managed forest that replicated a forest disturbance period category (Table D18; p values of Anovas undertaken to test differences in mean densities among land type associations ranged from 0.11 to 0.9, Table D19). All 3 land type associations replicating primary forest landscapes (Huron Mountains, Sylvania, and McCormick) showed consistently higher densities of blackburnian warbler than did all other land type associations replicating managed forest landscapes (Munising, Manistique, and Rapid River) and settled forest landscapes

(Chattam, Trenary and Stonington; Tables D16-D18).

Habitat relationships between the 2 species were further explored for individual forest strata. Means of TOTCON and of LMCON at bird census stations in which the blackburnian warbler and the black-throated respectively occurred at a density >30 birds/km2 were considered to represent the means of these 2 variables in habitat selected by each of the 2 bird species. Means of TOTCON and LMCON for each of the blackburnian warbler and the black-throated green warbler were compared with means of TOTCON and LMCON of each of the 7 northern hardwood forest strata. In these comparisons, means of TOTCON and LMCON at bird census stations in which the blackburnian warbler occurred at a density >30 birds/km2, was greater than means of TOTCON and LMCON in all strata of the northern hardwood forest except for primary forest landscapes and the older growth within managed forest landscapes [2] (Table D20). As expected from its high encounter rate and high density in managed forest, the black-throated green warbler did not differ from any of the strata except primary forest landscapes. In primary forest, mean LMCON in the habitat selected by the black-throated green warbler was lower than the mean LMCON for that stratum (Table D20).

Mean CANOPEN for the blackburnian warbler was larger than mean CANOPEN of each of the northern hardwood forest strata except logged 1-5 years ago and logged 6-12 years ago in managed forest landscapes[3] (Table D13, D16). This indicated that the blackburnian warbler was more limited by its selection for late maturity conifers and total conifers in the northern hardwood forest, rather than by any fragmentation related effect occurring at the micro habitat because of canopy opening. The additional decline in blackburnian warbler from managed forest landscapes to settled landscapes could not be due to a more severe loss of micro-habitat availability since the LMCON and TOTCON did not differ between the managed forest landscapes and settled forest landscapes. The effects brought about by a reduction in canopy opening would also not be a likely factor since the blackburnian warbler mean on CANOPEN did not significantly differ from the mean for settled forest landscapes at the 0 .1 level (p=0.169, Table D17). Blackburnian warbler density was also greater in forest disturbance period 1-5 years after logging than all other forest disturbance periods in managed forest except the older growth forest (Table D11). This stratum had the highest mean CANOPEN of all northern hardwood forest strata considered[4].

The blackburnian warbler and the black-throated green warbler differed with respect to TOTCON (p=0.001) and LMCON (p=0.002) (Tables D20 and D21). The black-throated green warbler was associated with habitat that was relatively more deciduous. The 2 species did not differ in terms of CANOPEN (p=0.937) or in terms of GAP>100 (p=0.22, Tables D20, D21). This indicated that the relationships between the 2 species at the micro habitat level did not have an aspect of habitat fragmentation. Habitat separation between the blackburnian warbler and the black-throated green warbler was only significant in managed forest excluding older growth (p=0.062). The 2 species overlapped the most in primary forest landscapes (p=0.365, Table D22), and the least in managed forest excluding older-growth (p=0.062)[5]. In regressions of blackburnian warbler on LMCON in different strata of the model, only in the strata of primary forest landscapes and in older-growth were the regressions statistically significant. This indicated that for most of the northern hardwood forest in managed landscapes the amount of LMCON was uniformly too low to affect the habitat selection of the blackburnian warbler.

Density patterns of bird species affected by a shrub-layer

Densities of the black-throated blue warbler, American redstart, chestnut-sided warbler, veery and scarlet tanager showed a significant response to the increase in shrub layer development as characterized by the number of woody stems WSDC<0.5 in forest disturbance periods 6-12 and >12-15 years following logging disturbance in managed forest (Figures 13, 14, 8). The black-throated blue warbler, chestnut-sided warbler and veery sharply increased 6-12 years after logging, but declined >12 years after that disturbance (Figures 13, 14, Table D11). The 3 species had mean densities in the period 6-12 years after logging that were significantly higher than their respective mean densities for the combined 4 other remaining strata ($p=0.001$ for the black-throated blue warbler, $p=0.004$ for the chestnut-sided warbler, and $p=0.003$ for the veery; Tables D11, D14). The American redstart increased (6- 12 years after logging) but attained even higher densities in the forest disturbance period >12-15 years after logging; (Figures 13 and 14; Tables D11, D14). Mean density of the American redstart during the period of >12-15 years after logging was significantly higher than mean density in the remaining combined other strata of managed forest (Table D14). Although the scarlet tanager showed a similar pattern of increase as the redstart in the period of 6-12 and >12-15 years after logging, it also had high densities in older growth forest within managed forest. Density increases of the scarlet tanager in forest disturbance periods 6-12 years and >12-15 years were not as distinct as were densities of other bird species associated with a shrub layer development (Tables D13, D14 and D15). Densities of the black-throated blue warbler, American redstart, chestnut-sided warbler and veery differed significantly among land type associations replicating either a land use (primary and settled forest) or a forest disturbance period in managed forest (Table D19). The pattern these species exhibited across land type associations reflected the variability of WSDC<0.5, canopy gaps and canopy opening across landscapes (Tables D7& D8).

The black-throated blue warbler's significant density increase between primary forest and managed forest (p=0.023, Table D13) is most likely a response to the increase in shrub layer development in managed forest landscapes following logging disturbance. The black-throated blue warbler's significant association with WSDC<0.5 (p=0.001; Table 4) and its significant density increase in disturbance period 6-12 years after logging (p= <0.001, in Anova comparing density in period 6-12 years after logging with density in the other pooled strata; Table D13) support this argument. Compelling arguments however exist that preclude shrub layer development from being a major factor in the precipitous decline of the black-throated blue warbler in settled forest landscapes. The American redstart and the chestnut-sided warbler, 2 species equally associated with WSDC<0.5 increased in settled forest landscapes. Additionally regressions of American redstart density, and of chestnut-sided warbler density, on WSDC<0.5 in 'settled forest landscapes'[6] were highly significant (p= 0.018 for each regression, Table D23). The significance of these regressions indicated that settled forest landscapes included some heterogeneity in the development of the shrub layer that the American redstart and chestnut-sided warbler were tracking, even though the level of shrub layer development when aggregated over the category of settled forest landscapes was significantly lower than in managed forest landscapes (p=0.03; Table D10).

Habitat relationships among the black-throated blue warbler, American redstart and chestnut-sided warbler

Microhabitat relationships among the black-throated blue warbler, American redstart and chestnut-sided warbler were quantified to test the hypothesis that forest fragmentation aspects and not simply the presence of a well developed sapling layer could be responsible for observed density and distribution patterns of the 3 species. Means of WSDC<0.5, CANOPEN and GAP>100 were calculated for locations in the forest where each respective species was encountered at a density >80 birds /km2 (Table D24) in order to elucidate how the 3 species partitioned the availability of microhabitat. The 3 species did not differ with respect to mean number of WSDC<0.5 ($p=0.8$) but differed in terms of CANOPEN ($p=0.001$) and GAP>100 ($p=0.006$, Table D25)[7].

The increase in American redstart and chestnut-sided warbler densities following logging corresponded to what would have been predicted based on their habitat association with reduced canopy cover and deciduous woody stems[8] (large canopy gaps >100m2 did not significantly increase with logging). The relative density patterns that the black-throated blue warbler, American redstart and chestnut-sided warbler exhibited in managed forest however, across forest disturbance periods affected by logging 1-5 years after logging, 6-12years after logging, and >12-15 years after logging, differed from what would have been expected based on their habitat ordination along a gradient of canopy cover. The black-throated blue warbler increased in forest disturbance period 6-12 years after logging when the canopy was still highly open, but declined in the forest disturbance period >12-15 years when the canopy was already closing. The American redstart on the other hand maintained a high density in forest disturbance period >12-15 years after logging when the canopy was already closing surpassing black-throated blue warbler density during that forest disturbance period (Figure 14; Tables D11, D9).

Basing habitat relationships among the 3 species on their distribution across the whole range of northern hardwood forest, the 3 species were well separated along the gradients of canopy opening and large canopy gaps. Within the managed forest however there was not a clear separation among the microhabitats selected by the black-throated blue warbler, American redstart and the chestnut-sided warbler. The 3 species overlapped with respect to canopy opening ($p=0.74$), canopy gaps>100m2 ($p=0.324$) and shrub layer development (Tables D26, D27)[9]. The fact that micro habitat differences among the black-throated blue warbler, American redstart and chestnut-sided warbler could not account for the pattern of their relative density increases after logging, suggested that factors other than micro habitat differences affected their density patterns.

Since the habitat relationships among the black-throated blue warbler, American redstart and chestnut-sided warbler across the whole range of northern hardwood forest sampled reflected a fragmentation component (different response to % canopy opening and canopy gaps and different patterns of density from primary forest to settled forest), it was of interest to elucidate their relative densities in the different land type associations following disturbance by logging. The effects of interactions of land type association and forest disturbance period (1-5 years, 6-12 years and >12-15 years following logging) on densities of the black-throated blue warbler, American redstart and chestnut-sided warbler were explored in 2- way ANOVAs. Although all 3 species responded positively to forest disturbance, the pattern of their relative densities and responses differed in the 3 land type associations (landscapes of Munising, Manistique and Rapid River) replicating managed forest landscapes (Figures 16,17,18). The effects of land type association, period of

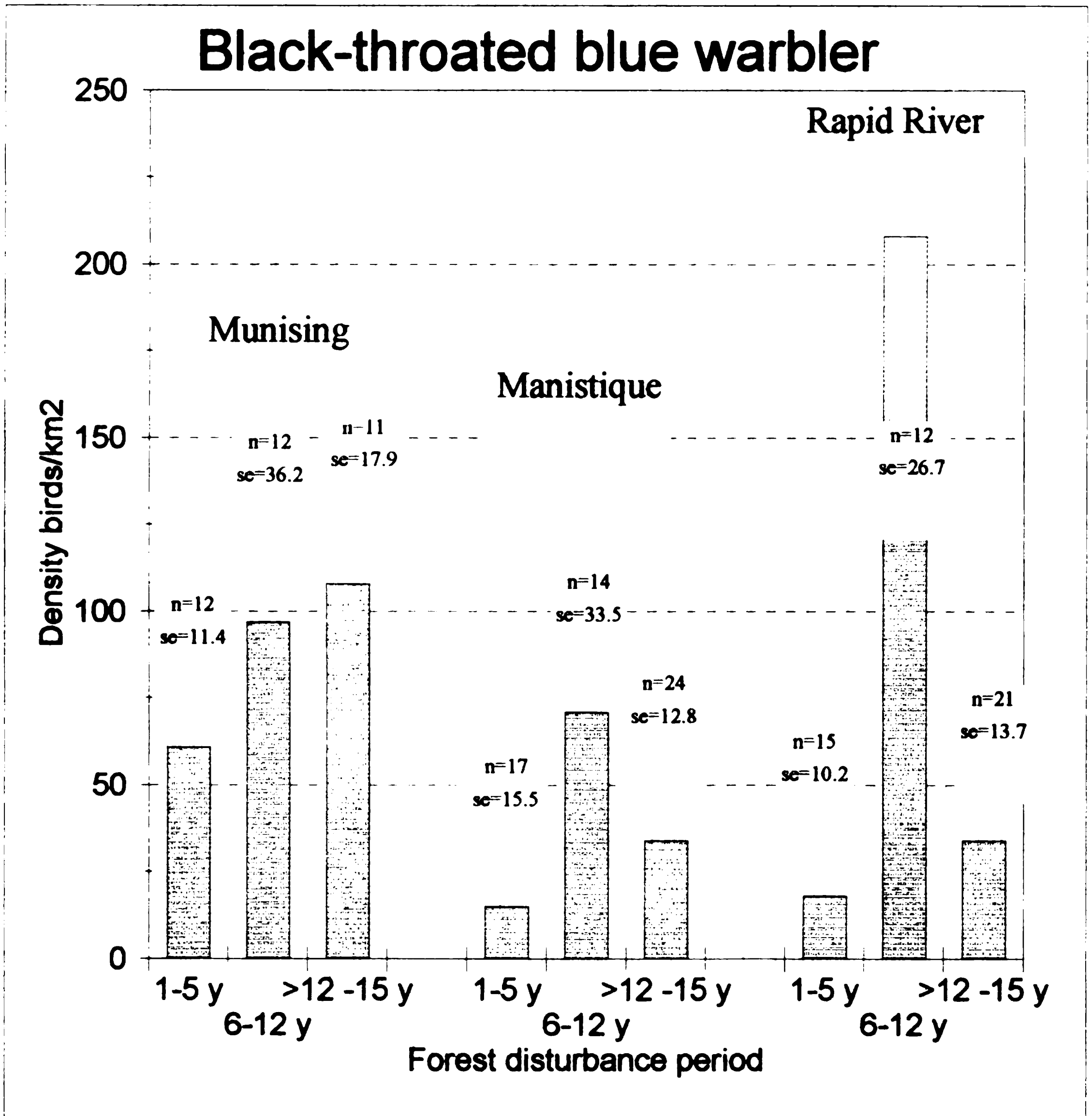


Figure 16. Mean densities of the black-throated blue warbler in strata of northern hardwood forest representing forest disturbance periods 1-5 years, 6-12 years and >12-15 years after logging in different land type associations replicating managed forest.

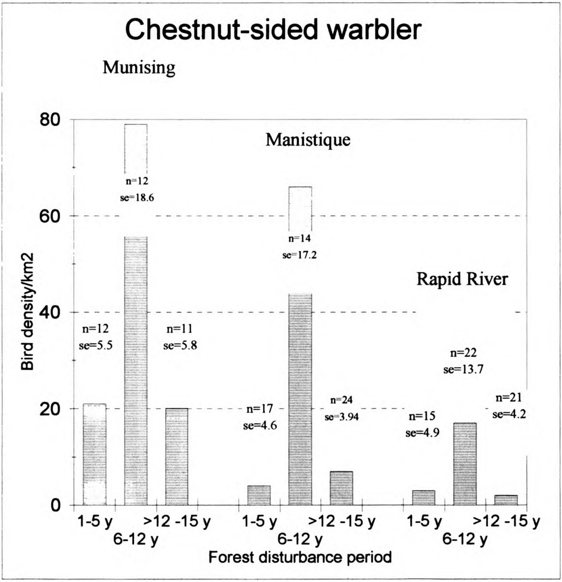


Figure 17. Mean densities of the chestnut-sided warbler in strata of northern hardwood forest representing forest disturbance periods 1-5 years, 6-12 years and >12-15 years after logging in different land type associations replicating managed forest.

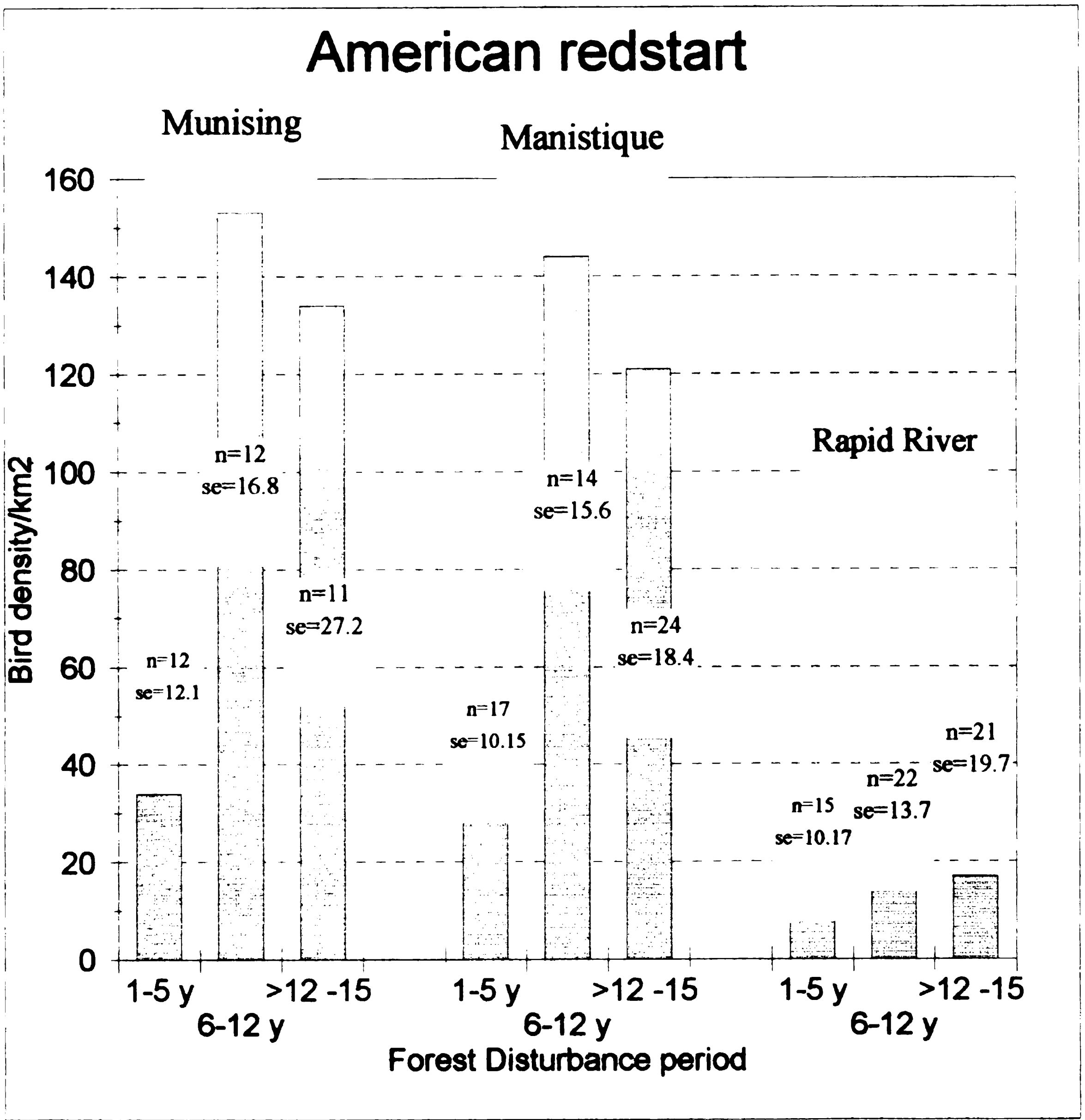


Figure 18. Mean densities of the American redstart in strata of northern hardwood forest representing forest disturbance periods 1-5 years, 6-12 years and >12-15 years after logging in different land type associations replicating managed forest.

disturbance and the interaction of land type association x period of disturbance were statistically significant for the 3 species (Table 7). The 3 landscapes differed with respect to the magnitude of a bird species density increase in any of the forest disturbance strata, and with respect to the relative densities of the 3 bird species across the 3 forest disturbance periods. The black-throated blue warbler density in forest disturbance period 6-12 years after logging in the Rapid River landscape, was 2-3 times its levels in that same forest disturbance period in either the Manistique or Munising landscapes (Figure 16 $p=<0.001$ for both pairwise comparisons by Tukey's post test). In contrast increases in chestnut-sided warbler and American redstart densities in the Rapid River landscape in forest disturbance periods 6-12 years after logging and >12 -15 years after logging were minimal compared to these same 2 forest disturbance periods in Manistique and Munising (Figures 17 and 18; $p<0.001$ for all 4 pairwise comparisons by Tukey's post test).

The variable BTARCS was considered as the difference between the black-throated blue warbler density and the combined densities of the American redstart and chestnut-sided warbler. This variable expressed a contrast between the forest interior black - throated blue warbler and the more edge tolerant chestnut-sided warbler and American redstart. Both the Manistique and Munising landscapes showed a negative (BTARCS) for almost all 3 forest disturbance period strata. In contrast, BTARCS was positive for all 3 strata of forest disturbance period in the Rapid River landscape (Figure 19).

Table 7. **P values of 2 way Anovas undertaken to compare the effects of land type association, period elapsed after logging and interaction between land type association and period elapsed after logging on mean densities of the black-throated blue warbler (BTBW), American redstart (AMRE), and chestnut-sided warbler (CSWA) and the mean of the derived variable (BTARCS) sampled 1992-1995 in the Upper Peninsula of Michigan.**

Effect	BTBW	AMRE	CSWA	BTARCS
Land type association	0.005	<0.001	0.001	0.231
Period elapsed after logging	<0.001	<0.001	<0.001	<0.001
Interaction Period elapsed after logging *Land type association	<0.001	0.005	0.047	<0.001

[1]BTARCS = density difference between the density of the black-throated blue warbler and the combined densities of the American redstart and the chestnut-sided warbler (BTBW-(AMRE+CSWA)).

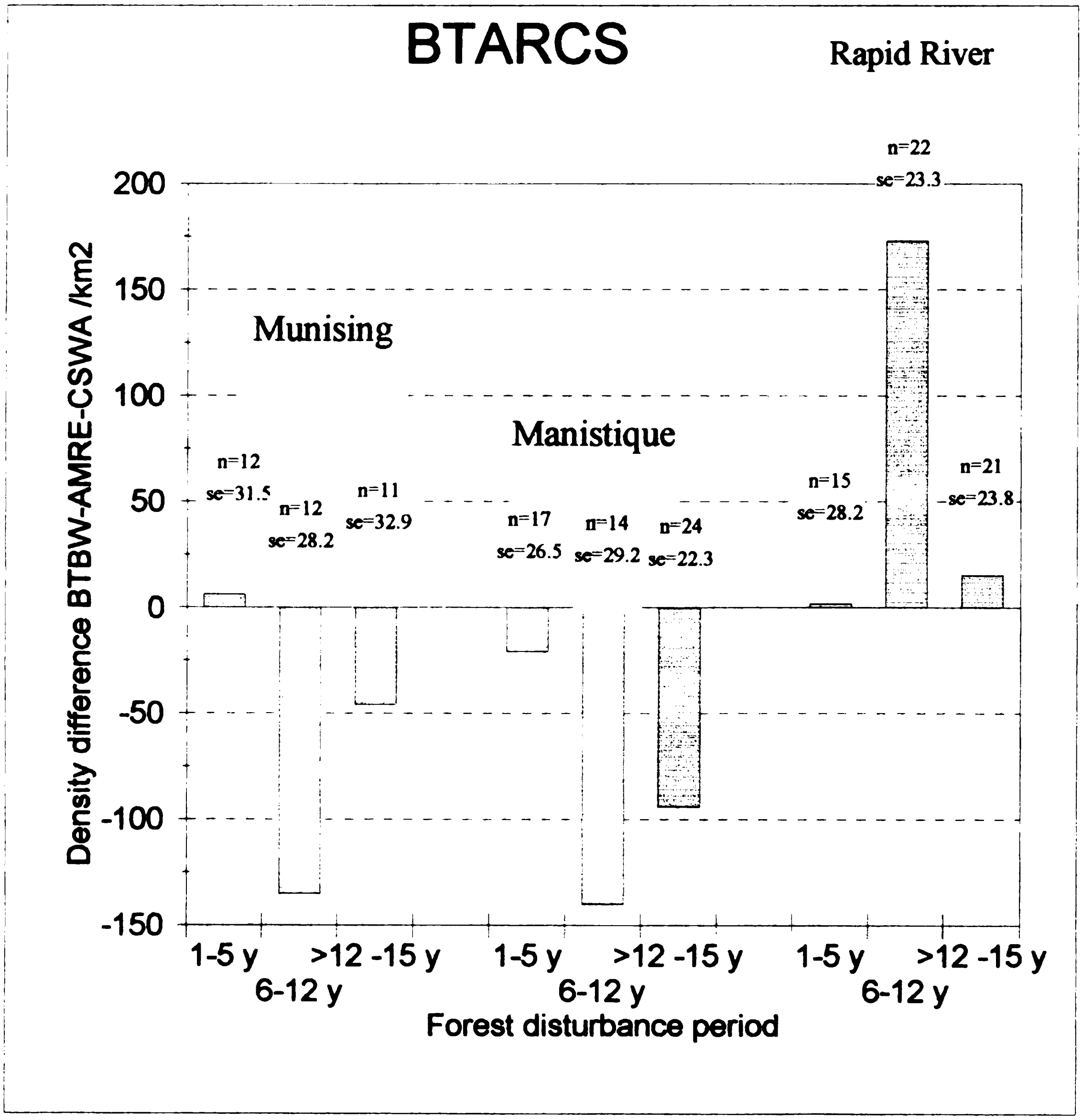


Figure 19. Mean densities of BTARCS (Density difference of the black-throated blue warbler - the combined densities of the American redstart and the chestnut-sided warbler) in strata of northern hardwood forest representing forest disturbance periods 1-5 years, 6-12 years and >12-15 years after logging in different land type associations replicating managed forest.

5. Effects of Landscape level and Micro habitat Variables on Density of the Black-throated Blue Warbler, American Redstart and the Derived Variable BTARCS.

Effects of forest edge, forest cover and shrub layer development

The effects of landscape level variables on the densities of the black-throated blue warbler and American redstart, and on the variable BTARCS were explored as micro-habitat level variables alone failed to provide a solid explanation for the variability of BTARCS among the 3 land type associations replicating managed forest. Landscape factors that were considered included 'forest cover within a 1- mile radius' (FC1MIL), and 'amount of forest edge within a 500m -radius from the bird census station' (EDGE). These effects were explored in managed forest and primary forest only[10] .

A 3-way ANOVA considered 3 levels of FC1MIL, 2 levels of EDGE and 2 levels of WSDC<0.5[11]. [The contribution of sampling points to each resultant group of forest cover, forest edge and woody stems from different land type associations, land use and forest disturbance period strata is given in Table D28]. The density of the black-throated blue warbler was mostly affected by WSDC<0.5 ($p<0.003$, Table D29) and to a lesser extent by FC1MIL ($p= 0.028$) and EDGE (0.10). The black-throated blue warbler density was also affected by interactions between FC1MIL and EDGE ($p=0.056$), between FC1MIL and WSDC<0.5 ($p= 0.025$) and among FC1MIL, EDGE and WSDC<0.5 ($p=0.022$). The effects of WSDC<0.5 on the black-throated blue warbler could be appreciated after the effects of EDGE and FC1MIL were randomized. The effect corresponded to a difference in density between 44.56 birds/km2 (n=90, se=9.8) for the group representing 'WSDC<0.5' = <50 stems and 85.32 birds/km2 (n=91, se=9.55) for the group of 'WSDC<0.5' = >50stems (Table D30).

Highest densities of the black-throated blue warbler were for the group of FC1MIL >80-90% and not as would be expected for FC1MIL >90% (Table D30). The seemingly contradictory decrease in density from 89.48 birds/km2 in FC1MIL >80-90% (n=68, se=10.47) to 53.86 birds/km2 (n=74 se=11.1 in FC1MIL >90% (Table D30) for a forest interior bird species was the result of a confounding of 2 effects (an artifact of this specific data set): the actual effect of forest cover within 1 mile and intensity of forest disturbance. Forest cover >90% was represented largely by primary forest and older growth forest within managed forest, while forest cover in the range of 80-90% was highly represented by managed forest[12]. The effect of EDGE on density of the black-throated blue warbler as a main factor was not as significant as its interactions with FC1MIL and WSDC<0.5. Interactions among FC1MIL, EDGE, and WSDC<0.5 however were assessed in more detail and are discussed later.

Density of the American redstart was significantly affected by FC1MIL, EDGE, and WSDC<0.5 ($p = 0.001$, <0.001, and 0.001 respectively, Table D29) in the ANOVA analysis that included all 3 variables as factors. Interactions between FC1MIL and EDGE and that between EDGE and WSDC<0.5 were also statistically significant ($p=0.001$ and 0.012 respectively; Table D29). When the effects of EDGE and WSDC<0.5 were randomized (one-way Anova with FC1MIL as factor), the least squares mean for American redstart density in FC1MIL >90% was 29.30 birds/km2 (n=74; se=8.62) in contrast to 81.43 birds/km2 (n=39; se=10.72) in FC1MIL > 70-80%. When the effects of FC1MIL and WSDC<0.5 were randomized (One way Anova with EDGE as factor), the effect of EDGE could be recognized as an increase in density from 22.66 birds/km2 (n=108 se=7.04) for EDGE <2000m to 73.95 birds/km2 (n = 73, se =8.0) for

EDGE>2000m. In a similar randomization of the other 2 factors (one way Anova WSDC<0.5 as factor), the effect of WSDC<0.5 was an increase from 31.01 birds/km2 (n = 90, se = 7.63) for 'WSDC<0.5' = <50 to 65.6 birds/km2 (n = 91, se = 7.4) for 'WSDC<0.5' = >50 (Table D30). The interaction of FC1MIL and EDGE increased American redstart density from 25.9 birds/km2 (n=53 se=9.11) for FC1MIL>90%, EDGE<2000m to 136.56 birds/km2 (n=20, se=14.9) for FC1MIL>70-80% and EDGE >2000m.

