

5-2003

Effects of Small-gap Timber Harvests on Songbird Community Composition and Site-fidelity

Mitschka John Hartley

Follow this and additional works at: <http://digitalcommons.library.umaine.edu/etd>

 Part of the [Forest Biology Commons](#), [Forest Management Commons](#), and the [Poultry or Avian Science Commons](#)

Recommended Citation

Hartley, Mitschka John, "Effects of Small-gap Timber Harvests on Songbird Community Composition and Site-fidelity" (2003). *Electronic Theses and Dissertations*. 644.
<http://digitalcommons.library.umaine.edu/etd/644>

This Open-Access Dissertation is brought to you for free and open access by DigitalCommons@UMaine. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of DigitalCommons@UMaine.

**EFFECTS OF SMALL-GAP TIMBER HARVESTS ON SONGBIRD
COMMUNITY COMPOSITION AND SITE-FIDELITY**

By

Mitschka John Hartley

B.S. Cornell University, 1992

M.S. Louisiana State University, 1994

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Doctor of Philosophy

(in Wildlife Ecology)

The Graduate School

The University of Maine

May, 2003

Advisory Committee:

Malcolm L. Hunter, Professor of Wildlife Ecology & Libra Professor of Conservation

Biology, Advisor

Raymond O'Connor, Professor of Wildlife Ecology

William Glanz, Associate Professor of Zoology

Alan White, Professor of Forest Ecology & Silviculture

William Halteman, Associate Professor of Mathematics

© 2003 Mitschka John Hartley
All Rights Reserved

**EFFECTS OF SMALL-GAP TIMBER HARVESTS ON SONGBIRD
COMMUNITY COMPOSITION AND SITE-FIDELITY**

By Mitschka John Hartley

Thesis Advisor: Dr. Malcolm L. Hunter, Jr.

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
(in Wildlife Ecology)
May, 2003

I investigated effects of small-gap timber harvests on bird communities at nine sites (10 ha each) within the Penobscot Experimental Forest (PEF), grouped into three replicated "blocks" (three sites each). Blocks were randomly treated with three treatments: 10% harvest, 20% harvest, and no harvest (i.e., control). I examined how treatments affected breeding songbird abundance, richness, and site-fidelity over four consecutive summers, including 1-3 years before and after each site was harvested. Ability to detect treatment effects was limited by the small number of replicates, but power analyses indicated that given the experimental design and observed variability, there was a high (>80%) probability to detect 20-30% differences in overall abundance among treatment groups. There was no evidence that treatments caused changes of this magnitude, or affected densities of individual species, avian richness, or which species were most abundant before versus after treatment. Annual variations in densities were much stronger than differences between treatment groups.

Of 96 male Hermit Thrushes and 74 male Ovenbirds captured within sites, an average of 62% and 28% of respective males were recaptured annually. Of these, 90% of male Hermit Thrushes and 94% of male Ovenbirds were recaptured on the same site in successive years, regardless of the site's treatment status. However, there was a significantly higher tendency for Hermit Thrush to disperse to new sites if they were previously captured on treated versus control sites.

In Chapter 3 I argue that annual fluctuations in bird densities may be driven largely by predator (i.e., red squirrel, *Tamiasciurus hudsonicus*) population dynamics. Previous research has shown that avian nest-predation by red squirrels strongly affects local breeding productivity of birds, and that red squirrel populations are regionally synchronous. I examined four lines of evidence that are consistent with the premise that squirrel population fluctuations can affect bird populations over large areas. Squirrel populations in the PEF peaked in 1995 and crashed in 1996, while bird densities decreased from 1995 to 1996, then increased sharply from 1996 to 1997. Breeding Bird Survey data showed a similar pattern of avian population change (especially for coniferous-forest birds) from 1995-1997 at much larger scales.

DEDICATION

This dissertation is dedicated to my Mother, Rosita Ella Hiscock Hartley, and my Grandmother, Gladys Inza Quimby Hiscock. More than anyone else in my life, these two women taught me to believe in myself and to pursue my dreams. Most importantly, they taught by example that effort is the currency of achievement, that hard work should be done without expectation of praise, and that difficulties must be endured with patience and without excessive complaint. I strive daily to keep these lessons in mind. Their contributions to my character and philosophy are beyond enumeration, as are my feelings of gratitude for their generosity, support, and love.

ACKNOWLEDGMENTS

My foremost thanks go to my advisor, Mac Hunter, for all of his patient support, encouragement, ideas, and help. His edits were always more rapid than I could have hoped for and his attention to detail and writing style were much appreciated. Perhaps most significantly I thank Mac for his friendship and for the many ways he has served as a role model in aspects both professional and personal. As much as I had enjoyed Maine before meeting Mac, he and his wife Aram showed me some of its most special places.

I am deeply grateful for the insights of all of my committee members. I learned a great deal from each of them, admired their abilities, and appreciated their friendship and good-natured interactions. I have especially fond memories of bird hunting, and hiking in Central America with Bill Glanz. I am indebted to my friends and fellow grad students who proofread my very worst writing before it went to anyone else. I especially thank Steve Campbell; he was as tireless with editorial assistance as with his companionship.

Bird and squirrel data in Chapter 3 were provided by Patuxent Wildlife Research Center (BBS trend data), R. Holmes (Dartmouth College), D. Harrison (University of Maine), A. Jobes (Trent University), Canada Agriculture (Fredericton, New Brunswick), C. Demers (SUNY-ESF, Huntington Forest) and R. Brooks (University of Guelph).

This research would not have been possible without the help of faculty and graduate students involved with the Forest Ecosystem Research Program (FERP) at the University of Maine. Bob Seymour especially was instrumental in shaping the FERP research and teaching me most of what I know about silviculture. My research was largely funded by the Maine Agriculture & Forest Experiment Station, through the FERP. The Maine Department of Inland Fisheries & Wildlife provided a vehicle for all four

summers of my field work. The USDA Forest Service Northeast Experiment Station, graciously provided my crew and I housing and other facilities in the Penobscot Experimental Forest for four summers. This work was also funded in part by grants from the Cooper Ornithological Society (through a Mewaldt-King Award), the American Wildlife Research Foundation, and the Association of Graduate Students at the University of Maine. During my graduate studies at UM I received funds for academic travel from the Swedish Information Service (through a Bicentennial Exchange Grant) and the American Bryological and Lichenological Society. I also received scholarship support from the New England Outdoor Writers' Association (through a Scholarship and an Arthur Sullivan Award), and the UM Department of Wildlife Ecology (through a Howard L. Mendall Memorial Scholarship and an Outstanding Wildlife Graduate Student Award). I was also supported by Audubon New York, a state office for the National Audubon Society, during part of my thesis writing.