The derived variable BTARCS was highly affected by forest cover FC1MIL (p<0.001, Table D29), by EDGE (p<0.001) and by the interactions between EDGE and FC1MIL (p=0.001) and among FC1MIL, EDGE, and 'WSDC<0.5'. BTARCS was negative for most groups of bird census stations for which FC1MIL was <80%, except for combinations of FC1MIL<80% and EDGE <2000m (Table D30). The least squares mean for BTARCS was negative (-34.18) for EDGE >2000m (n= 73, se=13.9) when the effects of FC1MIL and 'WSDC<0.5' were randomized (one way Anova with EDGE as factor). The highest (positive) value of BTARCS was for the group FC1MIL >80% - 90%; EDGE <2000m, and 'WSDC<0.5' = >50, which delineates the conditions under which the black-throated blue warbler fared best. The lowest value of BTARCS was for FC1MIL <80%; EDGE >2000m; 'WSDC<0.5' = >50. BTARCS was also negative for FC1MIL >80 - 90%, EDGE >2000m, 'WSDC<0.5' = >50 indicating that edge increases edge bird species even in relatively high forest cover.

The significant effect of the interaction between FC1MIL, EDGE, and WSDC<0.5 and the relevance of this relationship to management of forest bird species, warranted exploring the effects of edge and shrub layer development separately within each level of forest cover. Within forest cover >90%, the effect of EDGE and the effect of the interaction of EDGE with 'WSDC<0.5' were not significant for either the black-throated blue warbler or the American redstart (Table 8) and as a result these 2 effects were not significant for BTARCS. Densities of both the black-throated blue warbler and the American redstart increased at the higher level of WSDC<0.5. An increase in WSDC<0.5 affected the black-throated blue warbler more than it affected the American redstart. BTARCS remained positive for all combinations of EDGE and WSDC<0.5 within FC1MIL >90% (Figure 20).

Within forest cover 80-90%, the higher level of forest edge but the effect of EDGE was not significant (p=0.194). The American redstart density more than tripled between the lower and higher levels of EDGE (Figure 20a), an increase that was statistically highly significant (p=0.004, Table 8). The interaction between EDGE and 'WSDC<0.5' was significant for the black-throated blue warbler, and American redstart and was reflected in a high statistical significance for BTARCS. The American redstart densities remained relatively low for all combinations of WSDC<0.5 and EDGE except for the high levels of both EDGE and 'WSDC<0.5' (>2000m, >50 respectively). The black-throated blue warbler increased with a higher level

of 'WSDC<0.5' (p=0.006). That increase was greatest for the condition of EDGE <2000m (p=0.053 for the interaction between EDGE and 'WSDC<0.5)'. The Black-throated blue warbler density declined from 181 birds/km2 for the group WSDC<0.5 = >50; EDGE <2000 to 83 birds/km2 for the group ' WSDC<0.5' = >50; EDGE >2000m. This decline in the density of the black-throated blue warbler suggested a negative effect of high density of American redstart on the black-throated blue warbler. BTARCS was

Table 8. P values in Anovas undertaken to test the effects of EDGE[1] and WSDC<0.5[2] on mean densities of BTBW[3], AMRE[4] and mean of BTARCS[5] within 3 levels of FC1MIL[6]. Bird density and vegetation variables were sampled in 1992-1995 (Upper Peninsula, Michigan).

	BTBW	AMRE	BTARCS
Within FC1MIL>90			
EDGE	0.194	0.8	0.382
WSDC<0.5 0.003	0.017	0.619	
EDGE*WSDC<0.5	0.127	0.289	0.406
Within FC1MIL>80<90			
EDGE	0.39	0.004	0.024
WSDC<0.5 0.006	0.011	0.512	
EDGE*WSDC<0.5	0.053	0.015	0.005
Within FC1MIL>70<80			
EDGE	0.038	0.002	0.001
WSDC<0.5 0.687	0.364	0.436	
EDGE*WSDC<0.5	0.448	0.309	0.782

[1]EDGE = group based on length of forest edge within 500m radius.
[2]WSDC<0.5 = group based on number of woody stems within vegetation plots.
[3]BTBW = Black-throated blue warbler.
[4]AMRE = American redstart.
[5]BTARCS = difference in density between the Black-throated blue warbler and the combined densities of the American redstart and the chestnut-sided warbler.
[6]FC1MIL = group based on Forest cover within 1 mile radius.

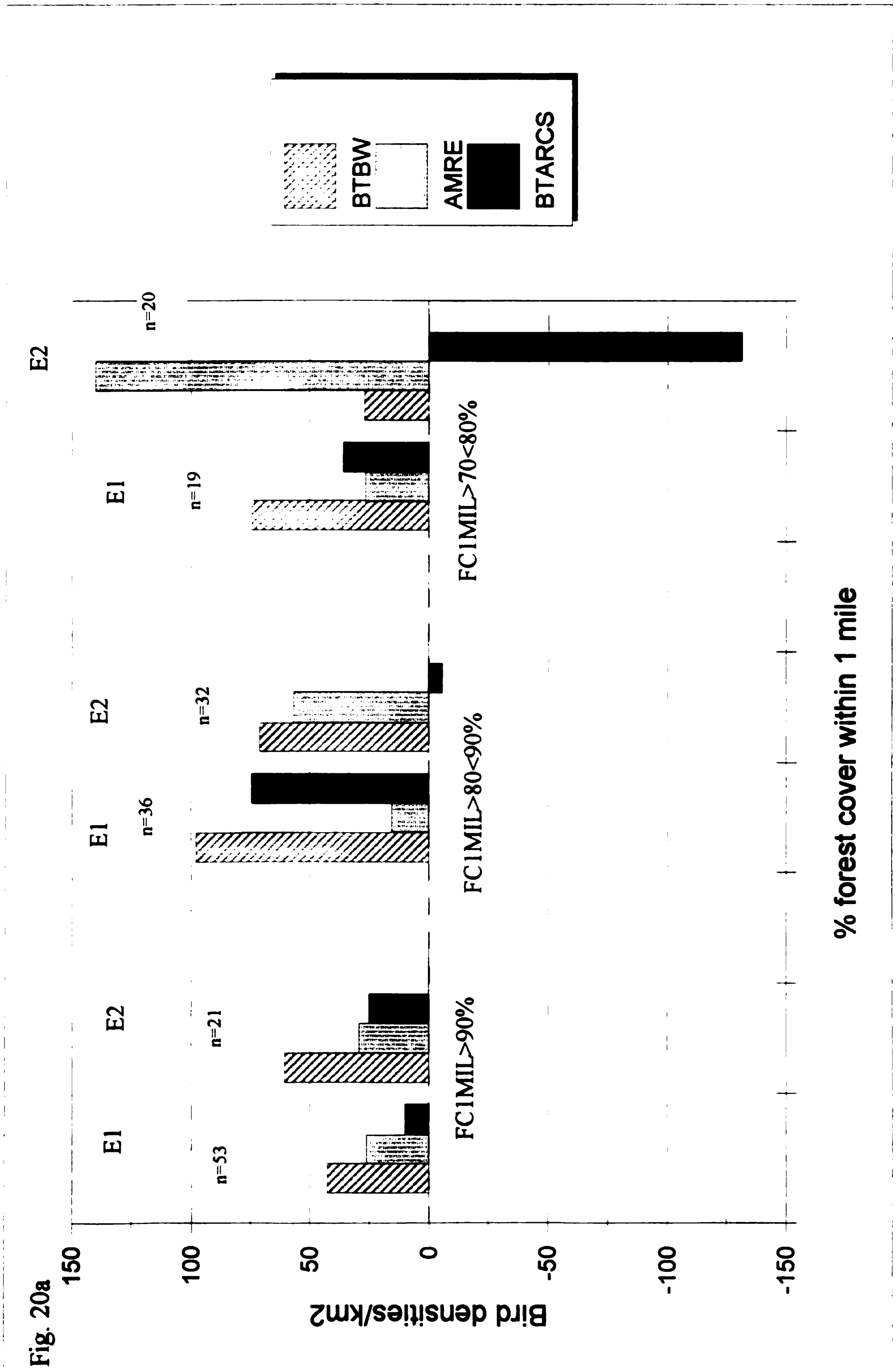


Fig. 20a
Bird densities/km2
150
100
50
0
-50
-100
-150
E1
E2
n=53
n=21
n=36
n=32
n=19
n=20
FC1MIL>90%
FC1MIL>80<90%
FC1MIL>70<80%
% forest cover within 1 mile
BTBW
AMRE
BTARCS

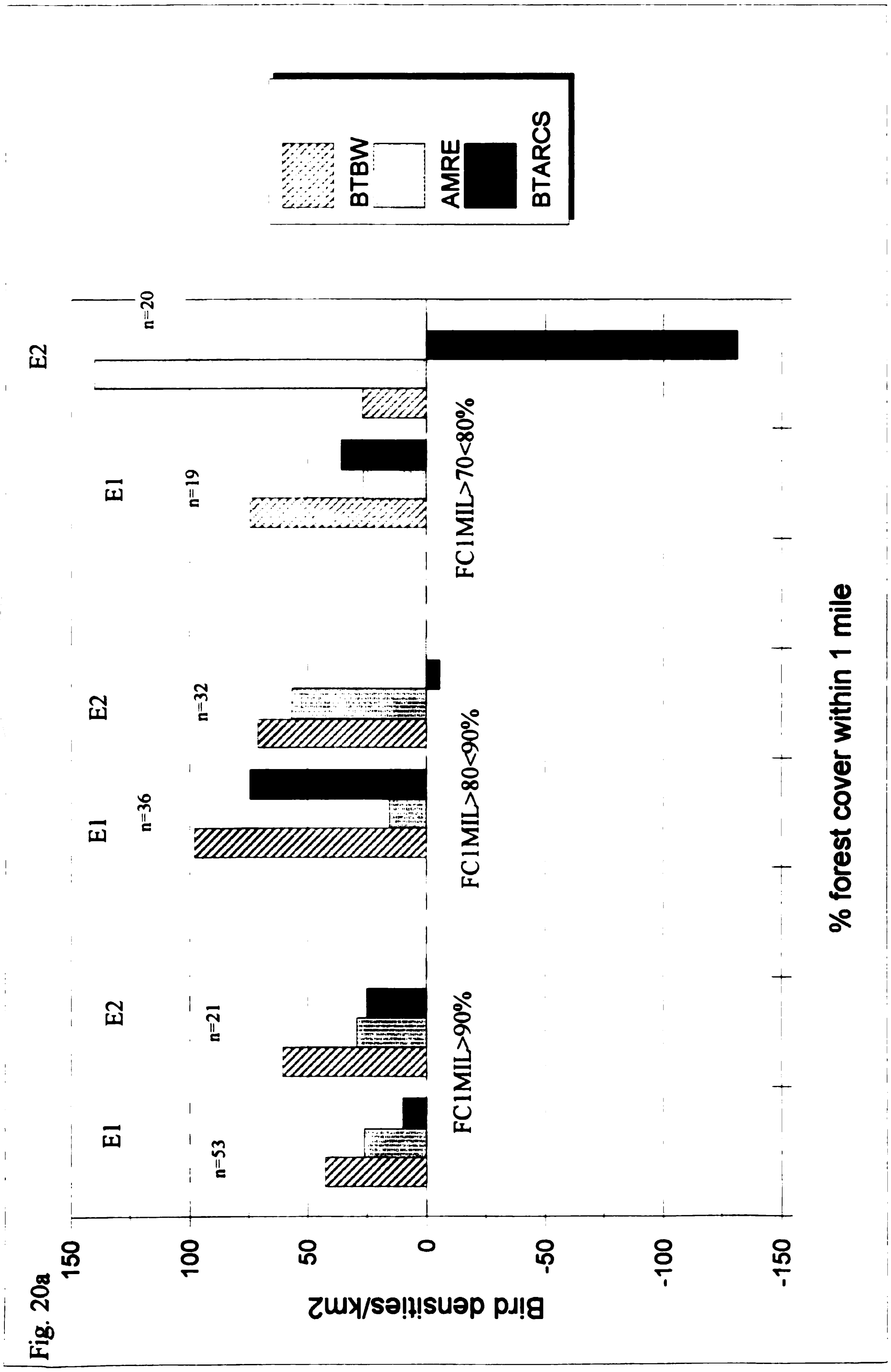
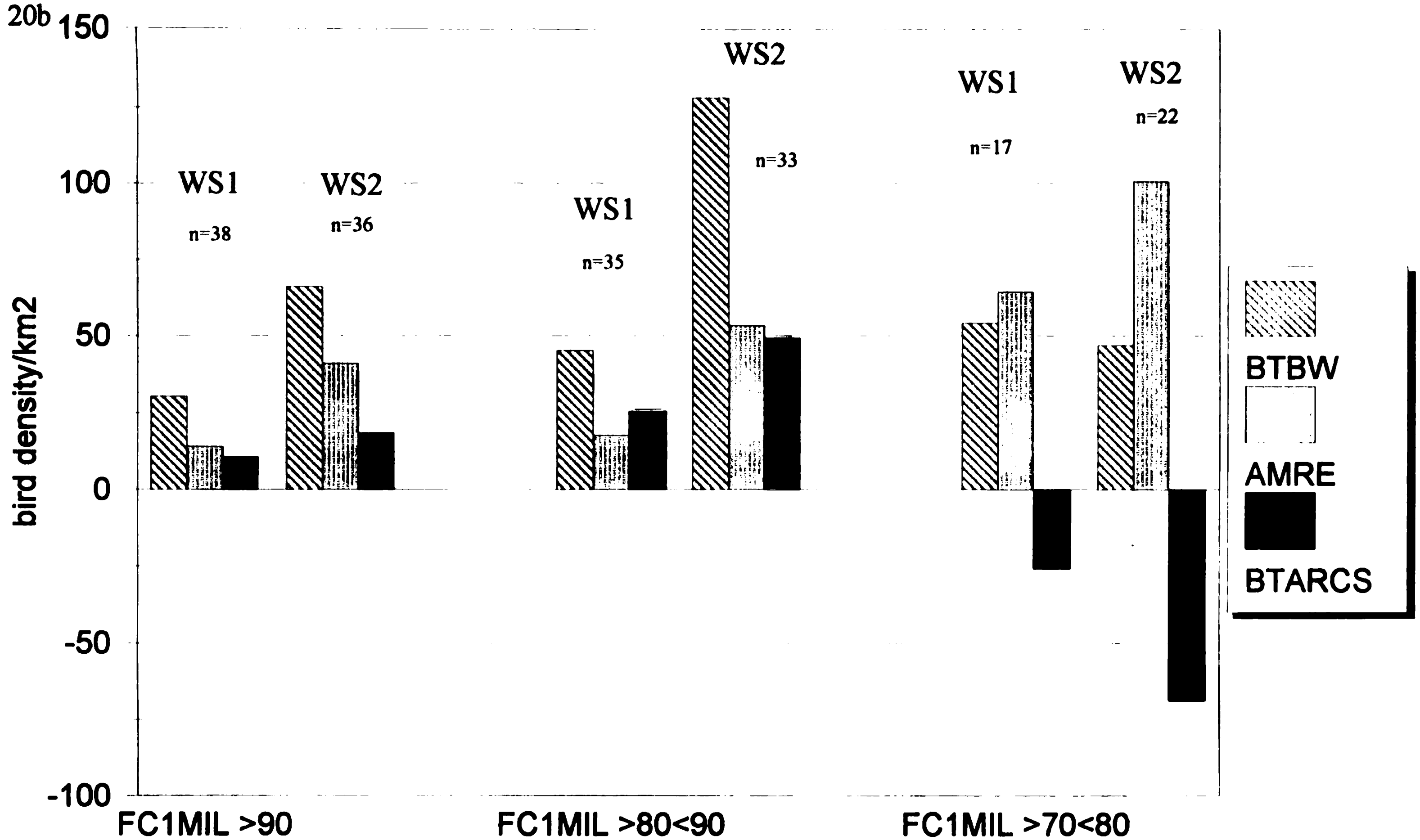

Bird densities/km2
150
100
50
0
-50
-100
-150
E1
E2
n=53
n=21
n=36
n=32
n=19
n=20
FC1MIL>90%
FC1MIL>80<90%
FC1MIL>70<80%
% forest cover within 1 mile
BTBW
AMRE
BTARCS

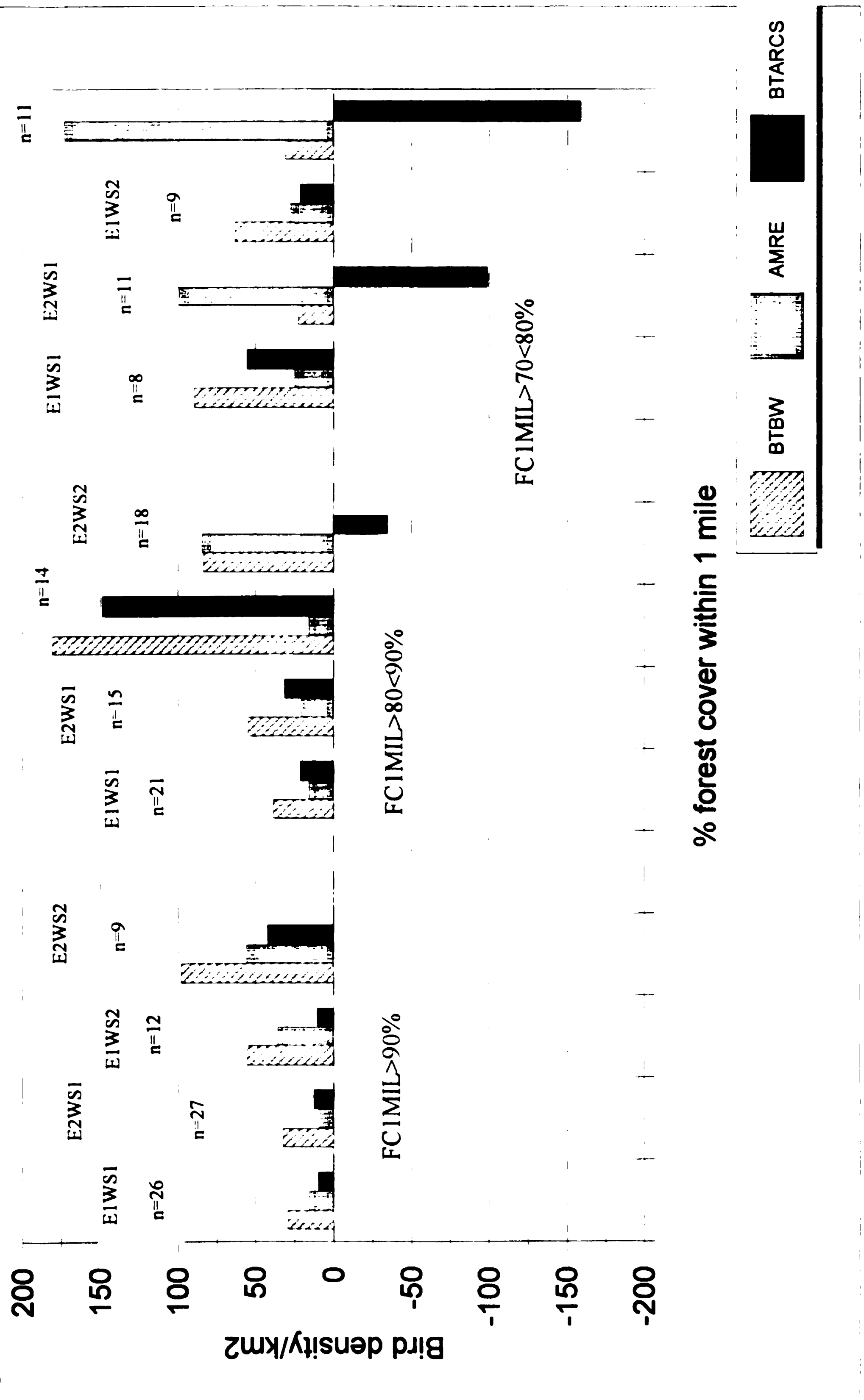
Fig. 20a

Fig. 20b



150
100
50
0
-50
-100
bird density/km2
WS1
n=38
WS2
n=36
WS1
n=35
WS2
n=33
WS1
n=17
WS2
n=22
FC1MIL >90
FC1MIL >80<90
FC1MIL >70<80
BTBW
AMRE
BTARCS

Fig. 20c



Bird density/km2
200
150
100
50
0
-50
-100
-150
-200
E1WS1
n=26
E2WS1
n=27
E1WS2
n=12
E2WS2
n=9
FC1MIL>90%
E1WS1
n=21
E2WS1
n=15
E1WS2
n=14
E2WS2
n=18
FC1MIL>80<90%
E1WS1
n=8
E2WS1
n=11
E1WS2
n=9
E2WS2
n=11
FC1MIL>70<80%
% forest cover within 1 mile
BTBW
AMRE
BTARCS

Figure 20 (continued)

Legend.

	Group of bird census stations for which
FC1MIL>90%	Forest cover within 1 mile >90%.
FC1MIL>80-<90%	Forest cover within 1 mile >80 <90%
FC1MIL>70-80%	Forest cover within 1 mile >70% -80%
E1	Forest edge within 500m <2000m
E2	Forest edge within 500m >2000m
WS1	Number of woody stems<0.5" <50
WS2	Number of woody stems<0.5" >50
E1WS1	Forest Edge<2000m & Number of woody stems<0.5" <50
E2 WS1	Forest Edge>2000m & Number of woody stems<0.5" <50
E1WS2	Forest Edge <2000m & Number of woody stems<0.5" >50
E2WS2	Forest Edge >2000m & Number of woody stems<0.5" >50

Figure 20. Effects of forest edge, and shrub layer development and their interactions on densities of the black-throated blue warbler and American redstart and on BTARCS in different conditions of forest cover within 1 mile.

positive (black-throated blue warbler winning) for all combinations of 'WSDC<0.5 and EDGE except for the combination of higher levels for 'WSDC<0.5' and EDGE.

In forest cover >70-80%, EDGE was the only factor that affected densities of the black-throated blue warbler and American redstart, and therefore BTARCS (p=0.038, 0.002 and 0.001 respectively). At this forest cover level, the black-throated blue warbler density showed no significant response to an increase in shrub layer development. Any development of shrub layer was preempted by the American redstart as its density increased with the increase in WSDC<0.5 (Figure 20 b). The combination of high EDGE and high 'WSDC<0.5' favored the American redstart as it did in FC1MIL >80-90% (Figure 20 c.). The effects in this case were however even more accentuated for all responses, for the increase in the American redstart and for the decrease of the black-throated blue warbler and for the more elevated negative value of the variable BTARCS.

Effects of extensiveness of the northern hardwood forest, canopy opening, shrub layer development, and forest edge.

The effect of the extensiveness of the northern hardwood forest within highly forested landscapes FC1MIL >80% on black-throated blue warbler and American redstart densities and on the variable BTARCS was explored. In 4-way ANOVAs, % of northern hardwood forest cover within a 1 mile-radius NHWD1MIL was considered along with length of forest edge within a radius of 500m EDGE as landscape factors, and the factors CANOPEN and WSDC<0.5 as micro habitat factors. In highly forested landscapes most combinations of the 4 factors favored the black-throated blue warbler as was evident by the positive values of BTARCS (Figure21a, 21b). The black-throated blue warbler density

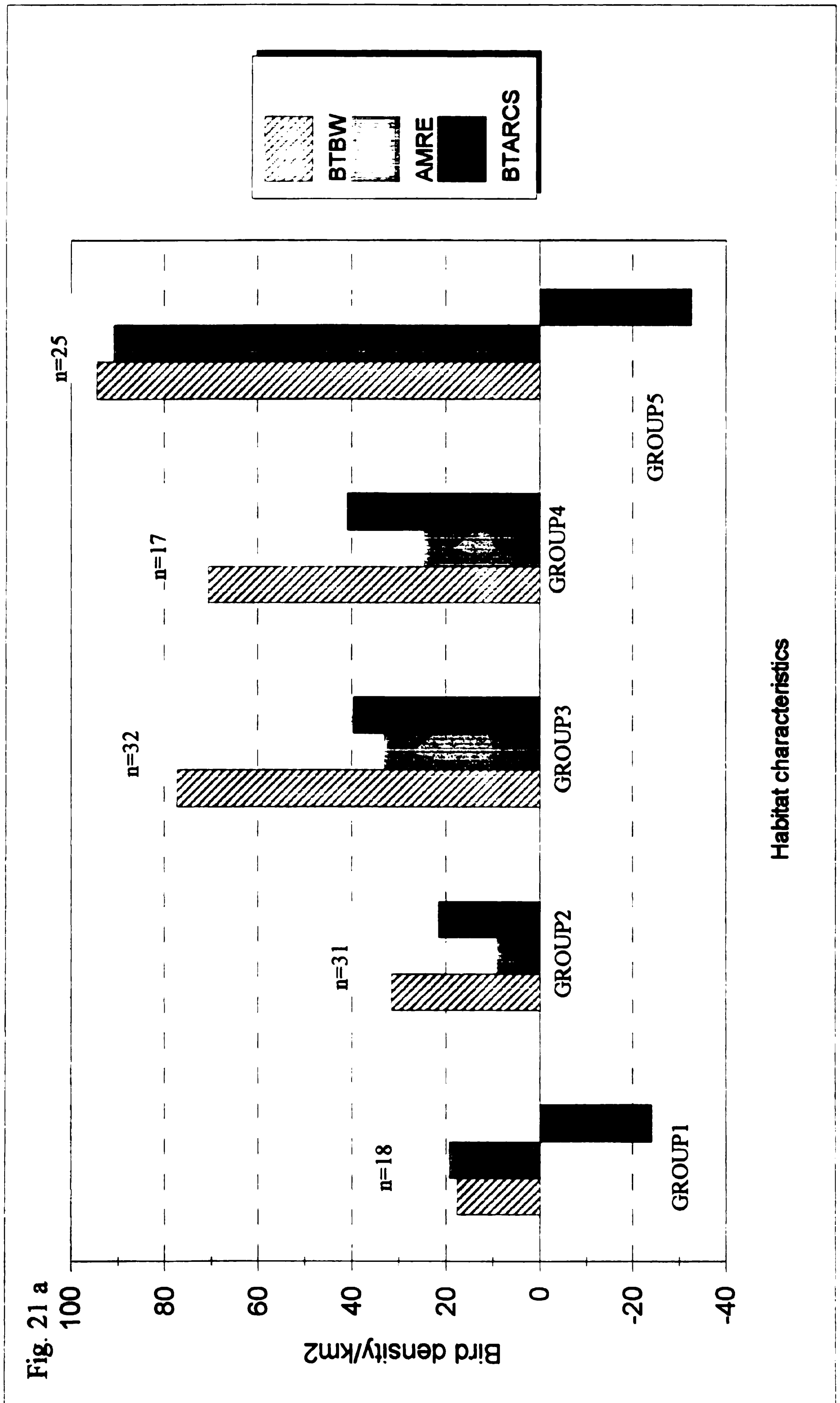

BTBW
AMRE
BTARCS
Bird density/km2
100
80
60
40
20
0
-20
-40
n=18
n=31
n=32
n=17
n=25
GROUP1
GROUP2
GROUP3
GROUP4
GROUP5
Habitat characteristics

Fig. 21 a

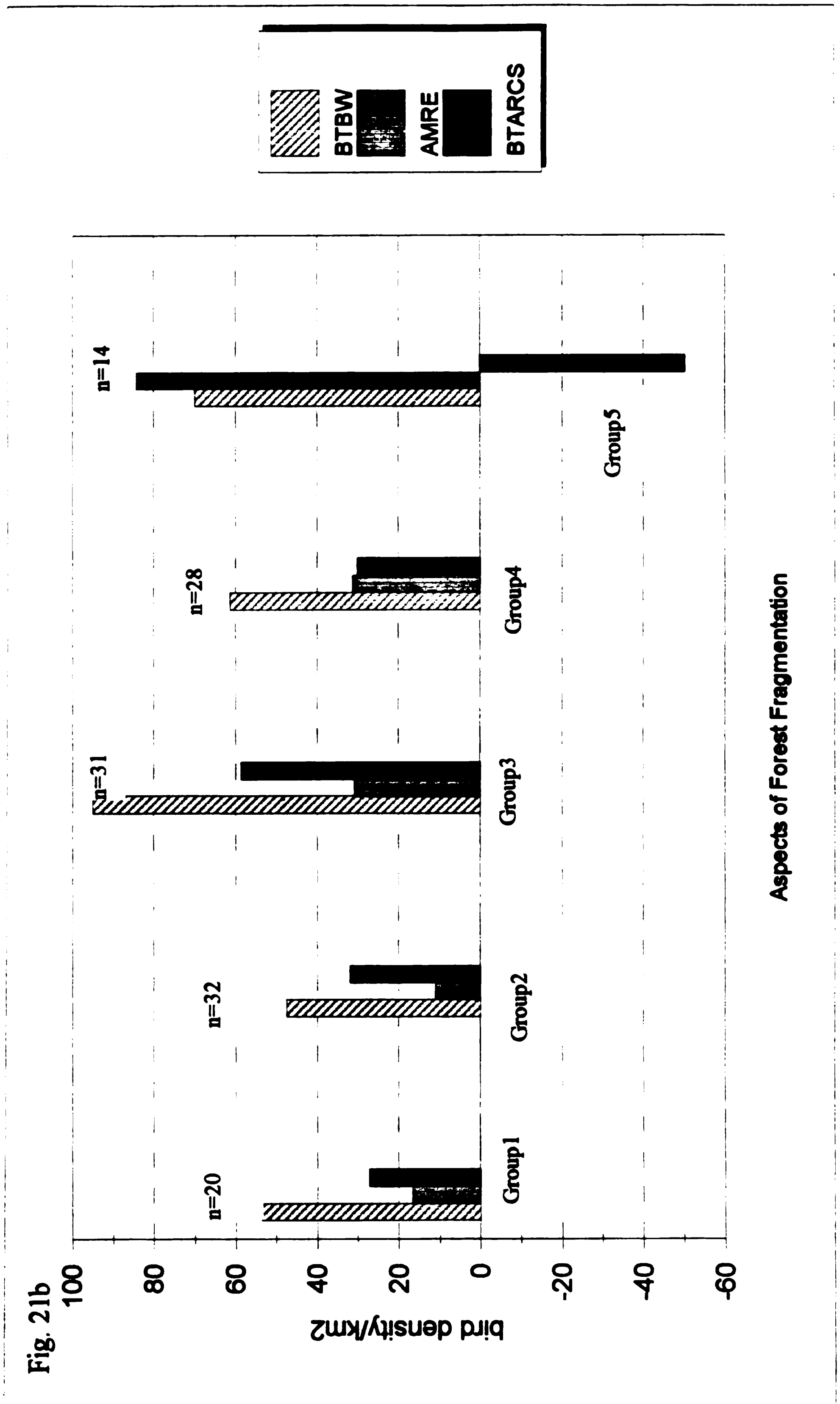


Fig. 21b
bird density/km2
100
80
60
40
20
0
-20
-40
-60
n=20
n=32
n=31
n=28
n=14
Group1
Group2
Group3
Group4
Group5
BTBW
AMRE
BTARCS
Aspects of Forest Fragmentation

Figure 21 (continued)

Legend.Figure 21a

Group 1
% Northern hardwood forest within 1 mile (NHWD1MIL) <30%
% Canopy opening (CANOPEN) <15%
Number of woody stems <0.5" (WSDC<0.5) <50

Group 2
% Northern hardwood forest within 1 mile (NHWD1MIL) >30%
% Canopy opening (CANOPEN) <15%
Number of woody stems <0.5" (WSDC<0.5) <50

Group 3
% Northern hardwood forest within 1 mile (NHWD1MIL) >30%
% Canopy opening (CANOPEN) <15%
Number of woody stems <0.5" (WSDC<0.5) >50

Group 4
% Northern hardwood forest within 1 mile (NHWD1MIL) >30%
% Canopy opening (CANOPEN) >15%
Number of woody stems <0.5" (WSDC<0.5) <50

Group 5
% Northern hardwood forest within 1 mile (NHWD1MIL) >30%
% Canopy opening (CANOPEN) >15%
Number of woody stems <0.5" (WSDC<0.5) >50

Legend for Figure 21b

Group1
% Northern hardwood forest within 1 mile (NHWD1MIL) <30%
% Canopy opening (CANOPEN) <15%
Edge within 500m <2000m

Group2
% Northern hardwood forest within 1 mile (NHWD1MIL)>30%
% Canopy opening (CANOPEN) <15%
Edge within 500m <2000m

(Fig 21 continued)

Group3
% Northern hardwood forest within 1 mile (NHWD1MIL)>30%
% Canopy opening (CANOPEN) <15%
Edge within 500m <2000m

Group4
% Northern hardwood forest within 1 mile (NHWD1MIL)>30%
% Canopy opening (CANOPEN) >15%
Edge within 500m <2000m

Group5
% Northern hardwood forest within 1 mile (NHWD1MIL)>30%
% Canopy opening (CANOPEN) >15%
Edge within 500m >2000m

Figure 21. Effects of interactions among NHWD1MIL, CANOPEN, and WSDC<0.5, and among NHWD1MIL, CANOPEN and EDGE on black-throated blue warbler and American redstart densities and on BTARCS. Data were obtained from bird censusing and vegetation sampling in 1992-1994 in the Upper Peninsula of Michigan.

was not affected by NHWD1MIL (p=0.69) or EDGE (p=0.816). The effects of EDGE on density of the American redstart bordered on the 1 % significance (p=0.11). BTARCS was also not affected by NHWD1MIL (p=0.513) or by EDGE (p=0.23). This indicated that in highly forested landscapes the effect of EDGE 'in general' and alone did not favor edge species over the more forest interior black-throated blue warbler. Both CANOPEN and WSDC<0.5 were highly significant for the black-throated blue warbler (p<0.006 and <0.001 respectively). An increase in CANOPEN and WSDC<0.5 increased black-throated blue warbler density from 24.65 birds/km2 (n= 49, se=16.29 for CANOPEN <15% and WSDC<0.50 = <50; to171 birds/ km2 (n=30, se=22.58). WSDC<0.5 was significant for the American redstart (p = 0.018) but the effects of CANOPEN were less pronounced than for the black-throated blue warbler. When the effects of all the other 3 variables were randomized, an increase in 'WSDC<0.5' favored the black-throated blue warbler as represented by the difference between 29.97 birds/km2 for 'WSDC<0.5'= <50 (n= 73, se =15.65) and 115.61 birds/km2 for 'WSDC<0.5' = >50 (n = 69, se = 15.20; Table D32). Density of the American redstart increased to a lesser magnitude with this range of increase in woody stem density (17.96 birds/km2, se =8.26; to 45.61 birds/km2, se = 8.02 respectively; Table D32).

The interaction between NHWD1MIL and WSDC<0.5 was significant for the black-throated blue warbler (p=0.021) and very significant for BTARCS (p=0.006). The highest density of the black-throated blue warbler was encountered in landscapes with a lower % of northern hardwood forest with a high level of WSDC<0.5[13]. The low value of 3.66 (n= 57, se = 14.44) for BTARCS for the group of bird census stations in the 2 factor combination NHWD1MIL >30%; WS<0.5 >50 indicates that overall (when the effects of

EDGE and CANOPEN were randomized), the black-throated blue warbler fared only slightly better than the combination of AMRE and CSWA in extensive northern hardwood areas in landscapes where total forest cover was high (>80%) and where there was good shrub development.

The interaction of NHWD1MIL x CANOPEN x EDGE was highly significant for BTARCS (p= 0.005). Of the 8 possible combinations of NHWD1MIL, CANOPEN, EDGE, 5 groups consisted of more than 10 bird census stations (Table D32). The higher level of EDGE favored the edge bird species when combined with the higher level of CANOPEN (American redstart density = 84.66 birds/km2 for EDGE >2000m, CANOPEN >15%, n=14; BTARCS = -50.09). EDGE was not associated with a high density of American redstart when canopy opening was low (CANOPEN <15%) (American redstart density = 31.28 birds/km2 for Edge>2000m, CANOPEN<15%; and BTARCS= 30.05 for that combination of edge and canopy opening). The difference in the variable BTARCS was significant (p=0.05; Bonferroni post test of pairwise comparisons) between the group NHWD1MIL>30; EDGE >2000m; and CANOPEN <15% (n=31) with the group NHWD1MIL =>30; EDGE= >2000m; CANOPEN >15% (n=14). The effect of a high level of edge and a high level of canopy opening in increasing edge species was even more accentuated with the combination of the high level of shrub layer development. For the group NHWD1MIL >30; EDGE >2000m; CANOPEN >15; WSDC<0.5 >50, the American redstart reached its highest density of 133.68 birds/km2 (n = 8, se =16.71), and BTARCS its lowest value of (-127.25, se= 36.72) with respect to all other 15 groups of 4 factor combinations. The black-throated blue warbler density for this combination of 4 factors was 70.99 birds/km2 (se 31.66) . This density for the black-throated blue in the combination of 4 factors NHWD1MIL >30; EDGE >2000m; CANOPEN >15; 'WSDC<0.5'= >50, was lower than its density of 11 birds/km2 8.75 for the same combination of factors except for the lower level of EDGE although the (Bonferroni post tests of pairwise comparisons was not significant). The density pattern that the black-throated blue warbler exhibited in highly forest landscapes indicated that it does not avoid edges and high canopy openings. A high level of canopy opening with the combination of a high level of edge however increased the density of edge species to a level that they surpassed the density of the forest interior black-throated blue warbler.

CHAPTER 4

DISCUSSION AND CONCLUSIONS

ECOSYSTEM LEVEL RELATIONSHIPS

Data analyses provided information on bird species associations with habitat variables and on patterns of bird density and habitat variable differences among strata of northern hardwood forest. Synthesis of this information permitted an ecosystem level view of relationships between bird species populations and the northern hardwood forest and among bird species. Ecosystem level properties affecting bird species in northern hardwood forest and resulting perspectives on forest fragmentation and forest bird species conservation are discussed below.

It is impossible to reconstruct the chronology of density changes that the blackburnian warbler and the black-throated green warbler underwent after much of the forest was clearcut and a second growth forest replaced the primary forest. That this change was detrimental to the blackburnian warbler and might have benefited the black-throated green warbler was indicated by habitat relationships between the 2 species that were apparent along a conifer-deciduous forest gradient and density patterns in primary forest and secondary forest. A prospect that the black-throated green warbler will invade blackburnian warbler habitat was suggested by its high selectivity for late successional forest conifer trees in settled forest[1] where it occurred in the absence of the blackburnian warbler and at a lower density than it did in managed forest. The fact that the black-throated green warbler reached its highest abundance in second-growth forest and not in primary forest or older growth in managed forest (strata that had a higher conifer component) suggested that the blackburnian warbler could have suppressed it in these northern hardwood forest strata.

Although land type associations that replicated managed forest and settled forest categories of land use were uniformly low in hemlock and hemlock-white pine that represent late successional forest, they varied with respect to total amount of conifer and to amounts of various other coniferous forest types (i.e. lowland conifers and pine forest). Landscape level effects relative to amount and types of coniferous forest at a land type association level were somewhat evident for the black-throated green warbler. In managed forest, the black-throated green warbler showed consistent higher densities (although not always significant) in the Rapid River landscape perhaps reflecting the higher amounts of lowland conifer forest types. The rarity of late sucessional forest conifers (at local sites) and the associated low encounter rate of the blackburnian warbler precluded the analysis of the effects of different landscape level conditions on its density. The density pattern that the blackburnian warbler exhibited across forest disturbance periods (Tables D11, D15) clearly demonstrated that it was not affected by frequent small scale forest disturbance that is representative of canopy and shrub layer dynamics [2]. An explanation why the blackburnian warbler was not affected by selective logging is that under present forest management (Hiawatha National Forest) patches of hemlock in northern hardwood forest are preserved. Thus without the decrease in sites containing a coniferous tree component, habitat availability at small scales would not be affected .

The increase in shrub layer development and densities of bird species (the black-throated blue warbler, American redstart, chestnut-sided warbler, scarlet tanager, and veery) associated with a shrub layer during time intervals of 6-12 and >12-15 years after logging indicated the close association between the dynamics of the shrub layer and bird populations. There are indications from density patterns that this increase in bird density following logging could be responsible for their greater densities in managed forest relative to primary forest. Higher densities of the black-throated blue warbler, American redstart and chestnut-sided warbler in unlogged second growth and older growth forest (Figure 14), and higher densities of all 5 species (black-throated blue warbler, American redstart, chestnut-sided warbler, veery and scarlet tanager, relative to primary forest (Figures 14, 15) that could not be accounted for by a shrub layer development suggested that habitat packing was occurring in the managed forest[3] .

Although all species associated with a shrub layer responded to the increase in shrub layer development following logging in managed forest, the density pattern of each species across all northern hardwood forest strata was unique. The bird species that were associated with a well developed shrub layer differed with respect to the degree to which they were affected positively or negatively by percent canopy opening and number of canopy gaps. If these species were ordinated along a gradient that combined canopy cover (at local site) and forest cover (at a landscape scale), the black-throated blue and scarlet tanager would receive highest scores, the veery and American redstart intermediate scores and the chestnut-sided warbler lowest scores on this gradient. The increase in scarlet tanager and black-throated blue warbler between 6-12 years and >12-15 years after logging relative to all other strata of northern hardwood forest indicated that poor shrub layer development was a limiting factor to shrub layer associated species in the interior of the forest. The increase in bird species that were favored by settled forest conditions within these strata after logging suggested that conditions were created that simulated settled forest conditions within the managed forest.

Significant differences in mean densities of shrub associated forest bird species were common among land type associations replicating a land use or a forest disturbance period. These differences reflected differences in shrub layer development. A question pertinent to forest management would be whether differences in the dynamics of the shrub associated bird species among different landscapes[4] reflected some inherent characteristics of the landscape or whether they stemmed from human induced disturbance. Increases of the American redstart and chestnut-sided warbler relative to the black-throated blue warbler after logging in the Munising and Manistique landscape as compared to the Rapid River landscape could be explained by their higher densities prior to logging. There were no known (previous) disturbance factors that would account for higher densities of edge species in either landscape. There were indications however that habitat conditions in general, in strata other than just those describing conditions following logging disturbance, were more favorable to these species in the Munising and Manistique landscape. The American redstart and chestnut-sided warbler had higher densities in forest disturbance strata >12-15 years and in unlogged second growth in the Munising and Manistique landscapes than they did in the Rapid River landscape. Although the Munising landscape overall had higher forest cover than either of the Rapid River and Manistique landscapes (many bird census stations in the Munising landscape had forest cover within a 1.6 km radius >90%, Table D28) which would favor the black-throated blue warbler, a more open forest canopy (in all forest disturbance period strata) and, a greater number of large canopy gaps, along with a better shrub layer development in all forest disturbance strata might have allowed edge species to persist in between logging events. [More favorable habitat to the American redstart and chestnut-sided warbler in the Manistique landscape was due to a higher amount of edge and lower forest cover in that landscape (Table D28)].

The greater number of large canopy gaps (100m^2 and >100m^2) in forest disturbance strata depicting recent logging activity (1-5 years; 6-12 years and >12-15 years) would at first suggest an effect of logging activity. Number of canopy gaps across these 3 forest disturbance strata however did not show a decrease in successive forest disturbance periods following logging as would be expected if the number of large canopy gaps was due directly to logging. The number of large canopy gaps also differed among land type associations within strata representing the same forest disturbance periods, possibly reflecting a difference in local climate. The higher number of gaps in the strata several years after logging (6-12 and >12-15 years after logging) could suggest an interaction of logging disturbance with weather activity in a process that involved standing trees left after the removal of others becoming more susceptible to toppling. Although large canopy gaps were also numerous in primary forest landscapes they were not associated with high densities of the American redstart and chestnut-sided warbler. As was shown in the Anova analysis of the effects of interactions between edge, canopy gaps, shrub layer development and forest cover, large canopy gaps alone were not associated with an increase in forest edge species. Although the Munising landscape did not have any more edge than the Rapid River landscape (it had lesser edge than the Manistique landscape), that amount of forest edge combined with a better shrub layer development and a more open canopy created more favorable conditions for edge species. The high density of black-throated blue warbler in the Rapid River landscape several years after logging could be due to habitat saturation. In the Rapid River landscape, shrub layer development was poor in all forest disturbance periods other than that of 6-12 years following logging[5]. The amount of northern hardwood forest was also limited in this landscape. [In this ridge swale land type association, the northern hardwood forest occurred on ridges surrounded by lowland conifer; the land type association itself was surrounded mostly by others that lacked northern hardwood forest].

ASPECTS OF FOREST FRAGMENTATION IN THE NORTHERN HARDWOOD FOREST

Examination of bird species densities along a range of forest conditions that included aspects of forest fragmentation, provided perspectives on habitat fragmentation from the end closer to intact ecosystems than those resulting from studies of highly disintegrated landscapes. The range of forest conditions that was herein spanned, included areas in which the northern hardwood forest had become separated from other forest by openland. Although among the 10 bird species considered several had declined and 2, the blackburnian warbler and the black-throated blue were largely absent from landscapes in which the forest was patchy, isolation was ruled out as an underlying cause of this decline on several grounds. All study sites in settled forest landscapes were close to the core of the Hiawatha National forest; many were less than 1 km away from contiguous northern hardwood forest. Since several forest interior bird species were abundant, there was no cause to believe that the dispersal ability of bird species that showed high densities differed from that of bird species that had declining densities. Another reason why dispersal was not an issue is that the black-throated blue warbler and the blackburnian warbler already had low densities under certain forest conditions within the managed northern hardwood forest.

Often cited causes of decline of forest bird species in fragmented landscapes are increased levels of predation and cowbird parasitism (Donovan et al. 1995). In the eastern deciduous biome declines of forest interior bird species with fragmentation have been blamed on their life history traits of nesting on or close to the ground in an open cup nest. Several bird species that remained abundant in settled forest or that increased, the ovenbird and veery nest on the ground and the American redstart and chestnut-sided warbler most often nest in the sapling layer close to the ground. The mostly absent blackburnian however nests in the canopy of conifer trees and the red-eyed vireo that showed declining densities in settled forest (although still abundant) nests in the canopy of deciduous trees. From these density and life history patterns there was no basis to suggest that either predation or nesting habits were major causes for bird species density declines.

Several studies have associated loss of habitat elements (i.e. microhabitats) from forest fragments as the cause of decline in the number of bird species (Freemark and Merriam 1986). The fact that the black-throated blue warbler was nearly absent in settled forest but the equally shrub layer associated American redstart and chestnut-sided warbler occurred at high densities suggested that the 2 latter species rather than a lack of habitat might have kept the black-throated blue warbler out of settled forest landscapes. The near absence of the black-throated blue warbler from settled forest landscapes however precluded the examination of any competitive interactions among the 3 species within this land use category. The relationship among these species however was revealed by their relative densities within a higher range of forest cover in primary and managed forest landscapes. Within a forest cover range of >70-90%, there was enough variability in the northern hardwood forest with respect to forest cover, edge and canopy gaps, to significantly affect the relative densities of American redstart, black-throated blue warbler and chestnut-sided warbler. The fact (shown in the results of different analyses), that densities of black-throated blue warbler were lower in the presence of high densities of the American redstart and chestnut-sided warbler suggested that an interaction was occurring among these species.

It has been suggested that bird species select habitat at different spatial scales (Gutzwiller and Anderson 1987; Steele 1992). It is possible that the black-throated blue warbler avoids landscapes with reduced forest cover as an inherent habitat selection behavior since these landscapes would have higher densities of edge and edge-interior bird species. Given the proximity of settled forest to contiguous forest in this case, it is more probable that the black-throated blue warbler was kept out of suitable microhabitat patches within settled forest landscapes through competitive interactions with the 2 other species that prevented it from settling[6]. The high densities of edge and habitat generalist bird species in these landscapes could discourage the black-throated blue warbler from establishing territories[7].

The blackburnian warbler was already rare in most of the managed forest even though this was contiguous forest and landscapes varied between 70- > 90% forest cover. The near absence of this species from settled forest could not be assessed in terms of loss of forest cover or forest fragmentation because of the confounding factor of loss of late forest maturity conifer. If Lord and Norton's (1990) definition of habitat fragmentation as simply the disruption of continuity at any spatial scale is considered, loss of late forest maturity conifers would be a habitat fragmentation aspect because this loss would increase distances between sites that have suitable habitat and the chance that some of them will not be discovered. There were aspects in the relationship between blackburnian warbler density and the occurrence of late forest maturity conifers that suggested that there were no effects beyond those of habitat availability. The fact that densities of the blackburnian warbler were proportional to amounts of late forest maturity conifers in different northern hardwood forest strata (regression explained >80% in blackburnian warbler variability) suggested that the population was in equilibrium with its habitat, that is the occupancy rate of habitat was even across the managed forest. The similarity of older growth forest and primary forest sites with respect to blackburnian warbler densities that reflected their similarity in the amount of late maturity conifers suggested that the more discontinuous habitat in managed forest did not reduce the blackburnian warbler's ability to locate suitable sites.

There are several arguments that could be contemplated as to why with this severe loss of hemlock and white pine there was no evidence of fragmentation effects. One consideration is that both white pine and hemlock are long lived and slow growing species, such that in the absence of cutting, many decades would have to pass before there would be any change in their availability. Following the initial selective logging of white pine and hemlock which reduced the types in the present managed forest, the availability of hemlock or old pine in the landscape remained constant under forest management practices that preserved these species within the northern hardwood forest. In contrast to the shrub nesting species that have to track constantly changing patches of shrub growth, the blackburnian faces less stochasticity in its search of late forest maturity hemlock and white pine.

In forested habitat the blackburnian could also be utilizing other coniferous forest patches which would allow it to persist in the landscape[8]. In contrast to more simplified habitat in which most structural components would have been already lost and the species might not find a different patch type as a substitute (Karr 1982). In forest areas different types of coniferous forest patches would have different habitat quality but would still provide alternative habitats for some individuals which could then establish in the higher quality habitat when these are vacated. In highly simplified ecosystem this gradation of habitats might not exist.

The presence of competitor bird species appears to be an important factor affecting the density and distribution of the black-throated blue warbler. Because the shrub layer was highly dynamic, by sampling forest at different time intervals after a logging disturbance, a temporal dimension for the densities and relative densities of the black-throated blue, American redstart and chestnut-sided warbler could be detected. Thus the relationship could be viewed along temporal and spatial dimensions. Although the black-throated green could be a potential competitor for the blackburnian[9], it was impossible to see their interactions in either temporal and spatial dimensions. How the species relate to each other along a temporal scale was precluded because of the length of time it takes conifer forest to establish. There was no sampling procedure that would allow observation of habitat dynamics, and the effects of the surrounding landscape on the interactions of the 2 species within the short time span of this study[10].

The most abundant bird species in managed forest landscapes, the red-eyed vireo, least flycatcher, ovenbird and black-throated green warbler, remained abundant in settled forest landscapes although the black-throated green warbler and red-eyed vireo showed statistically significant declines. The ovenbird, red-eyed vireo and black-throated green warbler can be considered forest interior bird species (Ambuel and Temple 1982, 1983; Lynch and Whigham 1984; Askins and Philbrick. 1987; Robbins 1989; Askins et al. 1990) showing declines in regions where the forest has been severely reduced or fragmented (Wilcove 1985; Askins and Philbrick 1987; Hill and Hagan 1991). Because density alone is not sufficient to indicate the productivity status of the population or reflect habitat quality (Van Horn 1983), other population parameters would need to be sampled before habitat suitability for forest interior bird species in settled forest can be assessed. Because of the proximity of settled forest landscapes to managed forest landscapes, it is possible that high densities of these species were in part due to overflows from the more contiguous managed forest. Another possibility would be that high densities were due to habitat saturation. Population levels in primary and managed forest landscapes could have been at saturation levels and all other landscapes would have poorer habitat quality for forest interior bird species.

The ovenbird, red-eyed vireo, and black-throated green warbler are associated with a closed canopy forest that characteristically has poor shrub-layer development. This association might explain their ability to persist in closed canopied northern hardwood fragments in the settled forest. This type of habitat is abundant in the interior of second growth northern hardwood patches in settled forest. Shrub nesting bird species such as the black-throated blue warbler, have to depend on some form of canopy disturbance to open it and stimulate the development of the sapling layer. In situations in which edge and edge -forest interior bird species are abundant such as occurred in the settled forest, edge bird species would be the species to first preempt the newly available habitat in the interior of the forest. Under closed canopy conditions, selected by the ovenbird, red-eyed vireo and black-throated green warbler, the interior of the forest patch is protected from edge bird species simply because these species do not find their necessary microhabitats under a closed forest canopy. That is the assemblage of species that are edge and edge interior birds that require a well developed shrub layer would not comprise any species that could invade the closed canopy forest fragments.

In bird conservation studies, the concepts involving forest fragmentation have evolved from landscapes in which the forest is reduced to fragments in a matrix that is nonforest. Models that have addressed the behavior of bird populations in such fragmented landscapes were largely influenced by the theory of island biogeography equilibrium proposed by MacArthur and Wilson (1967) in considering the spatial arrangement of fragments (for metapopulation models) or the distance from source populations, extinction and immigration rates as major factors affecting the persistence of a species in these environments.

Forest ecosystems however are subjected to periodic disturbance events that create temporary conditions in which fragmentation aspects could become elevated. In managed forest the northern hardwood forest is often interspersed with early successional forest that is periodically clearcut. Within the northern hardwood forest both selective logging and natural disturbance affect canopy cover and canopy gaps. The response of species to these disturbances would depend on their population levels at the time of disturbance (as was indicated by the response of the black-throated blue warbler, American redstart, and chestnut-sided warbler in different land type associations in managed forest). Population levels in turn reflect the events and conditions leading up to the time of disturbance. There is undoubtably an element of stochasticity associated with the coincidence of population levels of species with logging disturbance that would affect the outcome of which species will preempt the sudden availability of habitat. Disturbance patterns and processes that are characteristic of a specific environment however affect the frequency with which certain events occur and their coincidence with other events. Conditions and events that tend to favor one species at the expense of another would themselves become characteristic of certain landscapes. In forested ecosystems the assemblages of bird species are more complete such that species overlap in their habitat. Bird species that overlap in their habitat can persist in the northern hardwood forest because of heterogeneity of landscapes, and complex interactions among dynamics of landscape characteristics, habitat availability, bird species populations and relationships among species. A directional change (one that persists) applied over a large part of an ecosystem would move it in a direction of forest conditions that could favor one species (which also could be a forest associated species) over another.

It should also be noted that once a disturbance event has unfolded, it can lead to a different scenario. For example if a disturbance by logging introduces an edge species in the interior of the forest then the next cycle of logging might further increase the population of edge species especially if the species is able to persist until the next disturbance event. The frequency of canopy disturbance and the time it takes population to decline after suitable habitat produced by canopy disturbance begins to decline are likely factors determining whether edge species populations would remain in the interior of the forest at the beginning of another cycle.

In the second growth northern hardwood forest, the cycle of periodic logging started from habitat conditions that consisted of closed canopy, low edge and low shrub layer development. Although the density of the black-throated blue warbler would be limited by the lack of a good shrub layer development, the species would be protected from forest edge species. In the first cycle of logging shrub layer development would favor the black-throated blue warbler. Once edge species have established in the interior of the forest after the initial disturbance, it is likely their densities would build up with successive logging cycles until their densities and the density of the black-throated blue warbler reach an equilibrium. Because at this time most the second growth northern hardwood forest has only received one cycle of logging it is likely that the relative densities of the black-throated blue warbler, American redstart and chestnut-sided warbler have not yet reached a state of equilibrium. Even if the intensity of logging and the amount of forest remain constant, the relative densities of these 3 species will likely change in favor of edge species.

Not all aspects of change in forest conditions and subsequent declines in species involve forest fragmentation. The reduction in late forest maturity conifers is a long term effect that cannot be reversed without a well directed long term effort aimed at reestablishing this component back into the second growth northern hardwood forest. Yet in today's forest, this loss of the conifer component is not associated with a forest fragmentation dimension. The discontinuity in habitat of the blackburnian has occurred along a temporal dimension and not along a spatial one.

At this time vagueness still surrounds the concept of forest fragmentation (Faaborg et al. 1995) with controversy focusing on what biological processes to link to it (Fahrig 1997). Because habitat loss must necessary occur for habitat to become fragmented, debate has revolved on whether fragmentation should be restricted to effects that occur beyond the effects of habitat loss or whether fragmentation should also include habitat loss (Haila 1986, Fahrig 1997). Such debate is considered necessary because conservation strategies that would need to be implemented would differ between the 2 different premises.