Finally, this project was largely carried upon the pale, bug-bitten backs of a large and dedicated group of field assistants, to whom I owe a very large debt of gratitude. They endured difficult conditions for very low pay; with few exceptions they were a diligent and skilled bunch, dedicated not just to this research effort but to natural resources in general. My heartfelt thanks therefore go to Rhonda Weunsch, Ann Savage, Jen Norris, Boris, Brian Aust, Liz Burroughs, Chris Jacques, Chris Stauffer, Michelle Soenksen, Harry Kahler, Dan Schieman, Karen Tremper, Denise Moore, Jason Hummel, Megan Hughes, Mike Thibodeau, Kyle Apigian, Paul Miller, Erica Chipman, and Doug Smart.

TABLE OF CONTENTS

DEDICATION	iii
ACKNOWLEDGMENTS.....	iv
LIST OF TABLES	x
LIST OF FIGURES.....	xii

Chapter

1. EFFECTS OF 10% AND 20% TIMBER REMOVALS ON BIRD

COMMUNITY COMPOSTION.....	1
INTRODUCTION.....	1
Objectives.....	4
Hypotheses Tested.....	4
METHODS.....	4
Experimental Design	4
Treatments	6
Study Area.....	7
Avian Censuses	9
Analyses	10
Treatment Groups: Classic ANOVA Approach.....	11
Treatment Groups: Controlled Comparisons	13
Bird Community Ordination	14
Qualitative Assessments of Avifaunal Change	16
Power Analyses	16

RESULTS.....	17
Avian Richness and Abundance Among Years	17
Avian Richness and Abundance Within Years	19
Individual Species Abundances	21
Bird Community Ordination	24
Qualitative Changes in Avifauna	27
DISCUSSION	28
CONCLUSIONS.....	33
LITERATURE CITED	35

**2. EFFECTS OF EXPERIMENTAL HABITAT DISTURBANCES ON
BREEDING SITE-FIDELITY OF ADULT HERMIT THRUSHES**

<i>(Catharus guttatus)</i> AND OVENBIRDS <i>(Seiurus aurocapillus)</i>	38
INTRODUCTION.....	38
Objectives.....	40
Hypotheses Tested.....	40
METHODS.....	41
Avian Sampling.....	41
Analyses	44
Return Rates	45
Site-attachment.....	46
Survival and Recapture Rates	48

RESULTS.....	49
Return Rates	49
Site-attachment.....	55
Survival and Recapture Rates	59
DISCUSSION	59
Treatment Effects on Site-Fidelity	59
Survival and Recapture Rates	61
Undetected Emigrants	61
CJS and Short-Duration Studies.....	63
CONCLUSIONS.....	65
LITERATURE CITED	67
3. EFFECTS OF RED SQUIRREL (<i>Tamiasciurus hudsonicus</i>)	
POPULATION FLUCTUATIONS ON BIRD POPULATIONS	70
INTRODUCTION.....	70
METHODS.....	72
Local Analysis for Maine, 1995-1997.....	72
Regional Analysis, 1995-1997	73
Local Analysis for Ontario, 1998-2000.....	79
Local Analysis for New Brunswick, 1950-1959	82
RESULTS.....	85
Local Analysis for Maine, 1995-1997.....	85
Regional Analysis, 1995-1997	86
Red Squirrels.....	86
Birds	87

Local Analysis for Ontario, 1998-2000.....	89
Local Analysis for New Brunswick, 1949-1959.....	91
DISCUSSION	91
LITERATURE CITED	99
BIBLIOGRAPHY	103
APPENDICES.....	111
APPENDIX A. Data and Analyses Related to Chapter 1.....	112
APPENDIX B. Power Analyses Related to Chapter 1	123
APPENDIX C. Data and Analyses Related to Chapter 2.	129
APPENDIX D. Data and Analyses Related to Chapter 3.....	136
APPENDIX E. Scientific Names of Birds	139
BIOGRAPHY OF THE AUTHOR.....	141

LIST OF TABLES

Table 1.1.	Treatment schedule for nine research areas (RA) at the Penobscot Experimental Forest (PEF).....	6
Table 1.2.	Number and size of harvest gaps.....	8
Table 1.3.	Mean avian species richness for nine research areas in the PEF	23
Table 2.1.	Mistnet effort and number of captures per year	43
Table 2.2.	Recapture rate, by species and sex	51
Table 2.3.	Recapture rate by species, age, and sex	52
Table 2.4.	Contingency tables of recaptures by treatment for Hermit Thrush and Ovenbird.....	53
Table 2.5.	Numbers of recaptured male birds remaining on a site versus dispersing to a new site	54
Table 2.6.	Distances between capture locations of successive years	57
Table 2.7.	Summary of statistical test results for differences in site- attachment distances.....	58
Table 2.8.	Estimated survival (ϕ) and recapture (p) rates	60
Table 3.1.	Population trends for birds in northern New England.....	80
Table 3.2.	Regional comparison of number of bird species fitting hypothesized patterns of population change	81
Table 3.3.	Bird species fitting hypothesized pattern of population changes	90
Table A.1.	Abundance of bird territories in 1995.	113
Table A.2.	Abundance of bird territories in 1996	114
Table A.3.	Abundance of bird territories in 1997	115

Table A.4.	Abundance of bird territories in 1998	116
Table A.5.	Mean abundance of bird territories over all years (1995-1998).....	117
Table A.6.	Kruskal-Wallis tests of differences among treatment groups	118
Table A.7.	Analysis of variance (ANOVA) for richness and abundance	121
Table A.8.	Results of iterative analysis-of-variance (ANOVA) tests.....	122
Table C.1.	Differences in site-attachment distances by year	130
Table C.2.	Differences in site-attachment distances by treatment.....	131
Table C.3.	Differences in site-attachment distances by dispersal status.....	132
Table C.4.	Differences in site-attachment distances by treatment status.....	133
Table C.5.	Differences in site-attachment distances by treatment status (year “t+1”)	134
Table C.6.	Results of competing Cormack-Jolly Seber models for mark-recapture data analyzed with Program MARK.....	135
Table D.1.	Bird population trends for combined region	137
Table E.1.	Scientific names of birds	140