Some contentions about fragmentation would be relaxed if fragmentation was considered a process that had a temporal dimension. Fragmentation aspects in the northern hardwood forest which consisted of factors operating at different spatial scales suggested that fragmentation should be considered a complex process that involves different spatial scales and progresses with time to different levels. As a process fragmentation could be followed from initial stages starting with a highly forested system and would end in a highly fragmented ecosystem. This contrasts with most current conceptual models of fragmentation that have been developed for the end state of fragmentation and have had to progressively include more complexity to increase their representation of reality. Highly forested ecosystems, even when they are no longer representative of pristine forest conditions, as was herein described contain a compliment of forest bird species, and a diversity of landscape structures, far greater than what is typical in the more simplified landscapes consisting of woodlots imbedded in a landscape of nonforest. As was described for the black-throated blue warbler, processes that affect the decline of a bird species begin at such fine spatial scales that they are not detected as involving forest fragmentation effects until the process has advanced to a level at which it becomes detectable at larger scales. At what point in the disintegration process would the term fragmentation be applied is a matter of definition. At initial stages, only a slight change in habitat conditions can cause an edge species to begin preempting habitat that previously was occupied by a forest interior bird species. Thus the replacement of a forest interior bird species by another species (a process associated with fragmentation) can occur before a forest fragmentation process is recognizable.

Lord and Norton's definition of discontinuity of habitat that could occur at any scale overlaps the effects of habitat loss because any habitat loss would result in some discontinuity. Discontinuity of habitat in a spatial dimension would only have biological significance however if it starts to exceed the species' dispersal ability, or the increase in search time starts to impact its productivity. The effect of habitat discontinuity in a spatial dimension alone was not evident for any of the species that were declining across strata of northern hardwood forest. Discontinuity in a temporal dimension could be viewed from the perspective of habitat becoming more suitable to a competitor species for a long enough time that the competitor gains ground over the original species.

That many changes in deciduous forest ecosystems can appear to be related to forest fragmentation stem from the fact many bird species in this biome are associated with shrub layer development and their densities affected by shrub layer dynamics. These species also show habitat separation along a gradient of forest cover. However species can begin to decline before forest cover is lost. It should be evident that the multitude of events that lead to change in the relative densities of bird species and the eventual local extinction of species cannot be recovered from the stage of a fragmented landscape as was indicated in the case of the blackburnian warbler and black-throated blue warbler within settled forest. This aspect is one of the strongest arguments for the need to shift the emphasis in bird conservation from fragmented landscapes to forest ecosystems that are still functioning as forest ecosystems and to understand how these systems can disintegrate along temporal and spatial dimensions. It follows that while predation and cowbird parasitism could be important factors affecting the viability of forest bird species in highly fragmented landscapes, it is presuming to suggest that it is these factors that have caused the disintegration of the system and are the underlying cause of their current population levels.

BIRD CONSERVATION AND MANAGEMENT CONSIDERATIONS

1. Function of Primary Forest in Present Northern Hardwood Forest Ecosystems

The shortcoming of not having baseline data for forest disturbance processes, bird densities and habitat relationships among species, is the absence of models against which present day forest disturbances and forest temporal and spatial patterns can be assessed with respect to bird species adaptations. It is against such baseline data that directional change resulting from human induced disturbance can be assessed. There is a temptation to consider primary forest as a control to which human impacted forests can be compared. The amount of variability that was herein detected among northern hardwood landscapes within a single category of land use warns however against accepting differences between primary forest and secondary forest landscapes to be solely directional changes.

As results of comparisons of landscapes within a category of land use revealed, landscapes differed with respect to many small scale habitat elements within the northern hardwood forest. Differences in the dynamics and densities of the black-throated blue warbler, American redstart and chestnut-sided warbler among the 3 land type associations replicating managed forest were previously discussed in detail. The Munising landscape for example was more similar to primary forest landscapes with respect to number of large canopy gaps than it was to the Rapid River and Manistique landscapes. The amount of edge differed among primary forest landscapes, while it was non- existent in the McCormick Wilderness Area, shoreline in Sylvania and the Huron Mountains produced edge habitat. It should be evident that landscapes could vary in a multitude of ways because a multitude of habitat conditions can be produced by the interaction of different features that are inherent to geophysical characteristics of landscapes and disturbance activities superimposed over them.

Ecological classification systems such as the regionalization of Michigan landscapes (Albert et al. 1986; landscapes described by Pregitzer et al 1984; Simpson et al. 1990, Spies and Barnes (1985) and the land classification systems underway on the Hiawatha National Forest and the Ottawa National Forest, reveal a high level of variability among landscapes with respect to geomorphological features, and local climate. These differences in geomorphological features also produce differences in natural disturbance frequencies (Turner 1987, Simpson et al. 1990) which in turn affects the balance between northern hardwood forest succeeding to hemlock vs its persisting as a sugar maple dominated forest. For landscapes dominated by northern hardwood forest, the frequency of disturbance will determine the relative composition of the landscape in terms of late maturity conifers or more sugar dominated deciduous forest[11]. Because only a tiny fraction of the area formerly occupied by the original northern hardwood forest is left in the Upper Peninsula and across the Great Lakes Region, the range of variability that existed in the primary forest among landscapes has been reduced. Thus to infer that management induced changes have occurred from general comparisons between managed and remaining primary forest would be inadequate because the full range of variability of the primary forest would not have been captured.

Several facts can be used as arguments that the primary forest does not represent pristine conditions[12]. From a regional level (scale of the whole Upper Peninsula or Northern Great Lakes) a well documented change is the greater interspersion of forest with openland; a directional change that has favored edge species. The density of the white-tailed deer has increased many fold in the Upper Peninsula of Michigan after the large scale clearcutting and the growth of the secondary forest (Doepker et al. 1995). Deer in the Upper Peninsula of Michigan concentrate in hemlock forest during the winter. Because distances that white-tailed deer in the Upper Peninsula travel in their movements from summer range to winter yarding areas can be upwards of 30 km (Van Deelen 1995), all primary forest landscapes comprising extensive areas of hemlock forest are vulnerable. Thus even though large areas (several square miles) were selected to represent primary forest landscapes these would still be below the spatial scales of deer movements.

A large body of information exists concerning the impact of deer browsing in primary forest on the shrub layer (Anderson and Loucks 1979, Alverson et al. 1988, Miller et al. 1992). Heavy impacts of deer browsing in the Sylvania Recreational Area have been a long time concern (Webb et al. 1956). Directional changes in forest conditions that have affected shrub cover in primary northern hardwood ecosystems would have negatively affected the black-throated blue warbler and other shrub nesting bird species. Early accounts of the nesting habits of the black-throated blue warbler describe it as a specialized woodland bird (Pearson 1936). Bent (1963) also described it as commonly nesting in Canada yew in deep mature woods. Among the plant species that have nearly been decimated from changes in forest conditions is Canada yew (Braun 1950). The large scale decimation of Canada yew has been associated with changes in ecological conditions with the establishment of secondary forest following large scale clearcutting (Braun 1950). In primary forest however, deer browsing has been blamed for vegetation structure and compositional changes in understory vegetation including a broad scale decimation of Canada yew (Braun 1950, Anderson and Loucks 1979, Allison 1990).

An historical reduction in the shrub layer within the primary forest implies that densities of shrub layer associated bird species that were herein reported for the primary northern hardwood forest would not be representative of their former densities in pristine forest (former primary forest before the large scale ecological changes). The association of these species with the sapling layer that is largely renewed by logging in managed forest might also be a phenomenon that is part of the directional change that the northern hardwood forest has undergone after the large scale clearcutting.

Regional declines of forest interior bird species would affect their immigration rates into the primary forest. Cook (1904) described the black-throated blue warbler as one of the most common migrants at several migration passage points in the U.S. Early records describing the distribution of the black-throated blue warbler as abundant and its range extending well into southern Michigan (Pearson 1936). The distribution of the black-throated blue warbler has been shrinking in Michigan such that its present distribution is mostly restricted to the northern part of the state (Binford 1991). The reduction of the species distribution and early accounts of its nesting habits should caution about describing this species niche and habitat relationships from its present distribution and habitat. This point is important because not realizing the full potential of a species habitat use and the extent of the different environmental conditions under which it existed and associated with other bird species would limit management options because of forgotten information.

In today's forested landscapes primary forest landscapes adds to the total heterogeneity of the northern hardwood forest by stretching the gradients of forest cover at the landscape scale, amount of total late maturity conifers and forest edge (lower end). Significantly higher amounts of late forest maturity conifers presents the greatest opportunity to reserve habitat for the blackburnian warbler. Long term viability of the black-throated blue is most probable in primary forest because a high forest cover and in general lower amount of forest edge provide the greatest safeguard against edge species. Even when shrub layer development is limiting, the black-throated blue warbler will occur at low density but will be protected from high densities of edge species.

While there are limitations to what the primary forest could reveal about historical changes in the relative densities of bird species, primary forest landscapes can be setup as controls to monitor ongoing changes in the forest. Since less human disturbance occurs within primary forest reserves, long term monitoring of these landscapes would elucidate how changes in forest conditions at regional levels (or in surrounding landscapes) would affect species inflow into them and impact bird densities.

2. Function of the Managed Forest

Major characteristics of the managed forest that were uncovered by comparisons with primary forest and settled forest were related to shrub layer dynamics. Logging disturbance was a dominant organizing force in second growth forest at the level of a land type association that affected densities of shrub layer associated bird species. The effects of land type association acted in conjunction with logging disturbance to affect the relative response of bird species and the patterns of their response following logging. The fact that densities of both forest interior and area sensitive species as well as edge associated species peaked several years following logging disturbance revealed as was previously discussed that shrub layer development was limiting forest interior bird species densities in managed forest while logging disturbance enhanced the suitability of the interior of the forest to edge related bird species. Thus the managed forest can be looked upon as providing an environment that blended habitat suitability for edge species with that of forest interior bird species.

Heterogeneity of forest conditions in the managed forest became apparent through contrasts of habitat variables and bird species densities across its different forest disturbance period and land type associations strata. Heterogeneity of forest conditions with respect to how the black-throated blue warbler, American redstart and chestnut-sided warbler perceive the environment however became only apparent through contrasts of these species densities among strata that consisted of defined ranges for a combination of factors that included canopy opening, shrub layer development, length of forest edge and forest cover at a landscape basis. The fact densities of each of these 3 species differed significantly (at 0.05 level) among the strata delineated based on these specified criteria established that heterogeneity in forest conditions along these derived dimensions was of biological significance to a forest interior bird species and to its edge species potential competitors. The strata were not represented by geographically defined areas as stratification by land type association would be. The relative contribution of different geographical locations of the forest to these derived strata was not determined by this study[13]. The spatial pattern of different types of patches that define different forest conditions (that are differently suitable to the black-throated blue, American redstart and chestnut-sided warbler) thus could not be viewed spatially. A number of situations establish that the grain of such patchiness would be finer than the patchiness associated with the forest patch delineated based on the last logging operation event. Canopy reduction (one of the variables affecting habitat suitability that differently affected edge and area sensitive species) by selective logging produces finer patchiness than the delineated area for selective logging . In selective logging either single or several trees are removed from a small area. Thus because canopy reduction is patchy, bird census stations from within the same logged site would fall within different strata of canopy opening. Point samples from within a single site would also fall in different strata delineated on the basis of a mount of forest edge (within 500m) depending on whether they were close to forest edges or a great distance away. Forest cover patchiness was coarse grain in that it included patches of different forest types. Bird census stations from the same sampling site were frequently included within the same stratum defining an interval of forest cover.

The managed forest that was herein considered consisted of northern hardwood ecosystems within the core of the Hiawatha National Forest. The need to consider managed forest as an integral part of lands available for the conservation of forest bird species stems from the fact that most forested areas in the U.S. are managed. The range of forest cover that was available within the managed forest on the Hiawatha National Forest would likely overlap ranges of other managed forest areas across the northern Great Lakes. The heterogeneity in forest conditions encountered within the managed forest included ranges of forest conditions that were suitable to bird species that declined in settled forest. This confers upon the managed forest a potential for the conservation of forest interior and bird species that like the blackburnian warbler require specific habitat elements or like the black-throated blue warbler require large forest areas. The heterogeneity of managed forest however also increases the risk for these same species because it exposes them to increased levels of competition from more habitat generalist species. For the blackburnian warbler, the managed forest presented more suitable habitat to the black-throated green warbler. With respect to the black-throated blue warbler the managed forest presented suitable habitat to edge bird species.

3. Viewing the Northern Hardwood Forest as an Open System vs a Closed System, at Equilibrium or Undergoing Directional Change.

A hierarchical approach was used to organize the heterogeneity that exists in the northern hardwood forest. This northern hardwood forest ecosystem however is itself imbricated within higher level systems along with other ecosystems with which it exchanges materials, by which it is affected and which in turn it affects (see Tansley 1935, Reiners 1983, Delcourt et al. 1984, Noss 1992). Viewing the northern hardwood forest as an open system that exchanges populations with other hardwood forest and other forest systems has very different consequences with respect to bird conservation than viewing it as a closed system which exists by itself. In an open system view, the value conferred upon the northern hardwood forest depends upon its capacity to produce an overflow of species that have declined in other ecosystems. Thus the attributes that increase the capacity of the system to produce such species would be enhanced. Management of the ecosystem would seek to keep or restore a greater part of the system to a condition that can produce these species. In a closed system view, the emphasis would be in maintaining the greatest diversity of species. Forest management would emphasize enhancing heterogeneity in the system through human induced disturbance. This heterogeneity would include providing a range of conditions that would comprise the habitat suitability a large number of species. Differences in the 2 approaches can be easily illustrated with respect to the black-throated blue warbler that has declined in many ecosystems. In an open ecosystem view, properties of the ecosystem that enhances the protection and productivity of the black-throated blue warbler such as reduction of edge, maintenance of a low canopy cover, and high forest cover would be applied over most of the system. In a closed view of the northern hardwood forest ecosystem, heterogeneity of forest conditions would be maintained to enhance all species even if this consisted of applying disturbance levels and disturbance frequencies that deviate from intensities and frequencies of naturally occurring events.

The northern hardwood ecosystem was herein described within a minuscule time span (90+ years) with respect to the time it took the system to develop (see Davis 1981, Pielou 1991, Tyrell and Crow 1993). This time frame however was sufficient to provide some insight into some dynamics, patterns and structures within the ecosystem. It can be inferred that the system is progressing into the future, but the direction it is taking to some extent is determined by the structures, patterns and functions of present forest.

There are thus different ways to view a northern hardwood forest along a temporal dimension. Viewed on a short term basis management would only be concerned with immediate changes in the ecosystem. Effects of disturbance imposed by management would be assessed by monitoring changes at the individual project level by assessing the effects just prior and just after disturbance events. On a short term management basis little consideration is given to the state of the ecosystem decades into the future. It is evident that the assessment of disturbance effects would differ greatly between the 2 methods. In the short term basis any disturbance imposed by logging would appear to have a positive effect. The black-throated blue warbler would appear to be positively associated with disturbance of logging. However as has been described of its interactions between the American redstart, chestnut-sided warbler over the long term, the black-throated blue warbler might be loosing ground to the edge tolerant species. The long term effect of applying frequent disturbance on the northern hardwood forest would depend on the interaction of many factors and cannot be known from simple monitoring of before and after monitoring. Only modeling of population dynamics, habitat dynamics under different assumptions of forest disturbance level and under different assumptions of spatial and temporal arrangement of disturbance events and landscape conditions can a view emerge of what the long term future condition of the ecosystem would be like.

4. Aspects to Consider in the Development of Bird Conservation Strategies

1. A first step to the conservation of forest birds in the northern hardwood forest is to establish which bird species should receive management priority. Bird species that need to be prioritized are those that have suffered population declines from known directional changes in the northern hardwood forest ecosystem that have occurred at a regional level. The blackburnian warbler and the black-throated blue warbler should receive priority in the herein described northern hardwood forest ecosystem .

2. Assess the suitability of different land type associations comprising a component of northern hardwood forest with respect to their potential for providing large areas of habitat suitable for the long term sustainability of black-throated blue warbler and blackburnian warbler populations. For the black-throated blue warbler, suitable land type associations would comprise continuous forest that is dominated by northern hardwood forest and older growth northern hardwood forest. For the blackburnian warbler land type associations that contain large areas of older growth northern hardwood forest comprising components of hemlock and white pine and that is intermixed with hemlock and hemlock - white pine forest types would be most suitable.

3- Delineate core areas to provide areas for the long term sustainability of the black-throated blue warbler and blackburnian warbler. In these areas management strategies include the protection of black-throated blue warbler from edge species and enhancement of the hemlock component for the blackburnian warbler. Within a land type association, older growth northern hardwood forest areas and adjacent northern hardwood forest areas should be delineated as core areas for both the blackburnian and black-throated blue warbler. Early successional forest and forest openings within the core areas (area should be in the extent of a 1,000 ha) should be allowed to succeed to northern hardwood forest. Shrub layer development could be enhanced by light canopy disturbance in areas adjacent to older growth, while the older growth itself would act as a buffer against edge species. Enhancement of hemlock regeneration should occur within older growth forest where the blackburnian is already present and in forest areas adjacent to older growth. The reintroduction of Canada yew or its propagation should be encouraged. Management guidelines for areas adjacent to older growth should include maintenance of low edge, relatively low canopy disturbance (removal of single trees rather than group selection and shelterwood methods), and longer intervals between canopy disturbance events (>20 years). Canopy disturbance should occur in small areas at one time (5-10 hectares) separated by larger undisturbed areas. Logging operations that covers 100s of hectare at one time should not be undertaken in these core areas.

4. Develop general forest management guidelines for all northern hardwood forest and guidelines for all logging operations within northern hardwood forest. The interspersion of early successional forest, pine plantations and forest openings close to northern forest should be discouraged. Areas already in these states should be reverted back to northern hardwood forest. Smaller less intensive logging operations that are undertaken over a longer period of time should be encouraged over intensive logging operations. The treatment of 10s of hectares every 5-6 years in an area of several hundred hectares would be less likely to establish forest edge species within the interior of the forest than operations that treat hundreds of hectares at once every 15 years. Smaller less intensive operations spaced over a long time will maintain availability of a shrub layer in the interior of the forest without providing the opportunity for edge bird species to invade.

Logging roads should be maintained to the narrowest possible widths and openings in northern hardwood forest should be eliminated.

5. Develop sampling strategies to monitor long term changes in relative abundance of edge species and the black-throated blue warbler in core areas. Sampling strategies could also be used to evaluate densities of the black-throated blue warbler in core areas compared to its densities in other northern hardwood forest areas not slated specifically for its management. This sampling should however also be carried out over a long term basis because the black-throated blue warbler densities are likely to peak and then fall sharply with periodic logging. The long term relative response of populations of black-throated blue warbler and American redstart with successive logging cycles cannot be known from short term sampling. (It would take many decades for hemlock planting or regeneration to begin enhancing habitat availability for the blackburnian warbler. Monitoring of blackburnian warbler and black-throated green warbler populations however could be used to assess fluctuations in the relative population densities of the 2 bird species which over time would indicate if directional change is occurring).

CONCLUSIONS

1- Bird species declines in a northern hardwood forest ecosystem can occur long before the effects are recognized as forest fragmentation (involving loss of forest cover). When the degradation involves a habitat fragmentation dimension, the process can begin at small spatial scales and does not emerge at larger scales until it has become relatively advanced. In a forest ecosystem in which the assemblages of bird species is more complete, directional change in forest conditions is mediated by interactions between species. Species that are the most habitat specialist would likely be replaced by forest species that are more habitat generalist.

2- One reason why degradation of the deciduous forest biome has been associated with forest fragmentation might involve the association of many bird species with the shrub layer and their habitat distribution along gradients of canopy cover and forest cover. Changes of forest canopy cover and forest cover (at the landscape scale) exposes the most forest interior bird species to edge species.

3- Bird species that are associated with a closed canopy, low shrub layer development are less likely to be outcompeted by edge species. These species are likely to persist in closed canopied second growth, northern hardwood forest fragments as long as the canopy remains closed.

4. Degradation of the system (loss of species or habitat elements) can be along a gradient that is not related to forest fragmentation as the loss of late forest maturity conifers would be. For the blackburnian a discontinuity in availability of habitat along a temporal scale is more limiting that the spatial arrangement of habitat fragments. A severe loss of a habitat element that takes a long time to recover favors a more habitat generalist species (e.g. the black-throated green warbler). The presence of high densities of a habitat generalist might itself instill a further change in habitat conditions for the original species.

5. Because the northern hardwood forest is still recovering from the large scale clearcutting at the turn of the century and because the cycle of logging of the second growth forest is recent, the northern hardwood forest would not have likely reached an equilibrium with respect to the relative densities of the black-throated blue warbler, American redstart and chestnut-sided warbler. Long term effects of successive cycles of

logging in the northern hardwood forest on the relative abundance of these species cannot be determined from short term bird censuses that are designed to sample densities just before and just after a disturbance event.

6. The complex interaction of factors that create heterogeneity in the northern hardwood forest should warn against predicting the future state of bird species populations at an ecosystem level from forest disturbance effects observed within a narrow time interval and within a limited area.

FOOTNOTES

Footnotes for Chapter 1: Introduction

1. The term "northern hardwoods" is given to an association of many different tree species that includes sugar maple, American beech, yellow birch, hemlock, red maple, American basswood, white pine, black cherry, American elm, white ash, and balsam fir (Nichol 1935, Graham 1941, Braun 1950, Tubbs and Goodman 1983). Characteristic species however are sugar maple, American beech, yellow birch and hemlock.

2. A land type association is a land unit delineation in a hierarchical land classification system adopted by the US Forest Service. At the level of a land type association, delineations of the different units are based on local climate and landform. A more complete explanation of land type association and how it fits into a hierarchical land classification system is given in the chapter 'Methodology' under the heading 'Hierarchy of physical and climatic factors affecting forest heterogeneity'.

Footnotes for Chapter 2: Methodology

1. Wiens (1989) discussed how habitat relationships among species are dependent on the spatial scale at which these relationships are being investigated. An example he gave was of habitat relationships between the American redstart and the least flycatcher: a competitive relationship appears at a scale of 4 ha and that of positive association appears at larger scales (regional scales).

2. Schoener (1966) gives the size of feeding territories of several warbler species to be a fraction of a hectare. Morse (1976) gives a range of nesting territory sizes for black-throated green warbler and blackburnian to be in the range of 0.2 -0.5 ha and for the yellow-rumped warbler and magnolia warblers to be in the range between 0.7-0.9 ha. Cody (1978) gives an approximation of the size of territories of old world sylviid warbler species (counterparts to the parulid warblers in the new world) to be 0.5 ha.

3. The fine scale at which birds select habitat has been supported by many field studies (Hilden 1965) in which removal of an individual from its territory results in another of the same species replacing it.

4. An area around a singing male bird was often used to approximate the location of the nesting territory and to measure habitat selection by the species during the breeding season (James 1971).

5. Anderson and Shugart (1974), and Rotenberry and Wiens (1980) found differences between vegetation characteristics measured within sites occupied by individual bird species and unoccupied sites within study plots that would be considered homogeneous in vegetation structure and composition (at the study plot level). The spatial resolution at which most songbird species select their habitat is finer than the spatial resolution used for managing forest resources: that is birds can perceive patchiness within land areas that are considered uniform for management purposes. The averaging of vegetation measurements over a space that appears heterogeneous to bird species would mask vegetation characteristics that individual bird species select and habitat differences among bird species. This point was used by Wiens and Rotenberry (1981) to argue for the need to understand species specific habitat needs at relevant spatial scales in the management of bird communities rather than depend on bird community characteristics (species diversity and richness) or broader based habitat characteristics.

6. The concept of a landscape in organism-based biology is relatively recent. The concept of a landscape has long before been used in land classification. A landscape concept has been recently introduced into forest management to be a level above the unit of management which is the stand. A spatial scale in the range of 100s-1000s of hectares presents a perspective of higher level patchiness. At this level the spatial configuration of different management schemes and of different forest types (e.g. early successional forest vs long-lived forest types, old-growth vs managed forest) emerges.

7. The importance of population sources have been best revealed by the disappearance of forest bird species from woodlots in which the vegetation structure (at the microhabitat level) had not changed but forest had been lost from the larger landscape (Lynch and Whitcomb 1978; Askins and Philbrick 1987, Askins et al. 1987). Much of what is known about dispersal and the greater landscape has been revealed from landscapes in which the forest had become patchy invoking the theory of island biogeography (McArthur and Wilson 1967). In forested regions, environmental resistance and patchiness of source populations would be more difficult to assess because environmental patchiness would be perceived differently by different species.

8. The spatial scale of a region as used here is at a level of a large part of a state (level of a 'Section' in the definition of ecological units as presented in Ecomap (USDA-Forest Service 1993).

9. With the introduction of a hierarchy perspective (Allen and Star 1982), heterogeneity in the forest could be assigned to different scales. Many bird community studies were restricted to the level of a habitat and did not consider heterogeneity that would be due to differences in the spatial configuration of habitat patches at broader spatial scales. With the increase in spatial extent of more recent studies (covering different

regions) the need to consider a hierarchy becomes more evident. This is because the relationships found within lower levels (habitat types) might be affected by higher levels in the hierarchy. For example the relationship between a species and a habitat type might not be constant across regions.

10. The relationship of 2 species can be examined by assessing the relative occupancy of patches (territory level) of known characteristics by 2 species within a habitat type in a landscape of known characteristics; then moving to a different landscape (of different characteristics) and investigating the relative occupancy of same (territory level) habitat patches in the same habitat by the 2 species. Alternatively within the same habitat in the same landscape one could examine the occupancy of (territory level) patches of different characteristics by the 2 species. In either case looking at the occupancy of the 2 species in larger areas (larger than the scale at which discrimination between patches is occurring) would mask differences between the species. The 2 species will appear correlated (to the habitat type and not to individual types of smaller patches).

11. In the Robbins et al. (1989) study, of the 3 measures of % forest cover within 1 km, 2 km and 3 km from the point of bird censusing, the abundance of bird species were most correlated with forest cover within 2 km.

12. Readily available delineations of the forest based on habitat availability of different bird species at the microhabitat level, and forest fragmentation variables at both the microhabitat and landscape level (here considered within 1.6 km and 500 m) do not exist. Ideal delineations of strata that would be organism defined (that show either density or population productivity differences) could start from the bottom up by classifying land units the size of bird territories based on some vegetation structure characteristic associated with a population parameter of that particular species. Adjacent small size units that are similar with respect to the defined variable would be combined to form a patch. A spatial pattern of like patches becomes apparent at some higher spatial scale. Different patterns of patchiness could become obvious at increasingly higher levels of spatial scale. It might be possible in this manner to relate the pattern of patchiness at one level to some underlying environmental variables. For example the patches of coniferous trees within a patch of northern hardwood forest patch could be related to topography and aspect

13. The effects of forest changes on bird species have been described qualitatively in various treatises (Bond 1957, Brewer 1991) but these descriptive accounts do not provide the quantification needed for strong causal inference.

14. The Upper Great Lakes region has only recently been affected by anthropogenic activities and these have been minimal relative to human impacts in other geographical regions in the world.

15. Landuse is an extraneous factor to naturally occurring environmental factors that determine the hierarchical nature of ecosystems in the natural world as described by Allen and Star (1982). It is only the naturally occurring environmental factors which have

provided the theoretical basis for the hierarchy in ecological land classification systems. Land use however has a dominant influence in modifying the multi-scaled heterogeneity that has developed naturally at this geographic location. Forested ecosystems in the Northern Great Lakes provide unique opportunities to study the effects of human-caused disturbance because of the large patchiness in which different land uses occur and because of the fact primary forest still exists in several large areas.

16. The land use and land type association categories are large enough (in area) that bird density patterns that emerge at their scales would be expected to be affected more by intrinsic factors (i.e. habitat suitability and population productivity) affecting bird species operating within these patches and less by extrinsic factors (immigration from other source areas). [Information from biological reserves indicates that the larger the area the less it would be affected by outside processes such as bird immigration into the area (Blake and Karr 1984; Lord and Norton 1990, Harris and Silva-Lopez 1992, Noss 1983, Ambuel and Temple 1982, Robinson 1988)].

17. Because forest landscapes have been drastically altered outside of forest reserves, processes that occur over broad scales (e.g. deer migration) could still affect structure and composition of the forest inside forest reserves.

18. Logging creates canopy openings in locations where trees are removed. In these locations forest maturation processes are set back. The state of the vegetation structure therefore depends on the time that had elapsed since logging. The patchiness created by logging is laid over preexisting patchiness caused by other factors such as small scale soil variation, topography, aspect and past disturbance. Factors that have contributed to previously existing patchiness are likely to have different spatial scales than that in which logging is undertaken such that the overlaying of cutting creates a variety of new patchiness. Northern hardwood forest grows on mesic soils so it occupies those areas in the land type association in which mesic conditions dominate. The patches of northern hardwood forest within a land type association would match the level of 'land type' in the hierarchy of ecological units (Ecomap-USDA Forest Service 1993). Patchiness at this scale represents very fine variation in aspect, slope, soils, and plant associations. Small scale patchiness within the northern hardwood forest across a land type association would be similar because they occur on the same soil type, landform, rock type and are exposed to the same geomorphic processes and local climate. For the same silvicultural treatment (logging methodology) this small scale patchiness would only differ based on the time elapsed after logging disturbance.

19. The term older growth is used to refer to forest that forest managers recognize to have an age class and tree species composition that are more typical of the primary forest than of the secondary forest that developed after intense logging or clearcutting. The term older growth is however used rather than primary forest because it is not with absolute certainty that the area was not logged and the intensity or selectivity of logging (other than clearcutting) when it did occur is unknown.

20. Specific vegetation variables measured and methodology of sampling vegetation are described under Sampling of Microhabitat Variables in the Methodology Section of Field Methods.

21. A list of features that were considered forest edge is given in 'Locating Bird Census Stations' in the section of Field Methods in the chapter Methodology.

22. The specific variables that quantified fragmentation at different spatial scales and the statistical analyses used are discussed in 'Effects of Interactions of Habitat Fragmentation Related Aspects of Forest with Habitat Availability on Bird Species' in the Section Statistical Techniques in Methodology. Here only a broad overview of the study design is presented.

23. The details of these analyses are given in Statistical Techniques section of the Methodology chapter.

24. Alternatively some initial stratification of the sampling units could have been retained and the sampling units from each of the strata post stratified separately to new spatial scales. Sampling units from different strata of land use, managed forest, primary forest and settled forest, or from different land type associations could have been analyzed separately. The individual land use would not provide the full range of values for some fragmentation variables; for example settled forest might not have any sampling units that would fall in a stratum of high % forest cover. There would however be a management interest in comparisons of different land type associations within a land use category. Only the comparison of land type associations in primary forest would reveal the effects of land type association on forest fragmentation. For managed forest what would be revealed by a comparison of land type association is the intertwined effects of forest management with inherent land type association characteristics . The number of sampling units from each strata limited the possibility of carrying out separate analyses. Contribution of different land uses to groups representing different ranges of fragmentation values at the 2 spatial scales can however be uncovered by assessing the contribution of each land type association within a specific land use to the different groups.

25. The present delineation of stands has developed gradually. Through the years, different foresters have made decisions on where to place stand boundaries. Aerial photographs have been used to delineate boundaries of different forest types. Streams, rivers, roads have been used to subdivide areas that appear homogeneous in a photograph into smaller units. Because the delineation of stands have not followed consistent methodology through the years, it is now difficult to derive a well set of criteria to define how stands differ from one another or to find a consistent spatial resolution that went into the delineation of stands. Stands widely differ in size, usually between several hectares to hundreds of hectares. Some stands could comprise high heterogeneity in the vegetation structure, topography and could comprise many easily recognizable patch types.

26. The hierarchy of units below a spatial scale of a national forest include (as presented in USDA-Forest Service National Hierarchical Framework of Ecological Units 1993).

I) land type association in which landform complexes and local climate are dominant factors. These factors produce repeatable patterns of soil complexes and plant communities (USDA. 1993)

ii)land types differences in the units is based on soils, landform (example Kalkaska soil, end moraine). They are mapped in the field based on local topography and vegetation.

iii)Land type phase. Finer division of land types, based on very local site conditions, slope, aspect, topographic position.

27. Because factors causing the heterogeneity at different spatial scales, and the relationship between units at different scales are well defined, there is justification for relating the ecology of organisms to the physical-vegetative environment than do stands as they are delineated for management purposes.

28. Although parameters such as diameter at breast height and basal area are averaged over the area comprising a management unit (stand), this should not be considered an indication that the stand is homogeneous with respect to these parameters. Since the range of values and the variance of ecological parameters (soils, slope, vegetation communities) are not apriori set for their delineations, stands as management units do not represent consistent ecological units.

29. Although silvicultural treatments are usually applied over a whole management unit (stand), occasionally only a portion of a stand receives a treatment. In such a case only the area of the stand that has received the logging treatment would be suitable to represent the respective stratum of time elapsed after logging. Alternatively when several adjacent stands are treated at the same time, the total area receiving the treatment was included in the respective stratum of time elapsed after logging.

30. The 'CDS database' is incomplete for management prior to 1979 and for areas that had not received active management. Such information was found in old compartment records.

31. Presence of black cherry often indicates past logging and burning.

32. There were 2 instances in which a class of time elapsed since last disturbance was not represented in a land type association.

33. This is especially true for comparisons of vegetation variables and bird densities among 3 replicate land type associations within a land use category. For the category of

managed forest, separate comparisons among the 3 land type associations were undertaken for each class of time elapsed after disturbance.

34. In managed forest, each of the patches of continuous forest that represents a stratum of northern hardwood forest (e.g. logged 1-5 years ago) represented an area logged at one time. Traditional studies addressing the effects of logging on bird densities often consider a patch (stand or plot) as a replicate of that logging treatment. The perspective herein taken is not that of testing the effects of logging on areas of a specified size and shape, and of particular characteristics. The objective was to determine the general effects of (selective) logging when superimposed over many other factors of heterogeneity, on land units the size of bird territories and when viewed at the level of the entire northern hardwood forest ecosystem. Little was known about the individual logging treatments (only that it was selective logging and undertaken within a specified period of time). Furthermore, the size and the shape of the patches varied, thus the effects of individual treatments on different points within a patch varied depending on the larger vicinity of the point.

One aspect of spatial data is autocorrelation. It indicates points that are closer to each other to be more similar than points that are farther apart. Although the northern hardwood forest model did not include the effects of the patch (site), spatial autocorrelation and individual patch effects were later examined by testing for significance among different patches that were included within a stratum specified by the model . An F test examined if variability of bird census stations within a patch was less than the variability among patches. Within patch variability was compared to among patch variability of bird census stations in each of 2 strata of forest disturbance periods within each of 2 land type associations. All bird variables (10 bird species), and the vegetation variables representing % canopy opening, number of gaps >50-100m2, % ground cover by shrub layer, and number of coniferous trees were compared. Of 40 F tests of significance that compared within patch and among patch variance of bird densities, 4 were statistically significant at 0.05 level. None of the vegetation variables showed a significant difference among patches. A conclusion was therefore reached that the patch had no effect beyond the stratification already included in the model (that is lumping together of bird census stations from a single forest disturbance period within a land type association was justifiable).

35. In most cases, censuses by 2 individuals were treated as practice runs and were not part of the data set. In the cases where the census data became part of the data set, only the data from an assigned censuser (and not the companion's data) were considered.

36. The matching of bird density patterns with habitat availability patterns across model strata was part of the analytical pathway followed to assess the relative effects of habitat availability and habitat fragmentation aspects on bird density.

37. The strata of 'unlogged second growth forest' and 'older growth forest' were each represented in only 2 of the 3 replicate managed forest landscapes due to their unavailability in all 3 landscapes.

38. I used univariate rather than multivariate regression because the relationships among the habitat variables were not linear across strata of the northern hardwood forest system sampled. This non-linearity was later demonstrated by interactions among variables in different strata of the model that affected bird densities. Some variables affected a species density only within certain 'periods of forest disturbance' and certain ranges of forest cover. Variables that had an effect in one strata, failed to have an effect in the instance of another variable becoming more limiting under different forest conditions.

39. In these comparisons of managed forest with settled forest and primary forest, managed forest is assumed to comprise an equal proportion of the 5 forest disturbance periods. In reality the older growth stratum is over represented in the data since little older growth remains in the managed forest.

40. In the program Distance Sampling used to census birds, there was no way to identify whether the bird recorded at a station was breeding or simply occurred there as a vagrant. To reduce the probability of recording vagrants, only those bird census stations in which the species occurred at densities above 80 birds/km2 were selected to represent the breeding habitat of a species. The black-throated blue warbler was commonly encountered. Habitat conditions at bird census stations at which the species occurred above its mean density of (51.2 +/- 4.65) were considered representative of its habitat selection.

41. Because of the blackburnian warbler's low density in the forest, its presence even at very low densities could reflect its habitat selection. The assumption made here is that the probability of encountering the blackburnian as an overflow into marginal habitat is lower than it is for the more abundant American redstart and black-throated blue warbler.

Footnotes for Chapter 3: Results.

1. An Anova of mean density differences between settled forest and a hypothetical forest in which all 5 strata of forest disturbance periods were equally represented (including the older growth stratum) yielded a p value of 0.157 which is not significant at the 1% level. This p value would be even greater if the older growth forest strata was considered to be < 1/5 of the managed forest. That is there would be a smaller difference between the density of blackburnian warbler in managed forest than in settled forest. Under present conditions the older growth forest makes up only a very small percentage of the total managed forest.

2. These comparisons are not completely independent from the regression in which bird density and LMCON were averaged for the 7 strata of 'forest disturbance periods' and 'land use'. In regression however different patterns of the data can result in the same r^2 value and regression coefficient. These comparisons therefore give slightly more detail about the relationship of micro habitat availability and habitat selected by the blackburnian warbler and black-throated green warbler separately for each stratum.

3. In the stratum 'logged 1-5 years ago' the blackburnian density was higher than in the other strata of ' managed forest landscapes' excepting the older-growth stratum but these density differences were not statistically significant

4. It should be understood that a reduction of canopy cover in the strata of 1-5 years after logging does not imply that canopy cover was reduced in the habitat patches selected by the blackburnian. Habitat selection occurs at a spatial scale smaller than the area representing a stratum. The blackburnian can find patches of coniferous trees which differed in mean canopy cover from the mean canopy cover of the stratum. Mean density of the blackburnian warbler however aggregated over the stratum of disturbance period reflected the slightly higher mean for coniferous trees in this stratum in spite of the reduction in canopy cover.

5. The blackburnian warbler was only encountered once in settled forest landscapes and as a result it was not possible to compare its micro habitat selection with that of the black-throated green warbler in settled forest landscapes.

6. A separate regression was applied to regress bird densities on values of woody stems for each different strata of northern hardwood forest.

7. Differences between the black-throated blue warbler, American redstart and chestnut-sided warbler are for the whole range of northern hardwood forest heterogeneity covered in this study. As was previously presented, over the variability that appeared in the whole range of northern hardwood forest that was sampled, both the American redstart and chestnut-sided warbler were positively associated with % canopy opening CANOPEN, and with number of large canopy gaps >100m2 (GAP>100) in contrast to the black-throated blue warbler that showed no response to either CANOPEN or GAP>100 (Table 4).

8. Logging was not associated with an increase in the number of large canopy gaps >100m2

9. Mean number of canopy gaps>100m2, % canopy cover, and number of deciduous woody stems <0.5 were compared among the 3 species groups, black-throated blue warbler, American redstart, and chestnut-sided warbler. To calculate each of the 3 bird species means for these variables, only bird census stations at which the density of the respective bird species was > 80 birds / km2 were used

10. As previously discussed, the black-throated blue warbler dropped out in 'settled forest'. The fact micro habitat effects and landscape effects were confounded in settled forest also precluded further detailed investigation of individual variable effects.

11. Please see the section 'Statistical Techniques' and Table D28 for details about this 3-way ANOVA.

12 The effects of forest disturbance were incorporated by considering canopy gaps, shrub layer development and canopy opening. These however are micro-habitat level effects. Forest management effects at the landscape level such as edge were also incorporated. Factors that could have important effects on the density of a bird species at the local site but could not be incorporated were quantifications at the landscape level of the amount of habitat that contained the species specific micro habitat, and of that species population levels. Population levels in the landscape however could also be lags from previous events in the landscape prior to data collection.

13. The group of 12 bird census stations representing the combination of NHWD1MIL <30%, 'WSDC<0.5' >50 included 5 bird census stations from the land type association of Rapid River. Where shrub layer was developed the Rapid River LTA had unduly high densities of black-throated blue warblers. This high density might be explained by factors other than conferring a high habitat suitability for the species on a landscape which is highly forested but in which the northern hardwood forest makes up a low percentage of the total forest cover. The alternative explanation is that the population of black-throated blue warbler begins to saturate areas where the sapling layer has developed due to logging because of the limited sapling layer development elsewhere.

Footnotes for Chapter 4: Discussion and Conclusions.

1. The black-throated green means on total number of conifer trees and number of late forest maturity conifer trees for 19 sites in settled forest at which it occurred at a density>30 birds/ km2 were: TOTCON = 5.26 (se=0.72) and LMCO = 4.8 (se=0.62). This is compared to TOTCON= 2.8 (se=0.95) and LMCO = 2.6 (se=0.38) within the stratum of forest disturbance period 1-5 years ago. The 95% confidence limits for means of TOTCON and LMCON for the black-throated green in settled forest overlapped the 95% confidence intervals for TOTCON and LMCON means of blackburnian calculated across the whole northern hardwood forest. This shows that in settled forest in the absence of the blackburnian and where it occurred at low densities the black-throated green warbler could be more selective for conifers. In managed forest the black-throated green occurred in more deciduous habitat and showed less selectivity. (Means of TOTCON and LMCON for all northern hardwood forest strata and for the mean of the blackburnian and black-throated green across the whole range of northern hardwood forest are given in Table D 20).

2. The blackburnian warbler was not affected by the increased canopy opening caused by logging. Within the stratum of forest disturbance 1-5 years after logging, the stratum that has the greatest canopy cover reduction, % canopy opening at sites selected by the blackburnian did not differ from mean canopy opening for that stratum. Mean CANOPEN= 30% (sd= 19.5, n=12) at bird census stations at which the blackburnian density was >30 birds/km2; CANOPEN=22.55 (sd=15.9, n=46) for forest disturbance period 1-5 years after logging.

3. In the Rapid River land type association, the black-throated blue warbler had a relatively high density in unlogged second growth in spite of the very low number of woody stem. This situation might be reflecting an overflow into marginal habitat from proximate more suitable habitat because of the limited northern hardwood forest habitat in this landscape into which individuals could disperse.

4. Details of dynamics of the American redstart, black-throated blue warbler and chestnut-sided warbler in Munising, Manistique and Rapid River were presented in the Results section.

5. High deer populations are blamed for the poor shrub development on the Rapid River District on the Hiawatha National Forest. The study area receives high numbers of deer moving from lowland conifer areas from both the Whitefish River and Stonington deeryards. See Van Deelen (1995).

6. In some narrative accounts there are descriptions of the black-throated blue warbler using recently cut brushy forest areas in Canada (Godfrey 1986). This suggests that the black-throated blue warbler is adapted to a wider range conditions than what was revealed by its density pattern in the Upper Peninsula of Michigan.

7. All encounters of the black-throated blue warbler in settled forest occurred early in the season. That it was not encountered later in the breeding season in settled forest suggested that it did not establish territories. T. Donovan (pers. com) also observed that some bird species are prevented from establishing territories. Distance Sampling, the methodology used to estimate bird densities, does not differentiate between mated males and unmated males, or males that have actually established territories or simply passing through. All black-throated blue warblers that were encountered during bird censusing regardless of their true breeding status, were used to derive a density estimate .

8. In the Upper Peninsula the blackburnian warbler has been recorded in habitat types that include shrub with scattered conifers, northern white cedar, young black spruce and mature black spruce (Dawson 1979); Robert Doepker (Michigan DNR; Pers.Com) however found the blackburnian warbler to be most abundant in hemlock patches within the northern hardwood forest relative to other conifer forest habitat during his bird censusing for the Escanaba State Forest Plan development.

9. Several studies have indicated competition among the blackburnian and black-throated green warbler (MacArthur 1958; Morse 1976).

10. Since the microhabitat selected by the 2 species is relatively stable, their densities could be monitored at selected sites to establish interactions between them up along a temporal dimension.

11. This process has been described by Graham (1941). The frequency of disturbance for 2 primary forest landscapes Upper Peninsula has been described by Frelich and

Lorimer (1991). Davis (1995) describes present day stands of sugar maple that had no indication of ever including a hemlock component.

12. A stratum of primary forest landscapes was included in the conceptual model to stretch the range of forest conditions with respect to forest cover at landscape scales, presence of a coniferous component and low edge. This stratification was used to test if there were significant differences in the densities of individual forest interior bird species (black-throated blue warbler) and forest edge bird species (American redstart and chestnut-sided warbler) and in the relative abundance of the forest edge and forest interior bird species within this forest heterogeneity range. With respect to describing the sensitivity of bird species to habitat fragmentation aspects or to the presence of a coniferous component and to describing relationships among species along any environmental gradient, the primary forest did not need to be representative of pristine forest conditions that existed prior to the large scale disturbance at the turn of the century. It should however be emphasized that without strong evidence that the primary forest sampled in this study is representative of pristine forest conditions all relationships established in this study, are limited to describing relationships among species and between species density and habitat conditions existing in the present forest.

13. It is conceivable (although not practical and very tedious) that with a large quantity of data collected at small intervals to map isoclines of canopy opening, distances from edge, forest cover to produce different maps or GIS layers that will reveal the spatial arrangement of patches falling in specified ranges of a variable. The intersection of the different layers would produce a map in which patchiness of habitat conditions will delineate differential suitability of forest conditions to the black-throated blue warbler, American redstart and chestnut-sided warbler.

APPENDICES

APPENDIX A

Table A1. Relationship of the land type association to ecological units above and below its level in the National hierarchy of ecological units as given in Ecomap, USDA Forest Service, Washington, D.C. (1993), and to subdivisions identified in the regionalization of Michigan landscapes (Albert et al., 1986).

Planning and Analysis Scale	Ecological Units as Given in Ecomap	Regionalization of Michigan (Albert et al., 1986)	General Size Range
Ecoregion			
Global	Domain		1,000,000s to 10,000s of square miles
Continental	Division		
Regional	Province		
Subregion	Section	Regions I, II, III District	1,000s to 10s of square miles
	Subsection	Subdistrict	
Landscape	Land type association		1,000s to 100s of acres
Land unit	Land type		100s to less than 10 acres
	Landtype phase		

Table A2. Description of the land type associations of the West Unit of the Hiawatha National Forest, as they had been delineated (1992) in a draft ecological classification of the forest.

LTA#	LTA Name	Land Type Association Description
LTA 1*	Munising Moraine	Well developed upland sands and loamy sands of morainal or outwash origin supporting northern hardwood communities. Some areas shallow to sandstone bedrock. Strong climatic influence from Lake Superior.
LTA 2	Wetmore Outwash Plain	Well developed outwash upland sands of outwash and ice-contact origin. Mixed pine forests and medium to low quality hardwoods occur in this area.
LTA 3	Shingleton Fen	Large wetland complex formed in outwash sand reworked by Lake Algonquin.
LTA 4*	Steuben Segment, Newberry Moraine	Well developed loamy sands of morainal origin, supporting high quality northern hardwood communities. This segment is thought to be an interlobate feature between the Green Bay and Superior lobe of Late Wisconsin glaciation. Its elevation places it above Lake Algonquin shorelines.
LTA 5	Boot Lake Plain	Similar to Wetmore Outwash Plain; above Lake Algonquin level.
LTA 6	Whitefish-Autrain Lowlands	Drainage basin of the Whitefish River, with strong climatic influence from cold air drainage. Formed when receeding glacial ice in the Lake Superior basin raised water levels to a point where water flowed southward through this drainage into Little Bay de Noc. Mostly lowland conifers.

Table A2. (continued)

LTA#	LTA Name	Land Type Association Description
LTA 7*	Interior Sand Ridge-Swale Complex	Variable landscape pattern of beach ridges and dunes interspersed with wetlands, and vegetated with northern hardwood communities.
LTA 8	Cooks Moraine	Till moraine formed by the outermost position of the Green Bay Lobe. Mostly in private ownership.
LTA 9	Whitefish Delta	Sand delta from gladial drainage through the Whitefish-Autrain Lowlands. The native vegetation was tallgrass and shortgrass savannah; the area currently supports jack pine.
LTA 10	Stonington-Nahma	Thin till soils over limestone bedrock; variable landscape pattern of wetlands and uplands with wet areas supporting mostly coniferous forests and uplands supporting northern hardwood communities.
LTA 11	Stonington Outcrops	Thin till over limestone with common limestone outcrops; high water table, mostly coniferous forest.

*Landtype associations selected as study areas.

APPENDIX B

Table B1. Scientific names of animal and vegetation species.

Bird Species	
American redstart	*Setophaga ruticilla*
Black-throated blue warbler	*Dendroica cerulescens*
Black-throated green warbler	*Dendroica virens*
Blackburnian warbler	*Dendroica fusca*
Canada warbler	*Wilsonia canadensis*
Northern Parula	*Parula americana*
Brown-headed cowbird	*Molothrus ater*
Chestnut-sided warbler	*Dendroica pensylvanica*
Indigo bunting	*Passerina cyanea*
Least flycatcher	*Empidonax minimus*
Ovenbird	*Seiurus aurocapillus*
Red-eyed vireo	*Vireo olivaceus*
Scarlet tanager	*Pirangea ludoviciana*
Swainson's thrush	*Catharus ustulatus*
Veery	*Catharus fuscescens*
Mammal Species	
White-tailed deer	*Odocoileus virginianus*
Plant Species	
American beech	*Fagus grandifolia*
American elm	*Ulmus americana*
Blasam fir	*Abies balsamea*
Black cherry	*Prunus serotina*
Black spruce	*Picea mariana*
Canada yew	*Taxus canadensis*
Eastern hemlock	*Tsuga canadensis*
Eastern hophornbeam	*Ostrea virginiana*
Jack pine	*Pinus banksiana*
Northern white cedar	*Thuja occidentalus*
Paper birch	*Betual papyrifera*
Red oak	*Quercus rubra*
Red maple	*Acer rubrum*
Red pine	*Pinus resinosa*
Sugar maple	*Acer saccharum*
White ash	*Fraxinus americana*
White pine	*Pinus strobus*
White spruce	*Picea glauca*
Yellow birch	*Betula alleghaniensis*

Table B2. Variables considered in describing vegetation structure and composition at the microhabitat level.

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1 - tree species

2 - diameter of trees and snags

3 - tree height and snag height

4 - % canopy cover

5 - ground cover (% forb, grass, litter, base of shrub, base of coniferous shrub or tree)

6 - average height of shrub or sapling layer

7 - number of canopy gaps in 4 size categories

8 - distance to road, trail, opening, and other forest types

9 - number of deciduous stems <1cm and >1cm-3cm<

10 - number of coniferous stems <1cm and >1cm-3cm<

Table B3. Number of stands identified from USFS databases in 1992 that were available in the managed forest for the different strata of forest disturbance periods and land type associations that met the necessary criteria for establishment of bird census stations.

	Munising		Manistique		Rapid River	
	Available	Sampled	Available	Sampled	Available	Sampled
Managed forest logged 15 years ago	6	4	8	4	7	3
Managed forest logged 6-12 years ago	15	4	6	3	6	5
Managed forest logged >12-15 years ago	6	4	8	5	3	3
Untreated or treated >15 years ago	44		8		9	
Unlogged second growth		4		1		5
Older growth		4		3		0

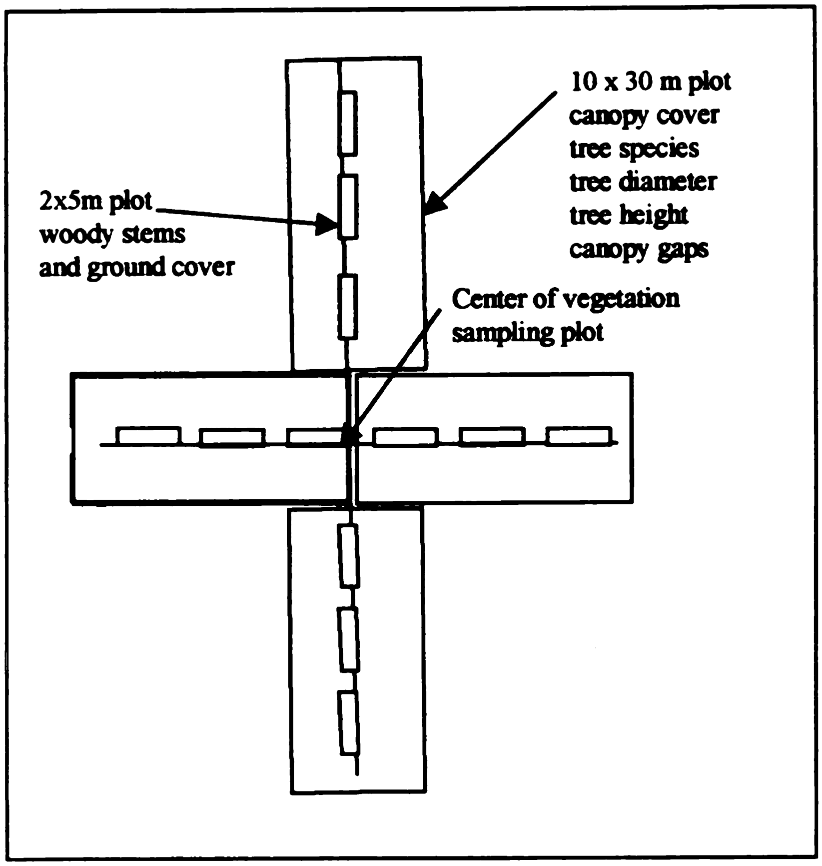

Figure B1. Vegetation plots centered at bird census stations in which microhabitat variables were measured.

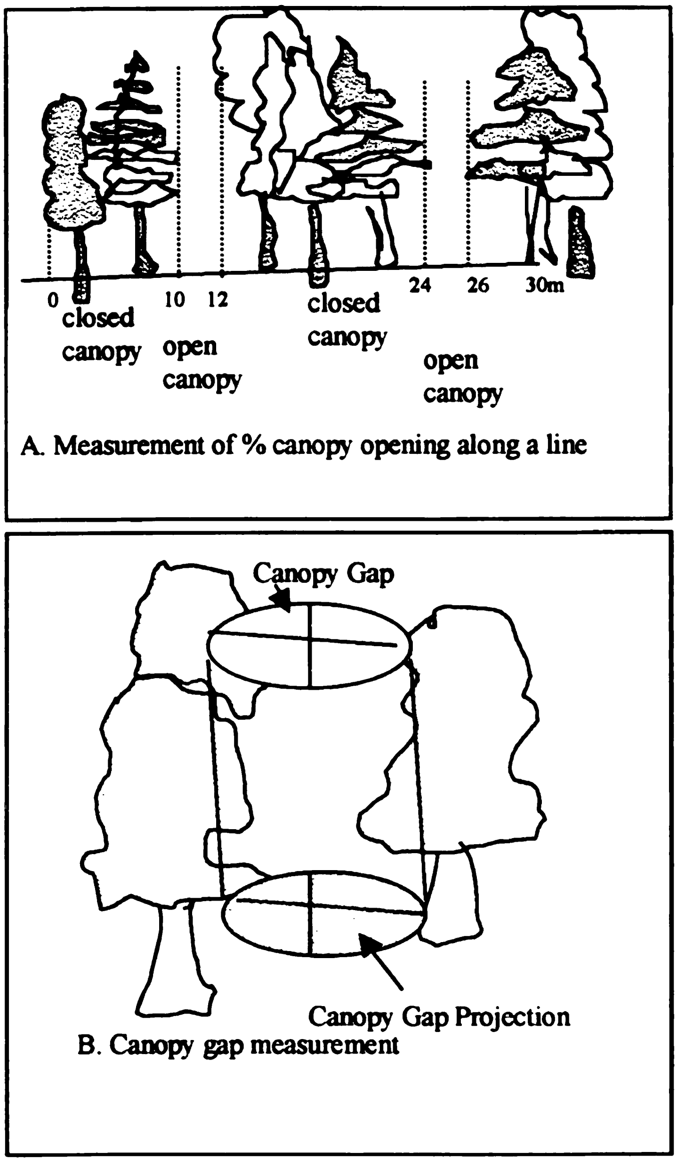

Figure B2. Measurement of % canopy opening and canopy gaps.

APPENDIX C

Table C1. Initial classification of cover types in the integration of land cover types from different land classification systems.