LIST OF FIGURES

Figure 1.1.	Location of research areas in the Penobscot Experimental Forest (PEF)	8
Figure 1.2.	Mean avian abundance (per 10 ha) for nine research areas in the PEF.....	18
Figure 1.3.	Difference in abundance between two control sites and six treated research sites	20
Figure 1.4.	Mean avian abundance (per 10 ha) by treatment group	22
Figure 1.5.	Mean density of species with apparent treatment preference	25
Figure 3.1.	Abundance of birds and red squirrels in the PEF.....	76
Figure 3.2.	Red squirrel abundance at five locations in northeastern North America.....	77
Figure 3.3.	Abundance of birds and red squirrels at Algonquin Provincial Park, Ontario, 1998-2000.....	83
Figure 3.4.	Spruce budworm (A), bird (B), and red squirrel (C) population changes from 1949-1959 in Green River, New Brunswick	84
Figure B.1.	Scenario 1, 1998 Data	125
Figure B.2.	Scenario 2, 1998 Data	126
Figure B.3.	Scenario 3, 1998 Data	126
Figure B.4.	Scenario 1, 1997 Data	127
Figure B.5.	Scenario 2, 1997 Data	128
Figure B.6.	Scenario 3, 1997 Data	128

Chapter 1

EFFECTS OF 10% AND 20% TIMBER REMOVALS ON BIRD COMMUNITY COMPOSITION: AN EXPERIMENTAL APPROACH

INTRODUCTION

In recent decades there has been considerable research into the effects of forest management on bird populations (Sallabanks and Marzluff 2000). However, the even-aged practice of clearcutting has been the focus of most of this research (Sallabanks et al. 2000), whereas other methods (e.g., partial cutting) have received much less attention (Thompson et al. 2000). Consequently, for most forest types and avian species we have a poor understanding of the level of timber removal that triggers abandonment or invasion of a forest patch, or density changes that can be considered a response to habitat alteration. To understand how timber harvest intensity affects bird communities within a relatively homogenous forest area (or “stand”) it is necessary to either: a) examine bird composition across many different stand replicates treated with a variety of harvest intensities or b) compare pre- and post-harvest bird communities on stands treated with specific levels of timber harvesting, and on unharvested controls. However, few studies have measured bird densities across a range of harvest intensities, and even fewer have examined pre- and post-harvest data from stands with randomly applied harvest treatments and a rigorous experimental design (Sallabanks et al. 2000).

Most of these studies have focused on partial harvests (e.g., Annand and Thompson 1997) that removed a large proportion (e.g., 40-60%) of mature timber rather uniformly throughout a stand (e.g., shelterwood cuts), or on stands that are mostly mature

and intact but contain one or more small-scale (e.g., 1 ha) clearcuts, often called patch cuts (Derleth et al. 1989, Lent and Capen 1995). These types of harvest are of lower intensity than is clearcutting because some mature trees are left unharvested in stands. Previous studies examining patch cuts defined the treatments as small-scale disturbances (Derleth et al. 1989, Lent and Capen 1995), but patch cuts really are high-intensity removals done on a scale (e.g., 0.5-2 ha) that is smaller than traditional, commercial clearcuts (e.g., 10-50 ha). Patch cuts examined in earlier studies were large enough to result in new patches of young forest that were invaded and occupied by a suite of pioneer species adapted to that habitat (Lent and Capen 1995, Buford and Capen 1999).

Annand and Thompson (1997) measured avian abundance in mature oak-pine stands and those harvested by clearcut, shelterwood, group selection, and individual-tree selection, and is one of the very few works that can help identify cutting levels that affect bird communities. However, it is unclear whether results from a study in Missouri oak-pine forests can be generalized to other forest types and regions such as my study area in Maine, though the bird community described by Annand and Thompson (1997) is generally similar to bird communities in Maine (Hagan et al. 1997).

Few studies have focused on how bird communities are affected by removing a relatively small proportion (e.g., 10-20%) of mature trees, especially when the size of cut patches is very small (e.g., 0.1 ha). Removing a few individual trees from a forest stand will probably not affect the breeding bird community in a stand, unless the trees provide a critical resource that is otherwise lacking in the forest. However, at some level, removal of mature trees will change the vertical and/or horizontal structure of a stand to a point at

which some species will find it unsuitable or less suitable habitat while others may invade or increase in density (Annand and Thompson 1997).

In a recent review of nearly 100 papers published over the last 25 years, Sallabanks et al. (2000) criticized the scientific rigor of research on forestry and birds. Studies with only one replicate per treatment were most common in the literature (27%), and only 27% of studies exceeded four replicates per treatment. Most studies (68%) were only 1-2 years in duration, with only seven of 95 studies lasting longer than four years (Sallabanks et al. 2000). Though most studies measured relationships between timber harvest and relative avian abundance, only 32% measured bird densities. Especially lacking have been studies using experimental manipulations that allow for direct comparisons of pre- and post-treatment data (Sallabanks et al. 2000). Only 16% of all studies collected data before and after timber harvests. Most significantly, not one paper published between 1972 and 1997 incorporated a manipulative experimental design in which treatments were assigned randomly to experimental units (Sallabanks et al. 2000).

The Forest Ecosystem Research Program (FERP) at the University of Maine started in 1993, to address the need for a rigorous approach to research on the effects of timber harvests on forest ecosystems. FERP researchers designed an experiment to examine how forest structure and function are affected by timber harvests that were explicitly designed to mimic natural disturbance patterns. Using the research areas and experimental design established by the FERP, my research examines whether low-intensity, small-scale timber harvests cause changes in the breeding bird community.

Objectives

The objective of my research was to determine whether FERP harvest treatments caused changes in the avifauna on 10 ha research areas (hereafter sites). This objective was subdivided into examination of effects on the entire bird community (all species considered simultaneously) and effects on individual species.

Hypotheses Tested

Using avian territory census data from nine sites during 1995-1998, I tested the following research hypotheses:

Null hypothesis 1: there is no difference in the abundance or richness of birds on control sites and sites treated with 10% or 20% harvests.

Null hypothesis 2: after 10% or 20% harvest treatments are implemented, no species becomes more or less abundant on treated versus control sites.

Null hypothesis 3: bird community composition, measured by dissimilarity matrices, is not different for treated versus control sites before or after harvest.

METHODS

Experimental Design

In 1994 the Forest Ecosystem Research Program (FERP) at the University of Maine began to evaluate effects of low-intensity timber harvests on forest ecosystem structure and function. The FERP designed silvicultural treatments that were meant to somewhat mimic the temporal and spatial pattern of natural disturbances in the northeastern United States. Natural disturbance frequencies range from 0.5-2% per year in temperate forests across North America (Runkle 1985), so the FERP chose two levels of harvest intensity to examine: 1% and 2% annual mortality of canopy trees. To

achieve these disturbance levels with a practical silvicultural system, the FERP planned for harvests every ten years that removed approximately 10% and 20% of canopy trees.

To evaluate the effects of these two harvest treatments on forest ecosystems, the FERP established a randomized complete block design (Sokal and Rohlf 2000) with replication of treatments in space and time. The FERP design included comparison of treated and untreated (i.e., control) sites, and pre- and post-treatment data collection. The FERP experiment was carried out on nine mature mixed conifer-deciduous forest sites that were 10 ha in size, and were similar in terms of soils, tree species composition, stocking, and time since harvest (>50 years). These nine sites were grouped in three blocks of three sites each. Sites within a block generally were in the same geographic area, and were thought to be most similar. These blocks thus represent three replicates, with the three treatments (i.e., two harvest levels and a control) randomly applied to one site in each block. For replication over time, treatments were imposed over three consecutive years (Table 1.1). The staggered-entry design for FERP treatments was due to constraints in funding, which allowed for pre-harvest baseline vegetation data collection on only one block of three sites each summer.

In 1995 pre-treatment bird data were collected on all sites, except one control (Research Area 8) that was not established until 1996. The following winter (i.e., February 1996) the first three research areas (#1-3) were randomly chosen to receive the 20% harvest, 10% harvest, or be an untreated control. During the next two successive winters, the second and third block of sites were randomly assigned treatments and harvested (except for controls). Thus, by the summer of 1998 all sites had been treated (Table 1.1).

Table 1.1. Treatment schedule for nine research areas (RA) at the Penobscot Experimental Forest (PEF). Treatments are labeled “10-30” and “20-10” respectively, as approximately 10% and 20% of timber is harvested every 10 years, and 30% and 10% of live trees are marked for permanent retention through a 100 year rotation. Treatments are listed in bold type for the first year treated, and their label remains unchanged for all years after treatment. Untreated stands are considered as a control until treated.

<u>Triplet</u>	<u>RA</u>	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1998</u>
1	1	control	20-10	20-10	20-10
	2	control	10-30	10-30	10-30
	3	control	control	control	control
2	4	control	control	control	control
	5	control	control	10-30	10-30
	6	control	control	20-10	20-10
3	7	control	control	control	10-30
	8	control	control	control	control
	9	control	control	control	20-10

Treatments

The spatial pattern of natural disturbances that predominate in eastern forests are on the scale of one or a few trees falling (Lorimer 1977), so FERP treatments were designed as a series of small (0.10-0.20 ha) harvest gaps distributed across each 10 ha site. The size and number of gaps varies slightly among sites within each treatment group (Table 1.2). After natural disturbances some mature trees often survive within a disturbed area (Lorimer 1977), which typically results in greater structural diversity than is found in many patch cuts after harvest (Hunter 1990). Therefore, FERP harvest gaps were marked before treatment so that some mature trees would be permanently retained throughout all harvest entries. Criteria for reserve-tree selection included one or more of the following: large-diameter trees, trees with existing cavities, representative species composition, and/or preservation of uncommon native species. The targeted level of retention was 10% of mature trees for the 20%-harvest treatment, and 30% of mature

trees for the 10% harvest treatment. Therefore, FERP treatments are labeled as “20-10” and “10-30,” to signify their level of harvest (every ten years) and retention, respectively (Fig. 1.1, Table 1.1).

Study Area

All FERP research areas (Fig. 1.1) are within the Penobscot Experimental Forest (PEF) located in the towns of Bradley and Eddington, Penobscot County, Maine (approximately 44°52.7' North, 68°39.2' West). This 1540 ha (3,800 acre) property has been managed by the USDA Forest Service from 1950-1994, and jointly by the Forest Service and the University of Maine from 1994 to the present. Approximately 30% of the land area of the PEF is occupied by long-term research sites managed for timber and monitored for research purposes by the USDA Forest Service. The forests of the PEF had experienced some light timber cutting for conifer sawlogs approximately 20-40 years before 1950, at which time most stands on the PEF were 60-100 years old, with older individual trees scattered throughout the area.

The climate at the PEF is cool and humid; the mean (1951-1980) annual temperature for nearby Bangor, Maine is 6.6°C. February, the coldest month, has an average daily temperature of -7.1°C, whereas July, the warmest month, averages 20°C. Mean annual precipitation is 1060 mm, with 48% falling from May-October. The PEF is within the Acadian forest type of the northeastern US and Canada. The forest vegetation across most of the PEF is predominately mixed conifers, mixed conifer-deciduous, or (rarely) deciduous-dominated. Dominant species include eastern hemlock (*Tsuga canadensis*), red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), aspen

Table 1.2. Number and size of harvest gaps. The number of gaps per research area (n), mean and median gap size, variance measures, 95% confidence interval around means, and total area harvested are listed for all six research areas (and all areas pooled), grouped by treatment (Treat.). All sites are in the Penobscot Experimental Forest, Bradley, Maine, and were treated from 1996-1998.

Research Area	Treat.	(n)	Mean Size (m ²)	Median Size (m ²)	Standard Deviation	Standard Error	95% Conf. Interval	Harvested Area (ha)
1	20-10	8	1542.33	1540	403.1953	142.5511	1205-1879	1.23
6	20-10	9	1280.91	1269	564.2914	188.0971	847-1715	1.15
9	20-10	10	971.53	906.15	484.1246	153.0936	625-1318	0.97
All three	20-10	27	1243.78	1269	528.47	101.71	1035-1453	Mean: 1.1
2	10-30	7	350.64	348.20	129.09	48.79	231-470	0.25
5	10-30	10	786.78	828.60	188.66	59.66	652-922	0.79
7	10-30	9	842.68	824.50	273.02	91.01	633-1053	0.76
All three	10-30	26	688.71	674.20	291.63	57.19	571-806	Mean: 0.6

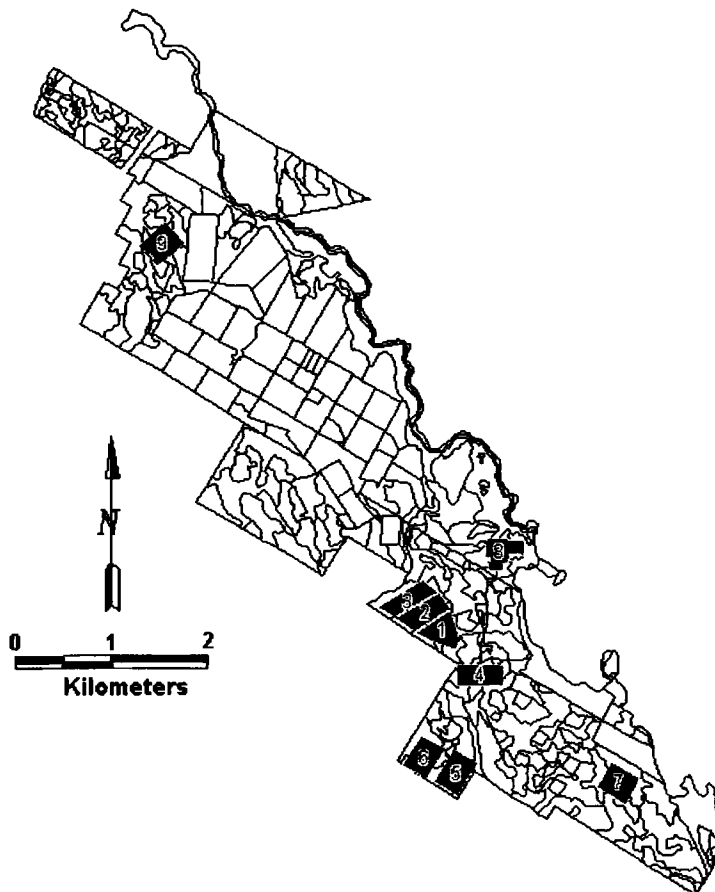


Figure 1.1. Location of research areas in the Penobscot Experimental Forest (PEF). PEF is located in Penobscot County, Maine.