USFS code	All cover types from National Forest, Huron Mountains, McCormick Wilderness Area, Sylvania Dukes Experimental Forest and private lands	Data Source	Classification for Landscape Analysis
013	Jack pine seedling	NF	Open; Bush; Upland
016	Jack pine pole	NF	Conifer; Upland; Dry; Pole; Early Successional; Plantation
019	Jack pine mature	NF	Conifer; Upland; Dry; Mature; Early Successional; Plantation
	Jack pine-natural	HM	Conifer; Upland; Dry; Mature; Early Successional; Natural
023	Red pine seedling	NF	Open; Bush; Upland
026	Red pine pole	NF	Conifer; Upland; Dry; Pole; Transitional; Plantation
029	Red pine mature	NF	Conifer; Upland; Dry; Mature; Transitional; Plantation
	Red pine natural	HM	Conifer; Upland; Dry; Mature; Transitional; Natural
	Red pine-white pine (natural)	HM	Conifer; Upland; Dry; Mature; Transitional; Natural
033	White pine seedling	NF	Open; Brush; Upland
036	White pine pole	NF	Conifer; Upland; Dry; Pole; Transitional; Plantation
039	White pine mature	NF	Conifer; Upland; Dry; Mature; Transitional; Plantation
	White pine/cladonia	MC	Conifer; Upland; Dry; Mature; Transitional; Natural
	Conifer/Cladonia	MC	Conifer; Upland; Dry; Mature; Transitional; Natural
049	White pine-hemlock	NF	Conifer; Upland; Mesic; Mature; Transitional; Natural
	White pine-hemlock-hardwood	HM	Conifer-Deciduous; Upland; Dry; Mature; Late Maturity; Natural
	White pine-hardwoods/Maianthemum	MC	Conifer-Deciduous; Upland; Dry; Mature; Late Maturity; Natural
	Pine-oak (whitepine-red oak-red pine)	HM	Conifer-Deciduous; Upland; Dry; Mature; Transitional; Natural
	White pine-red oak-hardwoods	MC	Conifer-Deciduous; Upland; Dry; Mature; Transitional; Natural
059	Hemlock	NF	Conifer; Upland; Mesic; Mature; Late Maturity; Natural
	Hemlock	HM	Conifer; Upland; Mesic; Mature; Late Maturity; Natural
	Hemlock-mountain maple	HM	Conifer; Upland; Mesic; Mature; Late Maturity; Natural
	Hemlock dominated hemlock-northern hardwoods	HM	Conifer-Deciduous; Upland; Mesic; Mature; Late Maturity; Natural
113	Balsam fir-aspen-paper birch young	NF,PL	Open; Brush; Lowland
116	Balsam fir-aspen-paper birch pole	NF,PL	Conifer-Deciduous; Lowland; Wet; Pole; Early Successional
119	Balsam fir-aspen-paper birch mature	NF,PL	Conifer-Deciduous; Lowland; Wet; Mature; Early Successional
	Conifer-hardwood/Myrica	MC	Conifer-Deciduous; Lowland; Wet; Mature; Early Successional

Table C1. (continued)

USFS code	All cover types from National Forest, Huron Mountains, McCormick Wilderness Area, Sylvania Dukes Experimental Forest and private lands	Data Source	Classification for Landscape Analysis
123	Black spruce young	NF,PL	Open; Brush; Lowland
126	Black spruce pole	NF,PL	Conifer; Lowland; Wet; Pole; Early Successional
129	Black spruce mature	NF,PL	Conifer; Lowland; Wet Mature; Early Successional
	Black spruce	HM	Conifer; Lowland; Wet; Mature; Early Successional
	Black spruce/Ledum	MC	Conifer; Lowland; Wet; Mature; Early Successional
143	Northern white cedar young	NF,PL	Conifer; Lowland; Wet; Pole; Transitional
146	Northern white cedar pole	NF,PL	Conifer; Lowland; Wet; Pole; Late Maturity
149	Northern white cedar mature	NF,PL	Conifer; Lowland; Wet; Mature; Late Maturity
	Northern white cedar	HM	Conifer; Lowland; Wet; Mature; Late Maturity
	Northern white cedar	HM	Conifer; Lowland; Wet; Mature; Late Maturity
156	Tamarack pole	NF	Conifer; Lowland; Wet; Pole; Transitional
159	Tamarak mature	NF,PL	Conifer; Lowland; Wet; Mature; Transitional
163	White spruce-balsam fir young	NF,PL	Open; Brush; Lowland
166	White spruce-balsam fir pole	NF,PL	Conifer; Lowland; Wet; Pole; Transitional
169	White spruce-balsam fir mature	NF,PL	Conifer; Lowland; Wet; Matur; Transitional
	Balsam fir-white spruce	HM	Conifer; Lowland; Wet; Mature; Transitional
183	Mixed swamp conifer young	NF,PL	Open; Brush; Lowland
186	Mixed swamp conifer pole	NF,PL	Conifer; Lowland; Wet; Pole; Transitional
189	Mixed swamp conifer mature	NF,PL	Conifer; Lowland; Wet; Mature; Transitional
	Yellow birch-hemlock-white cedar-red maple	HM	Conifer-Deciduous; Lowland; Wet; Mature; Transitional
193	Cedar-aspen-paper birch	NF,PL	Open; Brush; Lowland
196	Cedar-aspen-paper birch	NF,PL	Conifer-Deciduous; Lowland; Wet; Pole; Transitional
199	Cedar-aspen-paper birch	NF,PL	Conifer-Deciduous; Lowland; Wet; Mature; Transitional
	Conifer-hardwood (cedar-B.ash-w.spruce-y.birch-balsam fir)	HM	Conifer-Deciduous; Lowland; Wet; Mature; Transitional
	Conifer/hardwood/Aralia	MC	Conifer-Deciduous; Upland; Mesic; Mature; Transitional; Natural
553	Northern red oak young	NF,PL	Open; Brush; Upland

Table C1. (continued)

USFS code	All cover types from National Forest, Huron Mountains, McCormick Wilderness Area, Sylvania Dukes Experimental Forest and private lands	Data Source	Classification for Landscape Analysis
556	Northern red oak pole	NF,PL	Deciduous; Upland; Dry; Pole; Transitional
559	Northern red oak mature	NF,PL	Deciduous; Upland; Dry; Mature; Transitional
713	Blackash-American elm-red maple	NF,PL	Open; Brush; Lowland
716	Blackash-American elm-red maple	NF,PL	Deciduous; Lowland; Wet; Mature; Transitional
719	Blackash-American elm-red maple	NF,PL	Deciduous; Lowland; Wet; Mature; Transitional
	Blackash-elm	HM	Deciduous; Lowland; Wet; Mature; Transitional
766	Red maple pole (wet site)	NF,PL	Deciduous; Lowland; Wet Pole; Transitional
769	Red maple mature (wet site)	NF,PL,SYL	Deciduous; Lowland; Wet; Mature; Transitional
	Red maple-yellow birch-conifer/Circaea	MC	Deciduous; Lowland; Wet; Mature; Transitional
	Red maple-yellow birch-conifer/Clintonia	MC	Deciduous; Lowland; Wet; Mature; Transitional
	Red maple-yellow birch-conifer/Osmunda	MC	Deciduous; Lowland; Wet; Mature; Transitional
793	Lowland hardwoods	NF,PL	Open; Brush; Lowland
796	Lowland hardwoods	NF,PL	Deciduous; Lowland; Wet; Pole; Transitional
799	Lowland hardwoods	NF,PL	Deciduous; Lowland; Wet; Mature; Transitional
816	Sugar maple-beech-yellow birch (pole)	NF,PL	Deciduous; Upland; Mesic; Pole; Late Maturity
819	Sugar maple-beech-yellow birch (mature)	NF,PL	Deciduous; Upland; Mesic; Mature; Late Maturity
	Sugar maple/Botrychium	MC	Deciduous; Upland; Mesic; Mature; Late Maturity
	Sugar maple/Maianthemum	MC	Deciduous; Upland; Mesic; Mature; Late Maturity
	Sugar maple/Viola	MC	Deciduous; Upland; Mesic; Mature; Late Maturity
	Hardwood dominated-hemlock northern hardwoods	HM	Deciduous-Coniferous; Upland; Mesic; Mature; Late Maturity
	Sugar maple-hardwoods-hemlock (819-Hem)	NF,PL	Deciduous; Upland; Mesic; Mature; Late Maturity
	Sugar maple-conifer/Circaea	MC	Deciduous-Coniferous; Upland; Mesic; Mature; Transitional
	Sugar-maple (residential)	PL	
	Post clearcutting hardwoods (sugar maple-red maple-yellow birch and white ash)	HM	Deciduous; Upland; Mesic; Mature; Late Maturity
826	Sugar maple-basswood (pole)	NF,PL	Deciduous; Upland; Mesic; Pole; Late Maturity
829	Sugar maple-basswood (mature)	NF,PL	Deciduous; Upland; Mesic; Mature; Late Maturity

Table C1. (continued)

USFS code	All cover types from National Forest, Huron Mountains, McCormick Wilderness Area, Sylvania Dukes Experimental Forest and private lands	Data Source	Classification for Landscape Analysis
846	Red maple dry site (pole)	NF,PL	Deciduous; Upland; Mesic; Pole; Transitional
849	Red maple dry site (mature)	NF,PL	Deciduous; Upland; Mesic; Mature; Transitional
856	Sugar maple	NF,PL	Deciduous; Upland; Mesic; Pole; Late Maturity
859	Sugar maple	NF,PL	Deciduous; Upland; Mesic; Mature; Late Maturity
896	Mixed hardwoods (maple-basswood,	NF,PL	Deciduous; Lowland; Wet; Pole; Transitional
	white ash-paper birch)	NF,PL	
899	Mixed hardwoods (maple-basswood, white ash-paper birch)	NF,PL	Deciduous; Lowland; Wet; Mature; Transitional
	White ash	HM	Deciduous; Lowland; Wet; Mature; Transitional
	Elm-sugar maple-basswood	HM	Deciduous; Lowland; Wet; Mature; Transitional
913	Quaking aspen	NF,PL	Open; Brush; Upland
916	Quaking aspen pole	NF,PL	Deciduous; Upland; Mesic; Pole; Early Successional
919	Quaking aspen mature	NF,PO	Deciduous; Upland; Mesic; Mature; Early Successional
	Aspen	HM	Deciduous; Upland; Mesic; Mature; Early Successional
923	Paper birch young	NF,PL	Open; Brush; Upland
926	Paper birch pole	NF,PL	Deciduous; Upland; Mesic; Pole; Early Successional
929	Paper birch mature	NF,PL	Deciduous; Upland; Mesic; Mature; Early Successional
	White birch and yellow birch	HM	Deciduous; Upland; Mesic; Mature; Early Successional
	White birch-hemlock-red maple	HM	Deciduous-Coniferous; Lowland; Wet; Mature; Transitional
	Hardwood-conifer/Osmunda	MC	Deciduous-Coniferous; Lowland; Wet; Mature; Transitional
933	Bigtooth aspen young	NF,PL	Open; Brush; Upland
936	Bigtooth aspen pole	NF,PL	Deciduous; Upland; Mesic; Pole; Early Successional
939	Bigtooth aspen mature	NF,PL	Deciduous; Upland; Mesic; Mature; Early Successional
943	Balsam popular young	NF,PL	Open; Brush; Lowland
946	Balsam popular pole	NF,PL	Deciduous; Lowland; Wet; Pole; Early Successional
949	Balsam popular mature	NF,PL	Deciduous; Lowland; Wet; Mature; Early Successional
953	Aspen-white spruce balsam fir (young)	NF,PL	Open; Brush; Lowland

Table C1. (continued)

USFS code	All cover types from National Forest, Huron Mountains, McCormick Wilderness Area, Sylvania Dukes Experimental Forest and private lands	Data Source	Classification for Landscape Analysis
956	Aspen-white spruce-balsam fir (pole)	NF,PL	Deciduous-Coniferous; Lowland; Wet Pole; Early Successional
959	Aspen-white spruce-balsam fir (mature)	NF,PL	Deciduous-Coniferous; Lowland; Wet; Mature; Early Successional
97	Lowland brush	NF,PL	Open; Brush; Lowland
	Leatherleaf	HM	Open; Brush; Lowland
	Sweet gale-spirea	HM	Open; Brush; Lowland
	Alder	HM	Open; Brush; Lowland
99	Open	NF,PL	Open
	Open meadow	HM	Open

Table C2. Sources of geographical data covering study areas.

USGS Quadrangle	Coverage for Land Cover: US Forest Service Lands	Coverage for Roads: Private Lands	Water Bodies, Water Courses
Rapid River			
Rapid River	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Waco	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Tie Lake	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Poplar Lake	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Manistique			
Thunder Lake	Hiawatha National Forest-Pilot GIS	Manuscripted from aerial photos	USGS
Gooseneck	Hiawatha National Forest-Pilot GIS	Manuscripted from aerial photos	USGS
Waco	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Steuben	Hiawatha National Forest-Pilot GIS	Manuscripted from aerial photos	USGS
Corner Lake	Hiawatha National Forest-Pilot GIS	Manuscripted from aerial photos	USGS
Tie Lake	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Munising			
Chattam	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Rock River	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Forest Lake	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
AuTrain	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Sand River	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Tie Lake (Munising part)	Manuscripted from aerial photos	Manuscripted from aerial photos	USGS
Trenary			
Trenary	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Baker Creek	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Chattam			
Chattam	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Diffin	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS

Table C2. (continued)

USGS Quadrangle	Coverage for Land Cover US Forest Service Lands	Coverage for Roads Private Lands	Water Bodies, Water Courses
Stonington			
Maywood	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Ogontz	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Ensign	Hiawatha National Forest-tiff file of stands	Manuscripted from aerial photos	USGS
Dukes			
Carlshend	Manuscripted from aerial photos+stand map	Manuscripted from aerial photos	USGS
Skandia	Manuscripted from aerial photos+stand map	Manuscripted from aerial photos	USGS
Ladoga	Manuscripted from aerial photos+stand map	Manuscripted from aerial photos	USGS
Huron Mountains			
Mountain Lake	All private land	Manuscripted from aerial photos+cover map	Manuscripted (aerial photos)
Howe Lake	All private land	Manuscripted from aerial photos+cover map	Manuscripted (aerial photos)
Ives Hill	All private land	Manuscripted from aerial photos+cover map	Manuscripted (aerial photos)
Huron Mountain	All private land	Manuscripted from aerial photos+cover map	Manuscripted (aerial photos)
McCormick			
Silver Lake Basic	Manuscripted from aerial photos+cover map	Manuscripted from aerial photos	Manuscripted (aerial photos)
Bulldog Lake	Manuscripted from aerial photos+cover map	Manuscripted from aerial photos	Manuscripted (aerial photos)
Sylvania			
Black Oak Lake	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Land O'Lakes	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Beaton	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS
Watersmeet	Manuscripted from aerial photos+stand maps	Manuscripted from aerial photos	USGS

Table C3. Types of features in addition to primary and secondary roads, railroad tracks, powerlines and gaslines, included in the calculation of edge within 500m circle areas around bird census stations.

Code of Feature Used in CFF Files*	Description
106	Unimproved road class 4
402	Stream perennial
410	Lake or pond
515	Road, light duty class 3

*added to USGS quadrangle maps per US Forest Service specification.

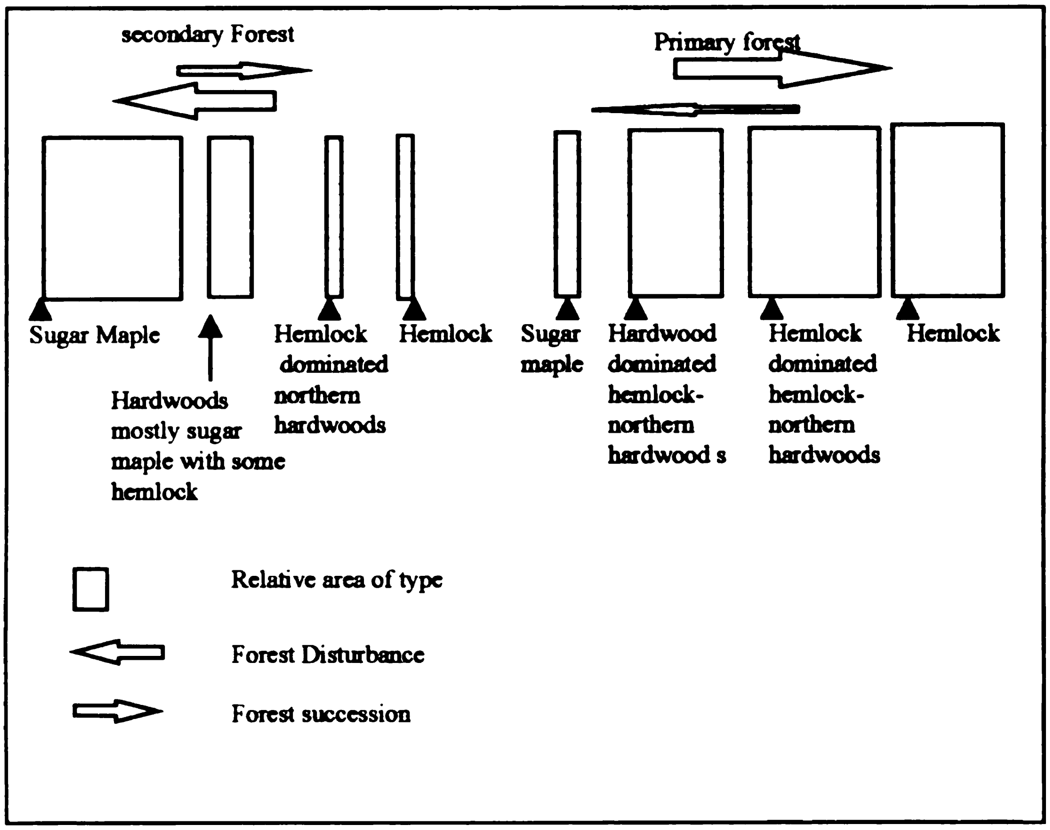

Figure C1. Schematic representation of the contrast in the successional relationship between sugar maple, hardwood dominated northern hardwoods, hemlock dominated northern hardwoods and hemlock in secondary and primary northern hardwood forest.

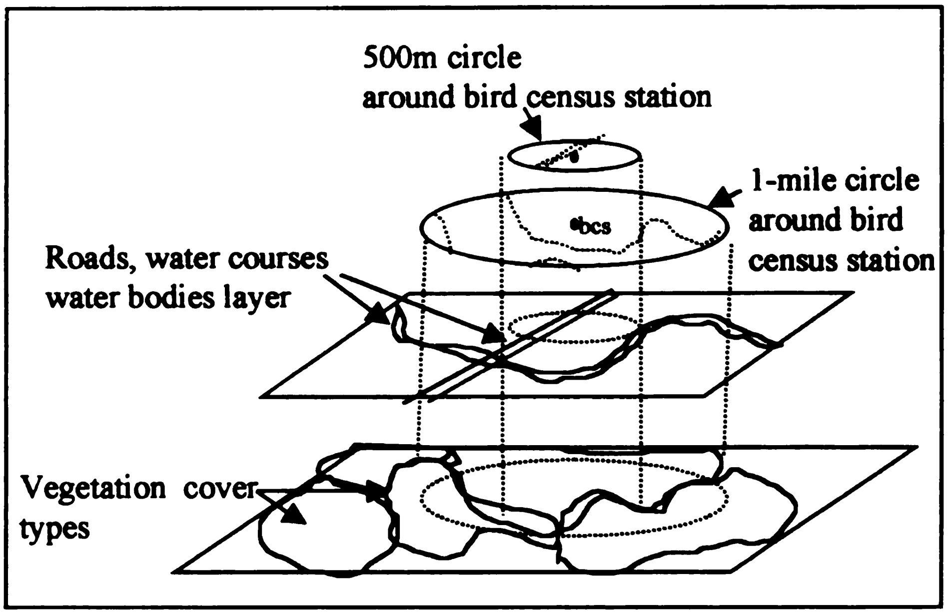

Figure C2. Relationship between vegetation cover and base features (roads, water courses), 1.6 km circle clips and 500 m clips around bird census stations.

APPENDIX D

Table D1. Model selected in the program Distance Sampling (Laake et al., 1994) and other specifications, in the estimation of a detection function for each of 10 bird species. Distance data were obtained from bird censuses conducted in 1992-1994 in northern hardwood forest in the Upper Peninsula of Michigan.

Bird Species	Model	Point of Truncation	Intervals	n[1]
Blackburnian warbler	Hazard Rate	60	25,35,45,60	161
Black-throated green warbler	Uniform	50	20,30,40,50	741
Black-throated blue warbler	Hazard/cosine	80	25,35,45,65	508
American redstart	Hazard/cosine	50	20,30,40,50	560
Chestnut-sided warbler	Uniform	50	20,30,40,50	208
Ovenbird	Half Normal	80	30,50,80	2137
Red-eyed vireo	Hazard/cosine	85	35,55,65,75,85	2314
Least flycatcher	Hazard/cosine	70	25,35,45,55,70	974
Veery	Hazard/cosine	100	25,40,55,70,100	592
Scarlet tanager	Hazard/cosine	150	35,50,65,80,120,150	312

[1]n = number of observations for species.

Table D2. Mean density/km2 and encounter rate of 10 songbird species censused at 321 bird census stations in northern hardwood forest. Northern hardwood forest was stratified into 7 strata. A roughly equal number of bird census stations were located in each stratum. Bird censuses were conducted in 1992-1994 in the Upper Peninsula of Michigan.

Bird Species	Mean Density	se[1]	Encounter Rate (% of bird census stations)
Blackburnian warbler	14.18	2.15	18.7
Black-throated green warbler	64.45	3.60	75.3
Black-throated blue warbler	51.2	4.65	49.5
American redstart	50.09	4.52	43.9
Chestnut-sided warbler	18.54	2.52	24.3
Ovenbird	96.02	2.96	96.9
Red-eyed vireo	101.11	2.76	97.8
Least flycatcher	201.11	18.59	57
Scarlet tanager	10.23	0.87	40.8
Veery	14.95	1.09	53.9

[1]se = standard error of the mean.

Table D3. P values of apriori contrasts in ANOVAs undertaken to test the statistical significance of differences in means of TOTCON and LMCON among land use and forest disturbance period strata. These contrasts are for a hypothetical northern hardwood forest in which the strata of primary forest, settled forest and 5 forest disturbance periods in managed forest were equally represented. Bird density data are from bird censuses conducted 1992-1994 in the Upper Peninsula of Michigan.

Strata Compared[1]	TOT$_{CON}$[2]	LM$_{CON}$[3,4]
Managed forest vs primary forest	0.001	<0.001
Managed forest vs settled forest	0.42	0.7
Primary forest 0.001 vs settled forest	0.001	
Managed forest logged <12 years ago vs all other managed forest strata	0.64	0.45
Managed forest logged <12 years ago vs primary forest	<0.001	<0.001
Managed forest logged <12 years ago vs settled forest	0.85	0.55
Managed forest older growth vs primary forest	0.143	0.31
Managed forest older growth vs all other managed forest strata	0.068	0.001

[1]Each stratum consisted of a random sample of 25 bird census stations from each stratum.
[2]TOTCON = total number of conifer trees.
[3]LMCON = total number of late maturity conifers (hemlock and white pine).
[4]TOTCON and LMCON were sampled within 1200m2 vegetation plots set at bird census stations.

Table D4. Mean of total number of conifer trees TOTCON, and total number of late maturity conifer trees LMCON, in different strata of forest disturbance period and land use. Vegetation was sampled in 1992-1994 in the Upper Peninsula of Michigan.

	TOTCON		LMCON		
Forest Disturbance	n[1]	x[2]	se[3]	x	se
Managed forest logged 1-5 years ago	46	3.09	1.05	1.28	0.87
Managed forest logged 6-12 years ago	55	2.38	0.96	0.8	0.79
Managed forest logged >12-15 years ago	58	2.46	0.94	1.37	0.78
Managed forest unlogged second growth	42	2.9	1.13	1.3	0.93
Managed forest older growth	25	5.84	1.43	5.52	1.18
Primary forest landscapes	46	7.56	1.05	6.65	0.87
Settled forest landscapes	43	2.88	1.09	1.74	0.9

[1]n = number of samples (bird census stations at which vegetation plots were set up).
[2]x = mean.
[3]se = standard error of the mean.

Table D5. Overall P values of Anovas undertaken to compare TOTCON and LMCON among different 'land type associations' replicating 'forest disturbance period' and 'historical divergence in land use'. Vegetation was sampled in the Upper Peninsula of Michigan 1992-1994.

Land Type Associations Compared	Disturbance Period	TOTCON	LMCON
Huron Mts * Sylvania * McCormick	Primary forest	0.608	0.426
Munising * Manistique * Rapid River	Logged 1-5 years ago	0.297	0.695
Munising * Manistique * Rapid River	Logged 6-12 years ago	0.124	0.254
Munising * Manistique * Rapid River	Logged >12 years ago	0.626	0.988
Munising * Rapid River	Second growth unlogged	0.698	0.865
Munising * Manistique	Older growth	0.992	0.98
Chattam * Trenary * Stonington	Settled forest	0.635	0.626

[1]TOTCON = total number of coniferous trees.
[2]LMCON = total number of late maturity coniferous trees.
[3]TOTCON and LMCON were counted in 1200m2 vegetation plots located at bird census stations.

Table D6. Means of TOTCON and LMCON in different land type associations replicating 'forest disturbance periods' and 'historical divergence in land use' strata. Vegetation was sampled in the Upper Peninsula of Michigan 1992-1994.

Land Type Association	Land Use Category or Forest Disturbance Period	n[1]	TOTCON[4] x[2]	TOTCON[4] se[3]	LMCON[5] x	LMCON[5] se
Huron Mts	Primary forest	14	10.21	3.28	7.86	2.44
McCormick	Primary forest	15	5.80	3.17	4.33	2.36
Sylvania	Primary forest	17	6.94	2.98	3.77	2.22
Munising	Managed forest logged 1-5 years ago	12	3.92	1.65	2.33	1.62
Manistique	Managed forest logged 1-5 years ago	17	1.59	0.99	1.47	0.88
Rapid	Managed forest logged 1-5 years ago	15	4.53	1.74	3.00	1.54
Munising	Managed forest logged 6-12 years ago	12	2.92	1.80	2.92	1.76
Manistique	Managed forest logged 6-12 years ago	14	5.57	1.62	4.43	1.63
Rapid	Managed forest logged 6-12 years ago	22	0.82	1.33	0.73	1.30
Munising	Managed forest logged >12 years ago	11	2.00	1.10	1.82	0.87
Manistique	Managed forest logged >12 years ago	24	2.17	0.74	1.71	0.59
Rapid	Managed forest logged >12 years ago	20	3.10	0.82	1.65	0.65
Munising	Managed forest 2nd growth unlogged	17	2.53	1.17	2.06	2.32
Rapid	Managed forest 2nd growth unlogged	20	3.16	1.10	1.09	1.03
Munising	Managed forest older growth	14	5.86	2.43	4.71	2.10
Manistique	Managed forest older growth	11	5.82	2.74	4.64	2.37
Trenary	Settled forest	17	3.35	1.73	2.77	1.55
Chattam	Settled forest	10	1.00	2.25	1.00	2.02
Stonington	Settled forest	15	3.56	1.78	3.50	1.60

[1]n = number of sampling units.All vegetation variables were sampled within 1200m2 vegetation plots located at bird census stations.
[2]x = mean number of trees.
[3]se = standard error of the mean.
[4]TOTCON = total number of coniferous trees.
[5]LMCON = total number of late maturity conifers.

Table D7. Overall P values of ANOVAs undertaken to compare CANOPEN[1], GAP100[2], GAP>100[3] and WSDC<0.5[4] among different 'land type associations' replicating 'forest disturbance period' and 'historical divergence in land use' strat of northern hardwood forest. Vegetation was sampled in the Upper Peninsula of Michigan 1992-1994.

Land Type Associations Compared	Disturbance Period	CANOPEN	GAP100	GAP>100	WSDC<0.5
Huron Mts * Sylvania * McCormick	Primary forest	0.251	0.637	0.563	0.023
Munising * Manistique * Rapid River	Managed forest logged 1-5 years ago	0.028	0.512	0.033	0.015
Munising * Manistique * Rapid River	Managed forest logged 6-12 years ago	0.185	0.034	0.167	0.747
Munising * Manistique * Rapid River	Managed forest logged >12 years ago	0.004	0.001	0.001	0.001
Munising * Rapid River	Managed forest second growth unlogged	0.099	0.542	0.883	0.061
Munising * Manistique	Managed forest older growth	0.002	0.067	0.11	0.003
Chattam * Trenary * Stonington	Settled forest	0.001	0.051	0.001	0.149

[1]CANOPEN = % of forest canopy that is open.
[2]GAP100 = number of canopy gaps of size class 100m2.
[3]GAP>100 = number of canopy gaps of size class >100m2.
[4]WSDC<0.5 = number of woody stems of diameter size class <0.5".
All vegetation variables were sampled within a 1200m2 vegetation plot located at bird census station.