(*Populus grandidentata* and *P. tremuloides*), and American beech (*Fagus grandifolia*).

FERP research areas are on moderately well-drained soils, and contain approximately 60% coniferous tree species and 40% deciduous tree species, though small areas within each site may contain higher (e.g., 90%) proportions of either type. It should be noted that a few small canopy gaps from natural disturbance events existed on all sites (i.e., treatments and controls) prior to implementation of any treatments. These natural gaps were similar in size to treatment harvest gaps, but were established before our study began, and therefore varied in terms of the amount or height of regenerated vegetation.

Avian Censuses

All nine FERP research areas in the PEF had marked, parallel transects that were spaced 50 m apart and ran the length (and around the perimeter) of the site; depending on the shape of the site and the orientation of the lines, there were 5-10 transects per site. From 1995-1998, each site was visited on 10 mornings from 21 May to 7 July by an observer who spent approximately two hours walking along each transect to map bird territories, using standardized spotmapping methods (IBCC 1970). I conducted 3-5 of the ten censuses on every site in all four years. Censuses were also conducted by 1-2 additional observers who differed each year. Each year all observers visited the nine sites in nearly equal proportions, with each observer counting birds on two sites per morning in good weather. Observer-bias was minimized by training and practice to ensure that techniques were similar among all observers in all years.

Consecutive visits to a site started at different corners, and transects were walked in a direction opposite to the previous visit. Bird observations were not collected during any precipitation, or when winds were >15 km/hr. Each site had a similar proportion of

early (beginning before 0400 EST) and later (beginning around 0700 EST) morning censuses. After all ten census visits were completed, all registrations for each species were examined to determine how many territories were occupied by each species.

A territory was defined by an individual of a species detected in the same area on at least six of ten visits (IBCC 1970). Multiple territories for a species typically were delineated by counter-singing registrations. A territory with $\geq 50\%$ of registrations outside the boundaries of a 10 ha research area was counted as 0.5 territories, as long as three registrations were within site boundaries. Birds observed < 6 times, or only seen flying over the forest were not considered to be territorial.

To supplement census data collected from 1995-1998, I made one early-morning visit to each treated site during the first week of June, 2002, and spent ten minutes observing birds at each of the harvest-created gaps in each research area. This single visit was intended to determine whether pioneer species had occupied any gaps since 1998, or whether any species was obviously numerically abundant in or around gaps.

Analyses

The avifaunal metrics I examined among treatment groups were: 1) species richness (i.e., number of species per site, with ≥ 0.5 territory); 2) total abundance (i.e., number of territories, pooling all species); 3) individual species abundance; 4) matrices with all pair-wise comparisons of sites in terms of their percent dissimilarity index, calculated from bird community abundance matrices. A fifth analytic approach was to qualitatively assess which species were numerically dominant on sites before and after harvest treatments, and determine whether any differences could be attributed to

treatments. Also, I determined whether “pioneer species” that prefer disturbed forests tended to be observed on treated versus control sites after harvesting.

Treatment Groups: Classic ANOVA Approach

To determine whether harvest treatments affected bird communities, analyses were conducted using two different approaches. The first was a “classic ANOVA approach” that divided the nine sites into three treatment groups, based on whether they received the 10-30 or 20-10 silvicultural treatment or were a control. Total avian richness and abundance values were examined for normality for all years combined and within each year. Both variables were normally distributed, so group differences were tested with analysis of variance (ANOVA) methods (Zar 1999). Each variable was tested in a factorial ANOVA model with ‘year’ and ‘treatment group’ as main effects and a ‘year*treatment’ interaction term (SAS 1990). The year-term generally was significant, but treatment and interaction terms were not (see Results), so avian abundance and richness were examined separately for each year. For each year, both abundance and richness were compared across sites with one-way ANOVA, with treatment group as the main-effect tested. Duncan’s multiple comparison test was used to determine which means differed significantly (SAS 1990) at an alpha level of 0.05.

In ANOVA models, I grouped sites by the treatment they would eventually receive and compared all variables of interest among these groups, in 1995 (before harvesting occurred), in 1998 (after all harvests), and in the intervening years when treatments were applied to some but not all of the replicated blocks. Comparing the same “fixed” treatment groups with data from before and after they are treated is necessary to distinguish between treatment effects *per se* and fundamental differences among the sites

that make up each treatment group. In the intervening years (i.e., 1996-1997), sites were analyzed by these same “fixed” treatment groups, to see whether there were tendencies for group differences in 1996 and 1997, when only one or two of the three sites within each group had been treated, respectively (Table 1.1).

It may seem counterintuitive to analyze data for each year with sites grouped by their eventual treatment, but there were no groups in 1995, as all sites were untreated. Likewise, in 1996 only one site had been treated in the 20-10 and 10-30 groups (Table 1.1), so tests for treatment effects were confounded with differences related to individual sites. By 1997, two of the three sites within each group had been treated (Table 1.1), so if treatment effects were sufficiently strong they may have been evident. For 1997 data, separate analyses were run using the “actual” treatment groups, and results are presented when they differ qualitatively from analyses with “fixed” treatment groups.

In addition to analyses on the pooled richness and abundance variables described above, I examined whether the abundance (per 10 ha) of individual species differed among treatments, for all species found on at least one site within each treatment group. Because abundance data for individual species were not normally distributed for many species in some or all years, treatment effects on individual species were examined using Kruskal-Wallis analyses. The power of Kruskal-Wallis tests generally was low because there were only three replicates per group, and the density per 10 ha for all species was ≤ 7 ; for most species it was ≤ 3 . Therefore, individual species tests for treatment effects were considered significant if $p \leq 0.10$ (Appendix A; Table A.6).