Table D8. Means of CANOPEN, GAP100, GAP>100 and WSDC<0.5 in different landtype associations replicating 'forest disturbance periods' and 'historical divergence in land use' strata. Vegetation was sampled in the Upper Peninsula of Michigan 1992-1994.

Land type Association	Land use category of Forest disturbance period	n[1]	CANOPEN[2]		GAP100[3]		GAP>100[4]		WSDC<0.5[5]	
			x	se	x	se	x	se	x	se
Huron Mountains	Primary forest	14	13.08	2.95	1.14	0.18	0.64	0.27	36.29	6.03
McCormick	Primary forest	15	15.19	2.52	0.93	0.30	0.87	0.33	41.80	6.86
Sylvania	Primary forest	17	9.61	1.76	0.77	0.32	0.41	0.30	20.88	3.51
Munising	Managed forest logged 1-5 years ago	12	32.7	5.52	0.33	0.24	0.92	0.29	46.17	12.03
Manistique	Managed forest logged 1-5 years ago	17	17.28	2.35	0.59	0.20	0.41	0.17	47.82	11.15
Rapid	Managed forest logged 1-5 years ago	15	23.19	3.97	0.27	0.21	0.13	0.13	10.93	4.52
Munising	Managed forest logged 6-12 years ago	12	26.43	3.48	1.00	0.30	0.75	0.31	73.33	9.99
Manistique	Managed forest logged 6-12 years ago	14	23.87	3.63	0.21	0.12	0.21	0.20	70.29	12.90
Rapid	Managed forest logged 6-12 years ago	22	18.78	2.35	0.46	0.16	0.32	0.15	84.36	14.71
Munising	Managed forest logged >12 years ago	11	26.98	2.98	1.64	0.41	1.46	0.31	117.36	29.12
Manistique	Managed forest logged >12 years ago	24	12.22	3.89	0.29	0.11	0.17	0.10	83.33	18.19
Rapid	Managed forest logged >12 years ago	20	9.09	1.35	0.25	0.20	0.25	0.10	40.85	9.26
Munising	Managed forest 2nd growth unlogged	17	8.22	3.14	0.11	0.12	0.24	0.14	24.35	6.90
Rapid	Managed forest 2nd growth unlogged	20	3.08	0.53	0.21	0.09	0.26	0.13	9.79	3.47
Munising	Managed forest older growth	14	13.38	2.82	0.50	0.17	0.21	0.11	28.79	3.70
Manistique	Managed forest older growth	11	2.09	0.67	0.09	0.09	0.00	0.00	61.45	9.92
Trenary	Settled forest	17	9.08	2.17	0.41	0.15	0.59	0.33	24.88	8.10
Chattam	Settled forest	10	15.55	3.60	0.90	0.34	0.40	0.16	45.60	13.99
Stonington	Settled forest	15	34.95	5.03	1.13	0.25	2.53	0.56	47.37	7.82

[1]n = number of sampling units.
[2]CANOPEN = % canopy opening.
[3]GAP100 = number of canopy gaps of size class 100m2.
[4]GAP>100 = number of canopy gaps of size class >100m2.
[5]WSDC<0.5 = number of woody stems <0.5" in diameter.
All vegetation variables were sampled within 1200m2 vegetation plots located at bird census stations.

Table D9. Mean of % canopy opening (CANOPEN), number of canopy gaps of different size classes (GAP50m2, GAP100m2, and GAP>100m2), and number of deciduous woody stems <0.5" (1.26 cm) WSDC<0.5, in different strata of forest disturbance period and land use. Vegetation was sampled in 1992-1994 in the Upper Peninsula of Michigan.

		CANOPEN[1]		$GAP50m_2$[2]		$GAP100m_2$[3]		$GAP>100m_2$[4]		WSDC<0.5[5]	
Forest Disturbance	n	x	se	x	se	x	se	x	se	x	se
Managed forest logged 1-5 years ago	46	22.55	1.99	1.56	0.19	0.39	0.13	0.43	0.15	33.37	7.2
Managed forest logged 6-12 years ago	55	19.7	1.83	1.34	0.17	0.47	0.11	0.4	0.14	68.51	6.58
Managed forest logged >12-15 years ago	57	13.56	1.79	1.14	0.17	0.53	0.11	0.44	0.13	72.19	6.47
Managed forest second growth unlogged	40	5.89	2.14	0.8	0.2	0.18	0.13	0.22	0.16	17.2	7.72
Managed forest old growth	25	8.41	2.71	0.6	0.25	0.32	0.17	0.2	0.2	43.16	9.76
Primary forest landscapes	46	12.49	1.99	1.09	0.19	0.93	0.13	0.63	0.15	32.39	7.2
Settled forest landscapes	43	20.29	2.1	1.39	0.19	0.81	0.13	1.33	0.16	38.07	7.44

[1]CANOPEN = % of forest canopy that is open
[2]GAP50 = number of gaps of size class 50m2
[3]GAP100 = number of gaps of size class 100m2
[4]GAP>100 = number of gaps of size class >100m2
[5]WSDC<0.5 = number of woody stems <0.5"
[6]n = number of samples (number of bird census stations at which vegetation plots were set up)
[7]x = mean

Table D10. P values of apriori contrasts in ANOVAs undertaken to test the statistical significance of differences in means of CANOPEN, GAP100, GAP>100 and WSDC<0.5 in a hypothetical northern hardwood forest in which the land use strata of primary forest and settled forest, and the 5 strata of forest disturbance period in managed forest are equally represented.[1]

Strata Compared	CANOPEN [2]	GAP_{100} [3]	$GAP_{>100}$ [4]	$WSDC_{<0.5}$ [5]
Managed forest vs primary forest	0.14	0.11	0.094	0.042
Managed forest vs settled forest	0.54	0.16	<0.001	0.031
Primary forest vs settled forest	0.11	0.85	0.08	0.93
MF-logged <12 y ago vs all other MF strata	<0.001	0.31	0.48	0.11
MF-logged <12 y ago vs primary forest	<0.001	0.37	0.31	0.08
MF-logged <12 y ago vs settled forest	0.041	0.48	0.003	0.031
MF-older growth vs primary forest	0.63	0.085	0.045	0.38
MF-older growth vs all other MF strata	0.01	0.46	0.006	0.26

[1]25 samples of bird density were taken from each of the 7 strata of primary forest, settled forest and 5 strata of forest disturbance period in managed forest.
[2]CANOPEN = % canopy that is open.
[3]GAP100 = number of gaps in size class 100m2.
[4]GAP>100 = number of gaps >100m2.
[5]WDSC<0.5 = number of deciduous woody stems <0.5".

Table D11. Mean density of 10 bird species, and mean value of the derived variable BTAMCS[1] in different northern hardwood forest strata representing different forest disturbance periods and historical divergence in landuse. Bird censuses were undertaken in 1992-1994 in the Upper Peninsula of Michigan.

Forest Disturbance Period		Blackburnian warbler		Black-throated green warbler		Veery		Scarlet Tanager	
	n	x	se	x	se	x	se	x	se
Managed forest logged 1-5 years ago	46	18.54	5.38	88.11	8.98	10.1	2.68	8.103	2.23
Managed forest logged 6-12 years ago	55	7.10	4.92	49.58	8.21	20.85	2.45	14.84	2.04
Managed forest logged >12 years ago	58	4.61	4.79	63.66	8	17.72	2.39	13.03	1.99
Managed forest second growth-unlogged	42	8.07	5.63	95.74	9.4	8.24	2.81	6.24	2.33
Managed forest older growth	25	38.23	7.3	63.24	12.18	14.52	3.64	12.49	3.02
Primary forest (landscape)	46	37.31	5.38	75.66	8.98	6.19	2.68	9.53	2.23
Settled forest	43	0.72	5.56	22.45	9.29	19.88	2.78	3.86	2.31

		Black-throated warbler		American redstart		Chestnut-sided warbler		BTAMCS	
	n	x	se	x	se	x	se	x	se
Managed forest logged 1-5 years ago	46	30.07	11.2	24.89	11.42	8.07	6.34	-2.89	18.8
Managed forest logged 6-12 years ago	55	124	10.2	77.32	10.44	41.67	5.8	4.99	17.2
Managed forest logged >12 years ago	58	46.8	9.96	82	10.17	7.13	5.64	-42.3	16.8
Managed forest second growth-unlogged	42	50.2	11.7	55.72	11.95	15.16	6.63	-20.7	19.7
Managed forest older growth	25	54.43	15.2	19.63	15.49	4.24	8.6	30.56	25.5
Primary forest (landscape)	46	28.28	11.2	15.32	11.42	9	6.34	3.97	18.8
Settled forest	43	8.34	11.6	53.25	11.81	39.97	6.55	-84.9	19.5

Table D11. (continued)

Forest Disturbance Period	n	Ovenbird		Least flycatcher		Red-eyed vireo	
		x	se	x	se	x	se
Managed forest logged 1-5 years ago	46	85.53	7.7	150.6	46.16	122.5	7.13
Managed forest logged 6-12 years ago	55	102.6	7.04	180.1	42.22	99.69	6.52
Managed forest logged >12 years ago	58	94.74	6.86	146.8	41.11	88.2	6.35
Managed forest second growth-unlogged	42	111.6	8.06	163.6	48.31	96.67	7.46
Managed forest older growth	25	75.26	10.4	182.8	62.62	87.35	9.67
Primary forest (landscape)	46	87.27	7.7	117.2	46.16	114.4	7.128
Settled forest	43	100.2	7.96	505.7	47.75	92.25	7.37

[1]BTAMCS = density difference of (black-throated blue warbler - (American redstart + Chestnut-sided warbler)).
[2]n = number of bird census stations.

Table D12. F and p values in Anovas undertaken to test the statistical significance of differences in means of bird density (Table D3) among 7 strata of northern hardwood forest representing landuse and forest distribution period. Bird censuses were undertaken in 1992-1994 in the Upper Peninsula of Michigan.

	F	p
Blackburnian warbler	6.28	<0.001
Black-throated green warbler	6.49	<0.001
Black-throated blue warbler	10.36	<0.001
American redstart	5.15	<0.001
Chestnut-sided warbler	5.69	<0.001
Ovenbird	2.4	0.021
Red-eyed vireo	3.13	0.003
Least flycatcher	6.92	<0.001
Veery	7.82	<0.001
Scarlet Tanager	3.78	0.001
BTAMCS	3.27	0.002

[1]BTAMCS = density difference of: (Black-throated blue warbler) - (American redstart + chestnut-sided warbler).

Table D13. Mean densities of 10 bird species and p values of Anovas of differences in bird density means landuse strata of a hypothetical northern hardwood forest in which strata of primary forest, settled forest, and 5 strata of forest disturbance periods[1] are equally represented. Birds were censused in 1992-1994 in the Upper Peninsula of Michigan.

	Primary Forest n=25		Managed Forest n=125		Settled Forest n=25		Primary vs Managed	Managed vs.Settled	Primary vs Settled
	x[2]	se[3]	x	se	x	se	p	p	p
Blackburnian warbler	45.21	14.47	15.21	7.15	1.23	1.23	0.003	0.157	0.001
Black-throated green warbler	76.39	12.61	66.37	7.43	25.46	7.58	0.423	0.002	0.003
Black-throated blue warbler	30.21	6.58	67.83	10.29	10.77	7.89	0.023	0.001	0.359
American redstart	10.07	5.19	59.49	9.87	59.39	15.56	0.006	0.996	0.034
Chestnut-sided warbler	9.76	4.97	16.04	4.58	41.59	14.84	0.522	0.010	0.013
Ovenbird	95.36	8.96	92.03	6.36	104.99	7.89	0.746	0.312	0.594
Least flycatcher	90.71	32.27	159.04	40.93	492.29	107.96	0.307	<0.001	<0.001
Red-eyed vireo	121.28	12.26	100.07	6.22	86.28	5.44	0.040	0.180	0.009
Veery	5.56	2.08	14.33	4.07	19.41	4.41	0.030	0.319	0.014
Scarlet Tanager	8.46	2.61	12.57	4.24	2.42	1.43	0.196	0.002	0.141

[1]n = number of samples which is 25 in each stratum.
[2]x = mean density/km2.
[3]se = standard error of the mean. For managed forest se was calculated using the following formula for the variance of the mean bird density in managed forest $V(\overline{Y_{st}})=\sum(\frac{n_h}{n})S^2_h(1/n_h)$ s^2 is the variance of bird species species density in each of the 5 strata of forest disturbance period; n_h is the number of samples (25) and n is the total samples in managed forest (125).

Table D14. P values of Anova planned apriori contrasts undertaken to test the statistical significance of differences in bird density means among landuse strata of a hypothetical northern hardwood forest in which strata of primary forest, settled forest and 5 strata of forest disturbance period within managed forest are equally represented. Bird density data are from bird censuses taken in 1992-1994 in the Upper Peninsula of Michigan.

Bird species	Strata Contrasted	DF	F	P	Justification for Contrast[2]
Blackburnian warbler	Managed forest-older growth vs primary forest	1&168	0.30	0.58	a
Blackburnian warbler	Managed forest-older growth vs all other strata in managed forest	1&168	8.23	0.01	b
Black-throated blue warbler	Managed Forest Logged 6-12 years ago vs all other strata in managed forest	1&168	43.33	<0.001	c
American redstart	Managed forest logged 6-12 years ago vs all other strata in managed forest	1&168	2.28	0.13	c
American redstart	Managed forest logged >12-15 years vs all other strata in managed forest	1&168	10.03	<0.001	c
Chestnut-sided warbler	Managed forest logged 6-12 years ago vs all other strata in managed forest	1&168	8.58	<0.001	c
Chestnut-sided warbler	Managed forest logged >12-15 years ago vs all other strata in managed forest	1&168	2.34	0.13	c

Table D14. (continued)

Bird species	Strata Contrasted	DF	F	P	Justification for Contrast[2]
Veery	Managed forest logged 6-12 years ago vs all other strata in managed forest	1&168	8.82	<0.001	c
	Managed forest logged >12-15 years ago vs all other strata in managed forest	1&168	0.05	0.82	c
Scarlet tanager	Managed forest logged 6-12 years ago vs all other strata in managed forest	1&168	3.68	0.06	c
	Managed forest logged >12 years ago vs all other strata in managed forest	1&168	2.83	0.09	c

[1]The 7 strata of northern hardwood forest were each represented by 25 samples

[2]Justification for apriori contrasts:

a = presence of late maturity conifers in the older growth within managed forest and in primary forest

b = low availability of late maturity conifers (hemlock-white pine) in all managed forest strata except in older growth stratum

c = significantly higher levels of deciduous woody stems <0.5" (1.27 cm) in the strata of managed forest logged 6-12 years ago, and logged >12-15 years ago.

Table D15. Bonferroni adjusted p values of ANOVA post tests undertaken to test the statistical significance of differences in bird density means and (BTARCS)[1] means in pairwise comparisons of northern hardwood forest strata. Bird data are from bird censuses undertaken 1992-1994 in the Upper Peninsula of Michigan.

Strata Compared	Blackburnian warbler	Black-throated green warbler	Black-throated blue warbler	American redstart	Chestnut-sided warbler
Primary forest vs Managed forest logged 1-5 years ago	1	1	1	1	1
Primary forest vs Managed forest logged 6-12 years ago	0.001	0.92	<0.001	0.002	0.005
Primary forest vs Managed forest logged >12-15 years ago	<0.001	1	1	<0.001	1
Primary forest vs Managed forest unlogged second growth	0.006	1	1	0.42	1
Primary forest vs Managed forest - older growth	1	1	1	1	1
Primary forest vs Settled forest	<0.001	0.001	1	0.6	0.02
Managed forest logged 1-5 years ago vs Managed forest logged 6-12 years ago	1	0.048	<0.001	0.02	0.003
Managed Forest logged 1-5 years ago vs Managed forest logged >12-15 years ago	1	1	1	0.006	1

Table D15 (continued)

Strata Compared	Blackburnian warbler	Black-throated green warbler	Black-throated blue warbler	American redstart	Chestnut-sided warbler
Managed Forest logged 1-5 years ago vs Managed forest unlogged second growth	1	1	1	1	1
Managed forest logged 1-5 years ago vs Managed forest older growth	0.85	1	1	1	1
Managed forest logged 6-12 years ago vs Managed forest logged >12-15 years ago	1	1	<0.001	1	0.001
Managed forest logged 6-12 years ago vs Managed forest unlogged second growth	1	0.007	<0.001	1	0.079
Managed forest logged 6-12 years ago vs Managed forest older growth	0.013	1	0.005	0.06	0.01
Managed forest logged >12-15 years ago vs Managed forest unlogged second growth	1	0.27	1	1	1
Managed forest logged >12-15 years ago vs Managed forest older growth	0.004	1	1	0.024	1
Managed forest unlogged second growth vs Managed forest older growth	0.03	0.99	1	1	1
Settled forest vs Managed forest logged 1-5 years ago	0.61	<0.01	1	1	0.01

Table D15. (continued)

Strata Compared	Blackburnian warbler	Black-throated green warbler	Black-throated blue warbler	American redstart	Chestnut-sided warbler
Settled forest vs Managed forest logged 6-12 years ago	1	0.825	<0.001	1	1
Settled forest vs Managed forest logged >12-15 years ago	1	0.024	0.34	1	0.005
Settled forest vs Managed forest unlogged second growth	1	<0.001	0.32	1	0.23
Settled forest vs Managed forest older growth	0.002	0.23	0.46	1	0.03

Strata Compared	Ovenbird	Least flycatcher	Red-eyed vireo	Veery	Scarlet Tanager	BTARCS
Primary forest vs Managed forest logged 1-5 years ago	1	1	1	1	1	1
Primary forest vs Managed forest logged 6-12 years ago	1	1	1	0.002	1	1
Primary forest vs Managed forest logged >12-15 years ago1	1	1	0.18	0.04	1	1
Primary forest vs Managed forest unlogged second growth	0.83	1	1	1	1	1

Table D15. (continued)

Strata Compared	Ovenbird	Least flycatcher	Red-eyed vireo	Veery	Scarlet tanager	BTARCS
Primary forest vs Managed forest older growth	1	1	0.7	1	1	1
Primary forest vs Settled forest	1	<0.001	0	0.013	1	0.03
Managed forest logged 1-5 years ago vs Managed forest logged 6-12 years ago	1	1	0.522	0.09	0.74	1
Managed forest logged 1-5 years ago vs Managed forest logged >12-15 years ago	1	1	0.01	0.97	1	1
Managed forest logged 1-5 years ago vs Managed forest unlogged second growth	0.55	1	0.36	1	1	1
Managed forest logged 1-5 years ago vs Managed forest older growth	1	1	0.1	1	1	1
Managed forest logged 6-12 years ago vs Managed forest logged >12-15 years ago	1	1	1	1	1	1
Managed forest logged 6-12 years ago vs Managed forest unlogged second growth	1	1	1	0.023	0.16	1
Managed forest logged 6-12 years ago vs Managed forest older growth	0.85	1	1	1	1	1

Table D15. (continued)

Strata Compared	Ovenbird	Least flycatcher	Red-eyed vireo	Veery	Scarlet tanager	BTARCS
Managed forest logged >12-15 years ago vs Managed forest unlogged second growth	1	1	1	0.3	0.77	1
Managed forest logged >12-15 years ago vs Managed forest older growth	1	1	1	1	1	0.49
Managed forest unlogged second growth vs Managed forest older growth	0.17	1	1	1	1	1
Settled forest vs Managed forest logged 1-5 years ago	1	<0.001	0.09	0.33	1	0.07
Settled forest vs Managed forest logged 6-12 years ago	1	<0.001	1	1	0.01	0.17
Settled forest vs Managed forest logged >12-15 years ago	1	<0.001	1	1	0.08	1
Settled forest vs Managed forest unlogged second growth	1	<0.001	1	0.1	1	0.59
Settled forest vs Managed forest older growth	1	0.001	1	1	0.67	0.01

[1]BTARCS is the density of (Black-throated blue warbler) - (American redstart + Chestnut-sided warbler).

Table D16. Mean density /km2 of 10 bird species in 3 landscapes (land type associations) replicating primary forest landscapes. Birds were censused in 1993-1994 in the Upper Peninsula of Michigan.

	Huron Mountains n=14		McCormick n=15		Sylvania n=17	
	x	se	x	se	x	se
Blackburnian warbler	51.38	15.8	35.62	15.27	27.2	14.35
Black-throated green warbler	77.3	16.63	70.73	16.06	78.64	15.09
Black-throated blue warbler	12.82	7.36	56.83	6.89	15.83	6.47
American redstart	30.56	7.2	3.35	6.96	13.32	6.58
Chestnut-sided warbler	15.15	5.84	4.95	5.65	7.49	5.3
Ovenbird	94.69	9.68	120.45	9.35	51.88	8.78
Least flycatcher	221.4	45.66	13.67	44.11	122.67	41.43
Red-eyed vireo	145.01	13.97	121.99	13.5	82.49	12.68
Scarlet tanager	10.07	3.25	11.75	3.15	7.11	2.95
Veery	9.69	2.71	7.92	2.62	1.8	2.46

Table D17. Mean density (birds/km2) of 10 bird species in 3 land type associations that are replicates of 'settled forest landscapes'. Birds were censused 1992-1994 in the Upper Peninsula of Michigan.

	Forest disturbance period = 6-12 years after logging					
	Chattam $n^1=10$		Trenary n=17		Stonington n=16	
	x^2	se^3	x	se	x	se
Blackburnian	3.03	1.46	0	0	0	0
Black-throated green warbler	16.98	10.67	31.83	8.18	15.91	8.43
Black-throated blue warbler	17.94	10.5	5.28	8.05	5.61	8.3
American redstart	62.91	22.42	19.98	17.19	82.57	17.72
Chestnut-sided warbler	41.38	21.07	5.62	16.16	75.6	16.65
Ovenbird	130.97	10.56	106.6	8.1	74.17	8.35
Least flycatcher	369.22	167.12	635.47	128.17	452.97	132.12
Red-eyed vireo	100.17	13.17	90.74	10.1	88.9	10.41
Scarlet tanager	1.51	2.54	2.67	1.95	6.6	2.01
Veery	29.52	6.67	11.97	5.12	22.2	5.28

[1]n = number of sampling units (bird census stations).
[2]x = mean density.
[3]se = standard error of the mean.

Table D18. Mean density (birds/km2) of 10 bird species in 3 land type associations that are replicates of 'forest disturbance period' strata in managed northern hardwood forest landscapes. Birds were censused 1992-1994 in the Upper Peninsula of Michigan.

	Forest disturbance period = 1-5 years after logging					
	Munising n[1]=12		Manistique n=17		Rapid River n=15	
	x[2]	se	x	se[3]	x	se
Blackburnian	12.84	11.97	22.97	10.05	20.55	10.70
Black-throated green warbler	84.88	18.44	52.43	15.49	137.23	16.49
Black-throated blue warbler	61.06	11.45	15.39	9.62	17.95	10.24
American redstart	33.55	12.08	31.82	10.15	13.42	10.81
Chestnut-sided warbler	21.22	5.52	4.37	4.63	2.83	4.93
Ovenbird	58.35	11.04	100.94	9.28	69.85	9.88
Least flycatcher	107.31	60.47	146.81	50.80	209.68	54.08
Red-eyed vireo	107.41	14.16	147.31	11.90	106.85	12.66
Scarlet tanager	5.46	3.63	4.44	3.05	15.45	3.25
Veery	23.75	4.11	5.79	3.45	4.52	3.67

Table D18. (continued)

	Forest disturbance period = 6-12 years after logging					
	Munising n=12		Manistique n=14		Rapid River n=22	
	x[2]	se	x	se[3]	x	se
Blackburnian	0	0	13.21	4.92	5.61	3.92
Black-throated green warbler	49.51	15.25	37.89	14.11	49.67	11.26
Black-throated blue warbler	97.83	36.20	70.49	33.51	208.00	26.73
American redstart	153.08	16.83	144.69	15.58	17.73	12.43
Chestnut-sided warbler	79.58	18.60	65.97	17.22	16.88	13.73
Ovenbird	89.98	13.09	95.46	12.12	76.29	49.44
Least flycatcher	102.56	71.40	124.54	66.10	292.19	52.73
Red-eyed vireo	65.11	12.48	107.80	11.56	112.31	9.22
Scarlet tanager	11.33	6.35	11.87	5.88	19.46	4.69
Veery	29.97	33.64	34.65	6.70	11.29	4.95

Table D18. (continued)

	Forest disturbance period logged >12-15 years ago					
	Munising n=11		Manistique n=24		Rapid River n=21	
	x	se	x	se	x	se
Blackburnian	2.80	2.94	2.57	1.99	4.4	2.13
Black-throated green warbler	60.77	18.97	50.40	12.85	74.27	13.74
Black-throated blue warbler	108.08	17.89	33.65	12.11	34.18	12.95
American redstart	133.83	27.25	121.10	18.45	17.97	19.72
Chestnut-sided warbler	20.26	5.81	6.63	3.94	1.52	4.21
Ovenbird	65.60	12.19	120.94	8.25	65.67	8.82
Least flycatcher	68.37	90.49	55.55	61.26	306.06	65.49
Red-eyed vireo	83.78	10.25	104.35	6.94	67.73	34.97
Scarlet tanager	8.24	5.42	11.33	3.67	18.71	3.92
Veery	21.28	4.80	25.44	3.25	8.72	3.47

Table D18. (continued)

	Forest disturbance period = unlogged second growth					
	Munising n=18		Manistique		Rapid River n=20	
	x	se	x	se	x	se
Blackburnian	0	0	not represented		16.95	44.14
Black-throated green warbler	76.04	18.51			113.53	17.56
Black-throated blue warbler	12.46	17.78			58.32	16.87
American redstart	92.27	25.87			24.54	24.54
Chestnut-sided warbler	33.60	8.30			0	
Ovenbird	135.42	11.22			100.50	10.64
Least flycatcher	77.87	59.01			252.97	55.98
Red-eyed vireo	94.61	53.58			24.53	59.92
Scarlet tanager	5.88	10.54			7.81	13.62
Veery	7.92	12.37			9.67	14.61

Table D18. (continued)

	Forest disturbance period = older growth forest					
	Munising n=14		Manistique n=11		Rapid River	
	x	se	x	se	x	se
Blackburnian	39.63	19.47	36.43	21.97	not represented	
Black-throated green warbler	60.63	12.25	66.55	13.82		
Black-throated blue warbler	39.52	13.05	73.41	14.72		
American redstart	29.66	8.92	6.86	10.07		
Chestnut-sided warbler	5.30	3.22	2.89	3.63		
Ovenbird	82.86	11.88	65.60	13.41		
Least flycatcher	62.68	101.03	335.65	113.98		
Red-eyed vireo	78.71	41.02	98.35	13.29		
Scarlet tanager	12.59	4.16	12.36	4.70		
Veery	17.21	4.63	11.10	12.43		

[1]n = number of sampling units (bird census stations).
[2]x = mean density.
[3]se = standard error of the mean.`

Table D19. P values in Anovas undertaken for comparing bird densities among land type associations replicating forest disturbance periods within managed forest landscapes and historical divergence in landuse.

	Blackburnian warbler	Black-throated green warbler	Black-throated warbler	American redstart	Veery
Among land type associations within the strata of:					
Primary forest landscapes	0.527	0.93	<0.001	0.031	0.083
Settled forest landscapes	0.195	0.34	0.584	0.046	0.11
Logged 1-5 years ago	0.804	0.002	0.008	0.364	0.002
Logged 6-12 years ago1	0.193	0.78	0.005	<0.001	0.01
Forest logged >12 years ago	0.807	0.45	0.002	<0.001	0.003
Unmanaged second growth forest	0.112	0.16	0.07	0.066	0.694
Older growth forest	0.914	0.75	0.098	0.104	0.677
	Chestnut-sided warbler	**Scarlet tanager**	**Red-eyed vireo**	**Ovenbird**	**Least Flycatcher**
Among land type associations within the strata of:					
Primary forest landscapes	0.43	0.554	0.006	0.001	0.008
Settled forest landscapes	0.017	0.224	0.785	<0.001	0.405
Logged 1-5 years ago	0.033	0.039	0.039	0.012	0.442
Logged 6-12 years ago	0.016	0.474	0.011	0.435	0.055
Forest logged >12 years ago	0.039	0.227	0.003	<0.001	0.017
Unmanaged second growth forest	0.007	0.631	0.677	0.03	0.038
Older growth forest	0.624	0.971	0.28	0.346	0.346

Table D20. Mean LMCON, TOTCON, CANOPEN, and GAP>100 of microhabitat sites selected by the blackburnian warbler and the black-throated green warbler and of each of 7 strata of northern hardwood forest. Data are from vegetation sampling and bird censusing 1992-1994 in the Upper Peninsula, Michigan.