Treatment Groups: Controlled Comparisons

The second approach to examining treatment effects took advantage of the fact that I had gathered before- and after-treatment data on all treated sites, and also sampled untreated controls in the same periods. This approach was designed to explicitly examine each variable of interest (e.g., pooled abundance), in terms of how it changed on treated sites relative to controls, from the summer before to the summer after it was first treated. No sites were examined two or three years post-treatment, because all three replicated blocks of treated sites had one year of post-treatment data, but only two sets of replicates had data from the second summer after treatment. As bird species richness was not expected to change much from year to year, compared to pooled abundance, only pooled abundance data were examined with the “controlled comparison” approach. As this analysis was supplemental to the classic ANOVA analyses described above, individual species abundances were compared between treatment groups (and to controls) only for those few species that were most numerically abundant on a site and/or species for which there was some evidence that treatments may have had an effect on their densities (see Results). Because only two control sites (i.e., RA 3 and 4) were sampled in all four years, the average of these two sites was used as the benchmark against which changes in treated stands were measured.

The controlled comparison approach examined changes in abundance variables from year “n” (the summer before treatment) to year “n-1” (after treatment) for each treated site, but these values were subtracted from the mean change experienced on control sites during the same period. Thus, if overall abundances dramatically decreased or increased from one year to the next, as happened during all years of this study, this

analysis is designed to account for that change by determining whether abundances increased or decreased more or less on treated sites relative to controls. Each replicate of the three treated blocks provided two values (one from each treated site) representing the change in abundance (relative to controls) that occurred after a site was treated.

The three pairs of comparisons (one for each block in each time period) were then analyzed in two different ways. First, the mean of the pooled set of six values was tested against the null hypothesis of zero, using a Student's t-test (Zar 1999). This tested whether the six treated sites (pooled) were different from controls. Also, means for each of the two treatment groups ($n = 3$ per group) were compared by a paired t-test (Zar 1999) to see if there was a difference in the relative change in abundance between the two harvest treatments.

Bird Community Ordination

I used Mantel tests (Sokal and Rohlf 1995) and Multi-response Permutation Procedures (MRPP) in PC-ORD (McCune and Mefford 1997) to assess bird community differences among sites, treatment groups, and years. These ordination techniques are based on comparisons of all pairs of sites in terms of their ecological distance or dissimilarity, which is calculated by comparing complete species-abundance matrices for the two sites. The statistical tests are performed on matrices of the pairwise-comparisons of ecological distance among all nine sites. I used the Sorensen (or Bray-Curtis) dissimilarity index (McCune and Mefford 1997) to measure percent dissimilarity between sites. Compared to traditional Euclidean distance, this coefficient retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune and Mefford 1997).

The Mantel test tested the null hypothesis of no relationship between two dissimilarity matrices (McCune and Mefford 1997), and was used in two different ways. First, I compared dissimilarity matrices for 1995 and 1998, for the eight sites sampled in both years. This test examined the extent to which relationships among sites in 1995 changed after harvesting. I also used Mantel tests to examine whether site-by-site dissimilarity matrices (for 1995 and 1998) were independent of treatment groups, by comparing the dissimilarity matrix and a design matrix with zeros for sites within a treatment group and ones for sites in different groups. This test is a nonparametric equivalent of analysis-of-variance with statistical power similar to ANOVA (Sokal and Rohlf 1995). Data from 1998 were analyzed with all nine sites, to maximize statistical power. Data from 1998 were also analyzed with the eight sites sampled in 1995, to enable direct comparisons of treatment effects between 1995 and 1998, and determine whether there were *a priori* group differences unrelated to treatments. Mantel tests were also run separately with sites in the 10-30 and 20-10 harvest treatment groups combined and compared with unharvested controls.

I also examined treatment effects using MRPP. This test compared the mean Sorensen dissimilarity index for sites within a treatment group to the mean for all groups (yielding the observed test statistic, delta) and compared this value with an expected delta, calculated to represent the mean delta for all possible partitions of the data (McCune and Mefford 1997). I ran MRPP for 1995 and 1998. As with the Mantel tests above, I ran MRPP for 1998 with all nine sites and with the same eight sites sampled in 1995, to enable direct comparison between results for 1995 and 1998. I also ran a set of

analyses with the two harvest treatments pooled into one group and compared to unharvested controls.

Qualitative Assessments of Avifaunal Change

For each of the eight sites with data from all four years (1995-1998), I compared lists of “numerically dominant” species for each site in 1995 and 1998, to see what proportion of the dominant species were the same before and after treatments were implemented. Numerical dominance was determined by tallying the shortest possible list of species which comprised more than 50% of the total abundance for a site in a given year. For all sites and years examined, a mean (and median) of six species dominated each site. I compared the similarity of each site’s list of dominant species in 1995 and 1998, to compare the extent of changes in dominance for treated versus control sites. In determining which species were most dominant in 1998, I allowed any species with the same abundance in 1998 to be substituted for each other.

Power Analyses

Tests for significant differences among treatment groups are not meaningful without an estimation of the effect size that was likely to be detected, given the experimental design and the variability of measured parameters. To estimate effect sizes detectable in this study, I used software PASS (Hintze 2001) to plot the statistical power of one-way ANOVA tests as a function of the within-group standard deviation of the response variable, with separate curves for alpha levels of 0.05 and 0.10. These tests were run iteratively with fixed effect sizes that reflected 10%, 20% and 30% differences between values of the response variable in one treatment group (e.g., the control) and values in one or both of the other groups. These curves can then be viewed in the context

of the standard deviations observed in this study for each treatment group, in each year of interest (Appendix B).

Formal power analyses were conducted for only one response variable: total avian abundance. Relative to total abundance, analyses of avian richness have much greater power because this variable had much lower variability. Conversely, analyses of individual species abundances were much more variable than total abundance; therefore it was a given that these tests had sufficient power to detect only differences of a large magnitude. An informal estimate of detectable effect size was also carried out for MRPP tests. This was done by iteratively re-running MRPP analyses ten times, after randomly selecting 10% and 20% of all individuals on sites that received the 10-30 and 20-10 treatments, respectively, and then recalculating species abundance matrices with these individuals removed.

RESULTS

Avian Richness and Abundance Among Years

Strong year-to-year fluctuations in both species richness and abundance were evident from 1995-1998 (Fig. 1.2), but these fluctuations were observed on all sites and could not be attributed to harvest treatments. Mean species richness (\pm standard error) per 10 ha site ranged from 20.8 (\pm 0.4) in 1995 to 25.3 (\pm 0.8) in 1997, with 95% confidence intervals overlapping from 1996-1998. An ANOVA model for species richness with year, treatment, and year*treatment interaction terms was significant ($p=0.025$), and had a highly significant year-term ($p=0.0006$), but treatment and interaction terms were not significant (Appendix A; Table A.7). Pooling across species and sites, mean abundance (\pm standard error) of territories per 10 ha decreased from 50.8 (\pm 1.4) in 1995 to

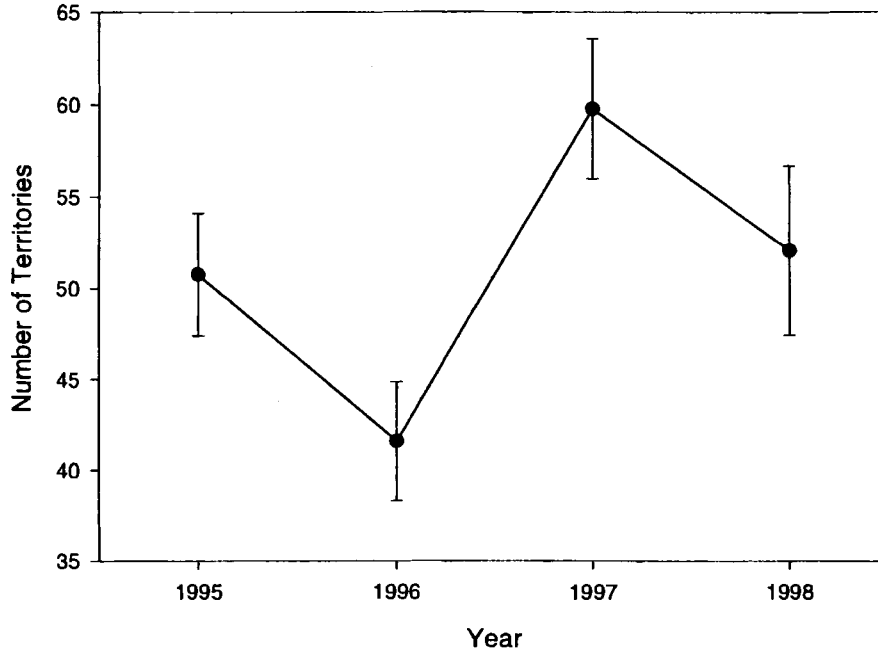


Figure 1.2. Mean avian abundance (per 10 ha) for nine research areas in the PEF. Error bars represent 95% confidence intervals.

41.6 (± 1.4) in 1996, then increased by 44% to 59.8 (± 1.6) in 1997, with no overlap in 95% confidence intervals around any of these three means (Fig. 1.2). In 1997 and 1998, 95% confidence intervals overlapped slightly. An ANOVA model for avian abundance with treatment, year, and treatment*year interaction terms was not significant ($p=0.497$), though a subsequent one-way test of year-effects was marginally significant ($p=0.06$; see Appendix A; Table A.7.). These strong year-effects are interesting, and are explored further in Chapter 3. Because year-effects from 1995-1998 were significant for both avian richness and abundance, subsequent analyses were conducted separately by year.

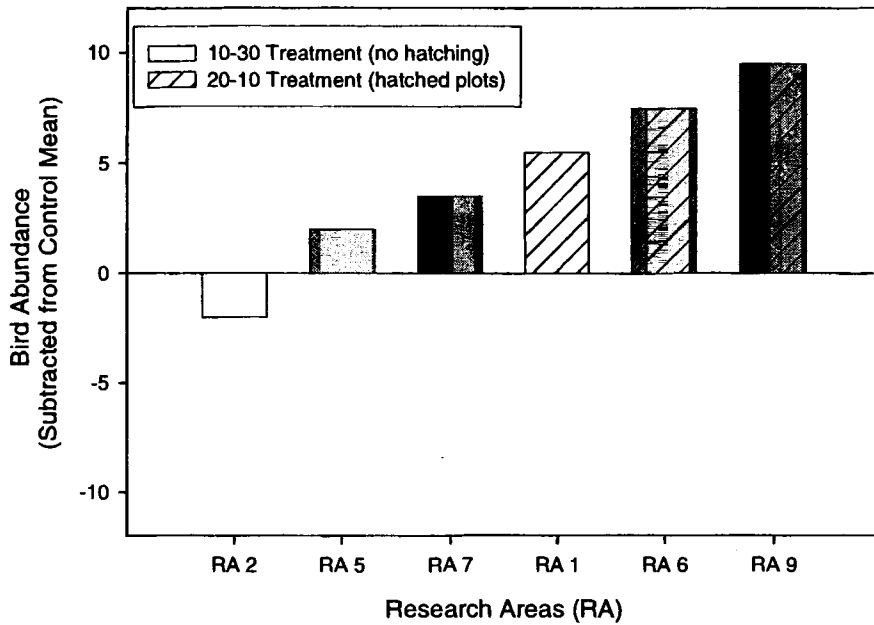
The controlled comparison of pooled abundance showed that changes in abundance from pre-treatment to the first summer post-treatment were significantly greater on the six treated sites than on two control sites (t-value 3.47, 5 d.f., $p = 0.02$).

On average, the annual changes in treated sites resulted in 6.75 more birds than on controls. This represents a 13% increase over the mean (pooling all sites and years) abundance of 51 birds per 10 ha site. However, changes in abundances on treated sites were high relative to controls only for the first summer after treatment; this pattern did not hold up in the second or third summer after harvest.

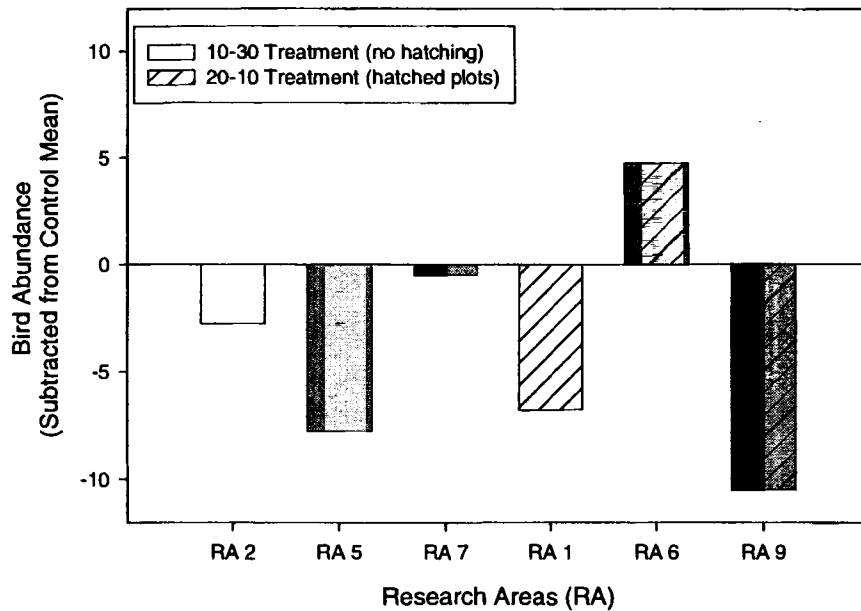
For example, from 1995 to 1996 all nine sites showed decreases in avian abundance, but the two treated sites (i.e., RA1 and RA2) decreased less than did controls. However, from 1996 to 1997 these same two sites increased more slowly than did controls (mean increase in total abundance = 11.75 for treated sites versus 19 for controls); from 1997 to 1998 abundances decreased similarly on treated and control sites (-7.75 versus -8.75, respectively). Similarly, the second block of sites (i.e., RA5 and RA6) showed higher increases in abundance than did controls from 1996 to 1997 (mean increase of 23.5 versus 19 in controls) but then decreased twice as much as controls from 1997 to 1998 (mean decrease of -17.5 versus -8.75 in controls). Nevertheless, before any sites were treated in 1995 the mean abundance for the two control sites was significantly higher than was the mean for six sites that were slated for eventual harvest, whereas in 1998 controls generally had lower abundances than did treated sites (Fig. 1.3), though the difference in 1998 was not significant.