		LMCON		TOTCON		CANOPEN		GAP>100	
	n	x	se	x	se	x	se	x	se
Black-throated green warbler	241	3.11	0.43	4.22	0.51	14.10	0.88	0.43	0.06
Blackburnian warbler	60	6.08	0.85	8.03	1.03	16.52	1.77	0.42	0.12
Managed forest logged 1-5 years ago	46	2.13	0.97	3.09	1.17	22.55	2.02	0.44	0.14
Managed forest logged 6-12 years ago	55	2.06	0.89	2.38	1.07	19.70	1.85	0.40	0.13
Managed forest logged >12>15 ago	57	1.67	0.87	2.46	1.05	13.56	1.81	0.44	0.13
Managed forest unlogged second growth	40	2.17	1.04	2.90	1.26	5.89	2.17	0.23	0.15
Managed forest older growth	25	4.68	1.32	5.84	1.59	8.41	2.74	0.12	0.19
Primary forest	46	5.19	0.97	7.57	1.17	12.49	2.02	0.63	0.14
Settled forest	43	2.62	1.01	2.88	1.21	20.29	2.09	1.32	0.14

[1]LMCON = number of late maturity conifer trees (Hemlock and white pine).
[2]TOTCON = total number of coniferous trees.
[3]CANOPEN = % canopy opening.
[4]GAP>100 = number of canopy gaps >100m2.
All vegetation variables were quantified in 1200m2 vegetation plots located at bird census stations.

Table D21. P values in ANOVAs representing the statistical significance of differences in LMCON, TOTCON, CANOPEN, and GAP>100 between each of the blackburnian warbler and the black-throated green warbler and individual strata of northern hardwood forest. Data are from vegetation sampling and bird censusing at 321 bird census stations undertaken in 1992-1994 in the Upper Peninsula of Michigan.

Northern hardwood forest strata	Blackburnian warbler				Black-throated green warbler			
for comparison	LMCON[1]	TOTCON[2]	CANOPEN[3]	GAP>100[4]	LMCON	TOTCON	CANOPEN	GAP>100
Managed forest logged 1-5 years ago	0.002	0.002	0.025	0.922	0.356	0.375	<0.001	0.961
Managed forest logged 6-12 years ago	0.001	<0.001	0.215	0.925	0.284	0.122	<0.001	0.846
Managed forest logged >12>15 years ago	<0.001	<0.001	0.242	0.9	0.137	0.132	0.789	0.936
Managed forest unlogged second growth	0.004	0.002	<0.001	0.32	0.406	0.33	<0.001	0.21
Managed forest older growth	0.372	0.247	0.013	0.187	0.258	0.334	0.048	0.122
Primary forest	0.49	0.764	0.133	0.248	0.05	0.009	0.464	0.182
Settled forest	0.009	0.001	0.169	<0.001	0.658	0.309	0.22	<0.001
Black-throated green warbler	0.002	0.001	0.937	0.22				

[1]LMCON = number of late maturity conifer trees (Hemlock and white pine).
[2]TOTCON = total number of coniferous trees.
[3]CANOPEN = % canopy opening.
[4]GAP>100 = number of canopy gaps >100m2.
All vegetation variables were quantified in 1200m2 vegetation plots located at bird census stations.

Table D22. Mean TOTCON and LMCON of microhabitats selected by the blackburnian warbler and the black-throated green warbler in different 'forest disturbance period' and 'historical divergence in land use' strata of northern hardwood forest and p values of ANOVAs indicating the statistical significant of differences in TOTCON and LMCON between the 2 bird species in the different northern hardwood forest strata. Data are from vegetation and bird censusing undertaken in 1992-1994 in the Upper Peninsula of Michigan.

	TOTCON[4]							LMCON[5]				
	Blackburnian warbler			Black-throated green warbler				Blackburnian warbler		Black-throated green warbler		
	x[2]	se[3]	n[1]	x	se	n	p	x	se	x	se	p
Managed forest excluding older growth	5.07	1	31	3.01	0.45	156	0.06	4	0.93	2.192	0.41	0.076
Older growth within managed forest landscapes	10.86	3.16	7	4.91	1.83	21	0.12	8.286	2.77	3.857	1.6	0.177
Primary forest landscapes	11.57	3.01	21	8.21	2.12	42	0.37	8.43	2.28	5.62	1.61	0.318
Settled forest landscapes	only one case			5.27	2.09	19				4.74	2.03	

[1]n = number of sampling units.
[2]x = mean number of trees.
[3]se = standard error of the mean.
[4]TOTCON = total number of coniferous trees.
[5]LMCON = total number of late maturity conifers.

Table D23. P values of regression coefficients in separate regressions of black-throated blue warbler (BTBW), American redstart (AMRE) and chestnut-sided warbler (CSWA) on woody stems <0.5" for the 7 'forest disturbance period' and 'historial divergence in landuse' strata. Bird densities and vegetation data were from bird censusing and vegetation sampling undertaken in 1992-1994 in the Upper Peninsula of Michigan.

Forest disturbance period	n	Woody Stems <0.5" BTBW	AMRE	CSWA
Managed forest logged 1-5 years ago	46	0.54	0.12	<0.001
Managed forest logged 6-12 years ago	55	<0.001	0.676	0.239
Managed forest logged >12 years ago	57	0.323	<0.001	0.98
Managed forest second growth forest	40	0.549	0.623	0.015
Managed forest older growth forest	25	0.142	0.864	0.43
Primary forest landscapes	46	0.01	0.676	0.385
Settled forest landscapes	43	0.613	0.018	0.018

Table D24. Means of canopy and shrub layer variables in habitat selected by the black-throated blue warbler, American redstart and chestnut-sided warbler. Characteristics of habitat selected by a species were identified by the characteristics of habitat around bird census stations at which the density of the respective bird species was >80 birds/km2. Data were obtained from bird censuses and vegetation sampling undertaken in 321 bird census stations during 1992-1994 in the Upper Peninsula of Michigan.

	BTBW n=85		AMRE n=66		CSWA n=27	
	x	se	x	se	x	se
WSDC<0.5	69.51	6.61	75.76	8.56	73.44	8.25
WSDC>0.5	22.63	2.43	30.4	3.74	2.11	4.38
CANOPEN	16.81	1.73	23.37	1.97	28.90	3.08
GAP50	1.27	0.14	1.12	0.14	1.11	0.29
GAP100	0.6	0.09	0.59	0.11	0.78	0.216
GAP>100	0.42	0.42	0.77	0.16	1.29	0.4

[1]x = mean.
[2]se = standard error of the mean.
[3]WSDC<0.5 = number of woody stems <0.5".
[4]WSDC>0.5 = number of woody stems >0.5"-1.5".
[5]CANOPEN = % of forest canopy that is open.
[6]GAP50 = number of gaps of size class 50m2.
[7]GAP100 = number of gaps of size class 100m2.
[8]GAP>100 = number of gaps of size class >100m2.

Table D25. P values of ANOVAs in planned tests undertaken to compare canopy opening, shrub layer development, and canopy gaps among northern hardwood forest habitats selected by the black-throated blue warbler (BTBW) American redstart (AMRE) and chestnut-sided warbler (CSWA). Data were obtained from bird censuses and vegetation sampling carried out in 1992-1994 in the Upper Peninsula of Michigan.

Groups compared	CANOPEN[1]	GAP_{50}[2]	GAP_{100}[3]	$GAP_{>100}$[4]	$WSDC_{<0.5}$[5]
Overall ANOVA	0.001	0.732	0.645	0.006	0.825
Test BTBW vs AMRE	0.013	ns	ns	0.087	ns
Test BTBW vs CSWA	0.001	ns	ns	0.002	ns
Test AMRE vs CSWA	0.132	ns	ns	0.066	ns

[1]CANOPEN = % of forest canopy that is open.
[2]GAP50 = number of gaps of size class 50m2.
[3]GAP100 = number of gaps of size class 100m2.
[4]GAP>100 = number of gaps of size class >100m2.
[5]WSDC<0.5 = number of woody stems <0.5".

Table D26. P values of ANOVAs undertaken to compare canopy opening and canopy gaps among the black-throated blue warbler, American redstart, and chestnut-sided warbler in 3 forest disturbance strata representing current logging disturbance. Data were obtained from bird censuses and vegetation sampling undertaken in 1992-1994 in the Upper Peninsula of Michigan.

Comparison	CANOPEN	GAP>100m2
Between BTBW & AMRE in forest logged 1-5 years ago	0.742	0.324
Among BTBW, AMRE & CSWA in forest logged 6-12 years ago	0.522	0.915
Between BTBW & AMRE in forest logged >12 years ago	0.716	0.693

[1]CANOPEN = % open canopy.
[2]GAP>100 = number of canopy gaps >100m2.

Table D27. Means of CANOPEN, GAP100, GAP>100, and WS<0.5 in habitats selected by the black-throated blue warbler (BTBW), American redstart (AMRE), and chestnut-sided warbler (CSWA) in northern hardwood forest strata representing 3 time intervals elapsed after recent logging. Data were obtained from bird censuses and vegetation sampling undertaken in 1992-1994 in the Upper Peninsula of Michigan.

Northern hardwood forest strata n	x	CANOPEN se	x	GAP100 se	x	GAP>100 se	x	WSDC<0.5 se	
Logged 1-5 years ago									
BTBW	9	27.68	2.52	0.33	0.24	0.89	0.39	39.67	19.62
AMRE	4	31.63	17.57	0	0	0.25	0.25	80.75	30.13
CSWA	*	not represented							
Logged 6-12 years ago									
BTBW	30	22.39	2.11	0.53	0.14	0.47	0.14	98.6	10.9
AMRE	26	24.26	2.58	0.35	0.09	0.38	0.15	67.85	8.6
CSWA	13	27.16	3.85	0.54	0.24	0.46	0.21	84.2	12.49
Logged >12 years ago									
BTBW	16	16.56	3.54	1.33	0.33	0.53	0.19	90.8	19.7
AMRE	18	21.91	5.27	0.78	0.28	0.72	0.23	117.78	24.16
CSWA	2	18.81	1.43	3.5	0.5	1	0	83	31

*(Mean values of microhabitat variables for each species group were derived from vegetation sampled at bird census stations within each forest disturbance at which the density of each respective species was >80 birds/km2). Only 1 case was encountered in the period of 'logged 1-5 years ago' for which the density of the chestnut-sided warbler was >80 birds/km2.

[1]n = number of bird census stations at which the density of the species was >80 birds/km2.

[2]x = mean value of variable.

[3]se = standard error of the mean.

[4]CANOPEN = % open canopy.

[5]GAP100 = number of canopy gaps in size class 100m2.

[6]GAP>100 = number of canopy gaps >100m2.

[7]WSDC<0.5 = number of woody stems <0.5".

Table D28. Contribution of different land type associations and forest disturbance periods to different groups of bird census stations aggregated based on forest cover within 1 mile (FC1MIL), length of forest edge EDGE, and shrub layer development, WSDC<0.5". Data were derived from vegetation sampling in 1992-1994 in the Upper Peninsula of Michigan and GIS coverage of study areas current for 1992.

		Land type association						
Groups	#BCS	HUM	MCC	SYL	DUK	MUN	MAN	RAP
Forest Cover 1; Edge 1; Shrub 1	26	3	4	4	1	11	0	3
Forest Cover 1; Edge 1; Shrub 2	27	2	5	1	3	13	0	3
Forest Cover 1; Edge 2; Shrub 1	12	3	0	0	4	5	0	0
Forest Cover 1; Edge 2; Shrub 2	9	1	1	1	2	3	0	2
Forest Cover 2; Edge 1; Shrub 1	21	0	0	5	1	0	3	12
Forest Cover 2; Edge 1; Shrub 2	15	0	0	0	0	0	6	8
Forest Cover 2; Edge 2; Shrub 1	14	0	0	0	2	3	4	5
Forest Cover 2; Edge 2; Shrub 2	18	0	0	0	0	0	15	3
Forest Cover 3; Edge 1; Shrub 1	8	0	0	0	0	0	5	3
Forest Cover 3; Edge 1; Shrub 2	11	0	0	0	0	1	6	4
Forest Cover 3; Edge 2; Shrub 1	9	0	0	0	0	0	5	3
Forest Cover 3; Edge 2; Shrub 2	11	0	0	0	0	2	6	3

Table D28. (continued)

	#BCS	Forest Disturbance Period Lg PF	Lg 1-5y	Lg 6-12y	Unl >12y	Older SG	G
Forest Cover 1; Edge 1; Shrub 1	26	12	6	0	0	3	5
Forest Cover 1; Edge 1; Shrub 2	27	11	2	0	9	0	5
Forest Cover 1; Edge 2; Shrub 1	12	3	5	0	2	0	2
Forest Cover 1; Edge 2; Shrub 2	9	5	0	0	2	0	2
Forest Cover 2; Edge 1; Shrub 1	21	5	5	3	0	7	0
Forest Cover 2; Edge 1; Shrub 2	15	0	2	8	0	1	4
Forest Cover 2; Edge 2; Shrub 1	14	0	2	3	3	5	1
Forest Cover 2; Edge 2; Shrub 2	18	0	0	6	9	0	3
Forest Cover 3; Edge 1; Shrub 1	8	0	5	0	0	3	0
Forest Cover 3; Edge 1; Shrub 2	11	0	1	1	4	3	2
Forest Cover 3; Edge 2; Shrub 1	9	0	5	0	3	0	0
Forest Cover 3; Edge 2; Shrub 2	11	0	1	2	5	3	0

[1]Forest Cover 1 FC1MIL = >90%. Forest Cover 2 FC1MIL = >80-90%. Forest Cover 3 FC1MIL = >70-80%.
[2]EDGE 1 EDGE <2000m. EDGE 2 EDGE >2000m.
[3]SHRUB 1 WSDC<0.05 = <50. SHRUB 1 WSDC<0.5 = >50.
[4]HUM = Huron Mountains.
[5]MCC = McCormick Wilderness Area.
[6]SYL = Sylvania Recreational Area.
[7]DUK = Dukes Experimental Forest.
[8]MUN = Munising.
[9]MAN = Manistique.
[10]RAP = Rapid River.
[11]PF = primary forest.
[12]Lg 1-5y = managed forest logged 1-5 years ago.
[13]Lg 6-12y = managed forest logged 6-12 years ago.
[14]Lg >12y = managed forest logged >12 years ago.
[15]Unl SG = managed forest unlogged second growth.
[16]Older G = managed forest older growth.

Table D29. P values in a 3-way ANOVA, indicating the statistical significance of effects of FC1MIL[1], EDGE[2] and WSDC<0.5[3] on densities of black-throated blue warbler (BTBW), American redstart (AMRE) and the variable BTARCS[4]. Bird densities and vegetation were sampled in 1992-1994 in the Upper Peninsula of Michigan.

Effect	BTBW	AMRE	BTARCS
FC1MIL	0.028	0	0.001
EDGE	0.101	0	0
WSDC<0.5	0.003	0.001	0.98
FC1MIL X EDGE	0.056	0.001	0.001
FC1MIL X WSDC<0.5	0.025	0.97	0.237
EDGE X WSDC<0.5	0.627	0.012	0.089
FC1MIL X EDGE X WSDC<0.5	0.022	0.64	0.023

[1]FC1MIL = group based on forest cover within 1 mile: >90%; <90->80%; >70-<80%.
[2]EDGE = effect of group based on length of edge within a 500m radius: >2000m; <2000m.
[3]WSDC<0.5 = effect of group based on number of deciduous woody stems: <50; >50.
[4]BTARCS = difference between the density of the black-throated blue warbler and the combined densities of the American redstart and chestnut-sided warbler.

Table D30. Mean densities of black-throated blue warbler (BTBW), and American redstart (AMRE), and mean values of B different groups of bird census stations formed by a stratification based on 3 levels of FC1MIL, 2 levels of EDGE, and 2 levels of WSDC<0.5. Bird densities and vegetation were sampled in 1992-1994 in the Upper Peninsula of Michigan.

Groups		#BCS	BTBW		AMRE		BTARCS	
			x	se	x	se	x	se
FC1MIL = >90%		74	53.9	11.1	29.3	8.6	18.6	15.0
FC1MIL = >80-90%		68	89.5	10.5	34.2	8.1	41.8	14.2
FC1MIL = >70-80%		39	51.5	13.8	81.4	10.7	-45.0	18.7
EDGE = <2000m		108	76.2	9.1	22.7	7.0	44.5	12.3
EDGE = >2000m		73	53.7	10.3	74.0	8.0	-34.2	13.9
WSDC<0.5 = <50		90	44.6	9.8	31.0	7.6	5.3	13.3
WSDC<0.5 = >50		91	85.3	9.6	65.6	7.4	5.0	12.9
FC1MIL = >90%;	EDGE <2000m	53	42.5	11.7	25.9	9.1	10.0	15.9
FC1MIL = >90%;	EDGE >2000m	21	65.2	18.8	32.7	14.6	27.2	25.5
FC1MIL = >80-90%;	EDGE <2000m	36	109.7	14.4	15.8	11.2	85.1	19.5
FC1MIL = >80-90%;	EDGE >2000m	32	69.3	15.2	52.6	11.8	-1.4	20.6
FC1MIL = >70-80%;	EDGE <2000m	19	76.5	19.8	26.3	15.4	38.3	26.8
FC1MIL = >70-80%;	EDGE >2000m	20	26.5	19.2	136.6	14.9	-128.4	26.0
FC1MIL = >90%;	WSDC<0.5 <50	38	30.9	14.9	12.7	11.6	11.0	20.2
FC1MIL = >90%;	WSDC<0.5 >50	36	76.8	16.4	45.9	12.8	26.2	22.2
FC1MIL = >80-90%;	WSDC<0.5 <50	35	46.7	14.7	18.1	11.4	26.3	19.9
FC1MIL = >80-90%;	WSDC<0.5 >50	33	132.2	14.9	50.3	11.6	57.3	20.2
FC1MIL = >70-80%;	WSDC<0.5 <50	17	56.1	20.7	62.2	16.1	-21.4	28.1
FC1MIL = >70-80%;	WSDC<0.5 >50	22	46.9	18.2	100.7	14.1	-68.7	24.6

Table D30. (continued)

Groups			#BCS	BTBW		AMRE		BTARCS	
				x	se	x	se	x	se
EDGE <2000m;	WSDC<0.5 <50		55	52.5	13.1	18.9	10.2	28.8	17.7
EDGE <2000m;	WSDC<0.5 >50		53	99.9	12.5	26.4	9.8	60.1	17.0
EDGE >2000m;	WSDC<0.5 <50		35	36.6	14.7	43.1	11.4	-18.1	19.8
EDGE >2000m;	WSDC<0.5 >50		38	70.7	14.4	104.8	11.2	-50.2	19.5
FC1MIL = 90%;	EDGE <2000m;	WS<0.5 <50	26	29.3	16.7	16.0	13.0	9.7	22.6
FC1MIL = >90%;	EDGE <2000m;	WS<0.5 >50	27	55.7	16.4	35.9	12.8	10.3	22.2
FC1MIL = >90%;	EDGE >2000m;	WS<0.5 <50	12	32.4	24.6	9.4	19.1	12.4	33.3
FC1MIL = >90%;	EDGE >2000m;	WS<0.5 >50	9	98.0	28.4	55.9	22.1	42.1	38.5
FC1MIL = >80-90%;	EDGE <2000m;	WS<0.5 <50	21	38.5	18.6	15.6	14.5	21.4	25.2
FC1MIL = >80-90%;	EDGE <2000m;	WS<0.5 >50	15	180.9	22.0	15.9	17.1	148.7	29.8
FC1MIL = >80-90%;	EDGE >2000m;	WS<0.5 <50	14	55.0	22.8	20.7	17.7	31.3	30.9
FC1MIL = >80-90%;	EDGE >2000m;	WS<0.5 >50	18	83.5	20.1	84.6	15.6	-34.1	27.2
FC1MIL = >70-80%;	EDGE <2000m;	WS<0.5 <50	8	89.7	30.1	25.2	23.5	55.3	40.8
FC1MIL = >70-80%;	EDGE <2000m;	WS<0.5 >50	11	63.2	25.7	27.5	20.0	21.3	34.8
FC1MIL = >70-80%;	EDGE >2000m;	WS<0.5 <50	9	22.4	28.4	99.3	22.1	-98.0	38.5
FC1MIL = >70-80%;	EDGE >2000m;	WS<0.5 >50	11	30.6	25.7	173.9	20.0	-158.7	34.8

[1]BTARCS = difference between the density of the black-throated blue warbler and the combined densities of the American redstart and chestnut-sided warbler.
[2]FC1MIL = group based on forest cover within 1 mile.
[3]EDGE = group based on length of edge within a 500m-radius from bird census station.
[4]WSDC<0.5 = group based on deciduous woody stems.
[5]#BCS = number of bird census stations.
[6]x = mean density.
[7]se = standard error of the mean.

Table D31. P values in 4 way ANOVAS in which the densities of the black-throated blue warbler, and American redstart and the variable BTARCS were compared among groups based on % of northern hardwood forest within 1 mile radius (NHWD1MIL), forest edge EDGE, % canopy opening CANOPEN, and number of woody stems (WSDC<0.5). Data were obtained from bird censusing and vegetation sampling undertaken in 1992-1994 and from GIS of study areas in the Upper Peninsula of Michigan current for 1992.

Factor	BTBW	AMRE	BTARCS
NHWD1MIL	0.69	0.185	0.513
EDGE	0.816	0.157	0.438
CANOPEN	0.006	0.114	0.226
WSDC<0.5	<0.001	0.018	0.092
NHWD1MIL x EDGE	0.621	0.076	0.166
NHWD1MIL x CANOPEN	0.127	0.114	0.026
NHWD1MIL X WSDC<0.5	0.021	0.129	0.006
EDGE x CANOPEN	0.31	0.927	0.477
EDGE x WSDC<0.5	0.749	0.113	0.68
CANOPEN x WSDC<0.5	0.02	0.354	0.433
NHWD1MIL x EDGE x CANOPEN	0.059	0.129	0.005
NHWD1MIL x EDGE x WSDC<0.5	0.225	0.408	0.059
NHWD1MIL x CANOPEN x WSDC<0.5	0.005	0.373	0.011
EDGE x CANOPEN x WSDC<0.5	0.335	0.672	0.963
NHWD1MIL x EDGE x CANOPEN x WSDC<0.5	0.253	0.932	0.355

[1]BTARCS = difference between the density of the black-throated blue warbler and the combined densities of the American redstart and chestnut-sided warbler.

Table D32. Least squares means of black-throated blue warbler and American redstart densities, and of (BTARCS)[1] in 4-way ANOVAs used to test the effects of NHWD1MIL, EDGE, CANOPEN, and WSDC<0.5. Least squares means of all groups of bird census stations that represent main effects of factors are presented but only means of groups that represent interactions among factors that were significant at the 0.1 level of significance and that comprised more than 10 bird census stations. Data presented are from bird censusing and vegetation sampling during 1992-1994 in the Upper Peninsula of Michigan.

Groups		#BCS	BTBW x	BTBW se	AMRE x	AMRE se	BTARCS x	BTARCS se
NHWD1MIL[2]<30		37	77.1	19.71	24.12	10.40	34.03	22.86
NHWD1MIL>30		105	68.47	9.34	39.45	4.93	17.45	10.83
EDGE[3] <2000m		89	70.253	11.43	23.58	6.03	35.58	13.25
EDGE >2000m		53	75.33	18.58	39.98	9.8	15.90	21.55
CANOPEN[4]<15%		88	42.02	13.03	22.61	6.88	10.36	15.11
CANOPEN>15%		54	103.56	17.49	40.95	9.23	41.12	20.29
WSDC[5]<0.5 <50		73	29.97	15.65	17.96	8.26	4.27	18.15
WSDC<0.5 >50		69	115.61	15.20	45.61	8.02	47.21	17.62
NHWD1MIL<30;	WSDC<0.5 <50	25	8.85	28.03	19.08	14.79	19.08	14.79
NHWD1MIL<30;	WSDC<0.5 >50	12	145.37	27.73	29.15	14.63	29.15	14.63
NHWD1MIL>30;	WSDC<0.5 <50	48	51.09	13.92	16.84	7.35	16.84	7.35
NHWD1MIL >30;	WSDC<0.5 >50	57	85.85	12.45	62.06	6.57	62.06	6.57

Table D32. (continued)

Groups		#BCS	BTBW x	BTBW se	AMRE x	AMRE se	BTARCS x	BTARCS se
CANOPEN<15%;	WSDC<0.5 <50	49	24.65	16.29	14.14	8.59	-1.16	18.89
CANOPEN<15%;	WSDC<0.5 >50	39	59.39	20.34	31.08	10.73	21.87	23.59
CANOPEN>15%;	WSDC<0.5 <50	24	35.29	26.72	21.78	14.01	9.69	30.99
CANOPEN>15%;	WSDC<0.5 >50	30	171.83	22.58	60.13	11.92	72.54	26.19
EDGE <2000;	WSDC<0.5 <50	47	30.93	13.99	18.95	7.39	8.87	16.24
EDGE <2000;	WSDC<0.5 >50	42	109.58	18.06	28.22	9.53	62.29	20.95
EDGE >2000;	WSDC<0.5 <50	26	29.01	27.99	16.97	14.77	-0.34	32.46
EDGE >2000;	WSDC<0.5 >50	27	121.64	24.44	62.99	12.90	32.13	28.35
NHWD1MIL<30%;	CANOPEN<15%	25	29.58	23.48	24.11	12.39	-9.90	27.23
NHWD1MIL<30%	CANOPEN>15%	12	124.62	31.66	24.12	16.71	77.96	36.72
NHWD1MIL>30%;	CANOPEN<15%	63	54.44	11.30	21.11	5.96	30.62	13.10
NHWD1MIL>30%;	CANOPEN>15%	42	82.50	14.88	57.79	7.85	4.28	17.25
NHWD1MIL<30%;	WSDC<0.5 <50	25	8.85	28.02	19.08	14.79	-22.70	32.50
NHWD1MIL<30%;	WSDC<0.5 >50	12	145.37	27.72	29.14	14.63	90.76	32.15
NHWD1MIL>30%;	WSDC<0.5 <50	48	51.09	13.92	16.84	7.34	31.23	16.15
NHWD1MIL>30%;	WSDC<0.5 >50	57	85.85	12.45	29.14	14.63	3.66	14.44

Table D32. (continued)

Groups			#BCS	BTBW		AMRE		BTARCS	
				x	se	x	se	x	se
NHWD1MIL<30%;	EDGE <2000;	CANOPEN<15%	20	53.58	23.12	16.78	12.20	27.26	26.82
NHWD1MIL>30%;	EDGE <2000;	CANOPEN<15%	32	47.62	15.86	11.00	8.37	31.19	18.40
NHWD1MIL>30%;	EDGE <2000;	CANOPEN>15%	28	95.06	17.28	30.92	9.14	58.64	20.10
NHWD1MIL>30%;	EDGE >2000;	CANOPEN<15%	31	61.27	16.09	31.22	8.49	30.05	18.67
NHWD1MIL>30%;	EDGE >2000;	CANOPEN>15%	14	69.94	24.18	84.67	12.76	-50.09	28.05
NHWD1MIL30;	CANOPEN<15%;	WS<0.5 <50	18	17.70	28.32	19.29	14.95	-23.88	32.85
NHWD1MIL>30;	CANOPEN<15%;	WS<0.5 <50	31	31.61	16.09	8.99	8.49	21.56	18.67
NHWD1MIL>30;	CANOPEN<15%;	WS<0.5 >50	32	77.28	15.86	33.23	8.37	39.68	18.40
NHWD1MIL>30;	CANOPEN>15%;	WS<0.5 <50	17	70.58	22.73	24.69	11.99	40.91	26.36
NHWD1MIL>30;	CANOPEN>15%;	WS<0.5 >50	25	94.43	19.20	90.90	10.13	-32.36	22.27

[1]BTARCS = density of black-throated blue warbler - (density of American redstart + chestnut-sided warbler).
[2]NHWD1MIL =group based on % of northern hardwood forest within 1 mile radius
[3]EDGE = group based on length of edge within a 500m-radius from bird census station.
[4] CANOPEN = group based on canopy opening
[5]WSDC<0.5 = group based on deciduous woody stems

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