Avian Richness and Abundance Within Years

When sites were grouped by their eventual treatment, bird abundance in 1995 (i.e., before any treatments had been applied) differed significantly among the three treatment groups ($p=0.02$), with higher abundance in the control ($n = 2$ sites) and 10-30 group ($n = 3$) than in the 20-10 group ($n = 3$; Fig. 1.4). In 1997, if sites were



A.



B.

Figure 1.3. Difference in abundance between two control sites and six treated research sites. Measured as the control mean minus the abundance on each site. Data are from 1995 (Fig. 1.3A) before treatments had occurred, and from the summer after each site had been treated (Fig. 1.3B). T-tests of the null hypothesis of zero difference were significant in 1995 ($t = 2.58$, 5 d.f., $p = 0.05$), but not for post-treatment ($t = -1.73$, 5 d.f., $p = 0.14$).

grouped by the actual treatments received, there was a marginally significant difference among groups ($p=0.107$). Duncan's Multiple Comparison test indicated that the 10-30 group ($n = 2$) had significantly more territories than the 20-10 group ($n = 2$), with the control group ($n = 5$) intermediate between (and not significantly different from) the two harvest treatments. However, there were no differences among these treatment groups (all with $n = 3$ sites) in 1998, after all sites had been treated (Fig. 1.4).

Power analyses indicated that at an alpha level of 0.10 there was very low power to detect 10% differences among treatment groups, based on data from 1997 (power ≈ 0.45) and 1998 (power ≈ 0.20), using average within-group standard deviation. Power to detect 20% differences among groups was much higher for both 1997 (power ≈ 0.93) and 1998 (power ≈ 0.60). For detecting intergroup differences of 30%, power was very high for 1997 even at an alpha of 0.05 (power ≈ 1.0); it was also high for 1998 data (power ≈ 0.88 at alpha = 0.10). Therefore, the lack of significant treatment effects, viewed in the context of power analyses, indicates that treatments probably did not reduce total avian abundance by 20-30% for any treatment.

Mean species richness for sites grouped by treatment were similar among years, and usually differed by <1 species per 10 ha (Table 1.3). One-way ANOVA's with species richness as the dependent variable and treatment group as the main-effect were not significant in any year (Table 1.3), nor were multiple comparison tests.

Individual Species Abundances

Densities of individual species observed on each of the nine sites from 1995-1998 (Appendix A; Tables A.1-A.4) were averaged over all years (Appendix A; Table A.5) and by treatment group within each year (Appendix A; Table A.6). Kruskal-

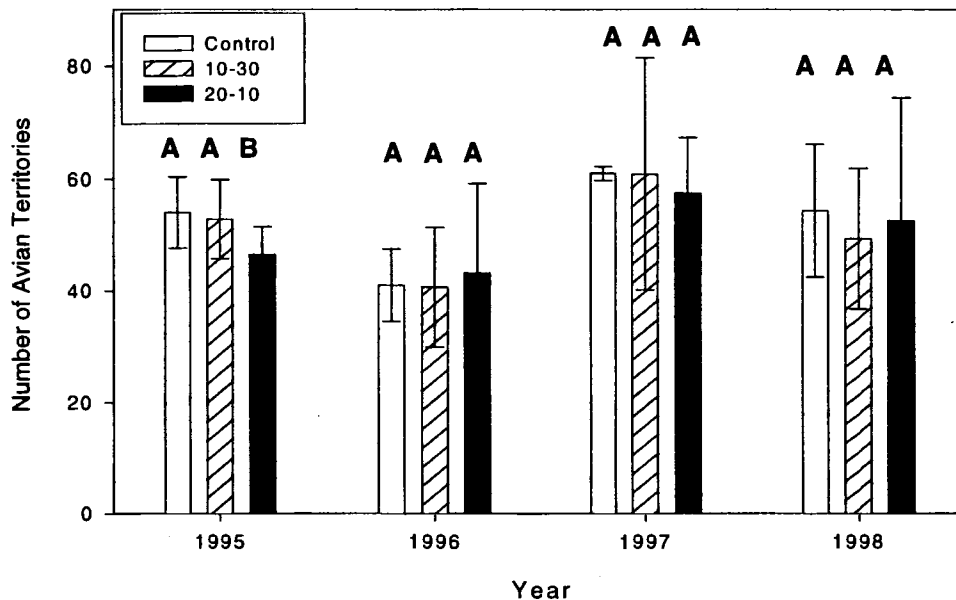


Figure 1.4. Mean avian abundance (per 10 ha) by treatment group. Sites grouped by the treatment they will receive, regardless of actual treatment status in a given year. Sample size is three sites per group, except for controls in 1995 (n=2). Error bars represent 95% confidence intervals. In each year, bars with the same letter do not differ significantly according to Duncan Comparison Tests.

Wallis tests for treatment effects on each species and year (Appendix A; Table A.6) showed very few species for which densities were significantly different, at an alpha level of 0.10. No species showed treatment effects in >1 year. The two species for which Kruskal-Wallis results were most significant ($p < 0.05$) were the Blue Jay (*Cyanocitta cristata*) and Brown-headed Cowbird (*Molothrus ater*). In 1997, Blue Jays were twice as abundant ($p=0.02$) on two stands with the 10-30 treatment compared to other groups. However, Blue Jay mean densities were generally low and similar across groups and years (Appendix A; Table A.6), so the statistical significance of this result is of little ecological interest. Likewise, Brown-headed Cowbirds were significantly ($p=0.05$) more abundant in the control group in 1997, but were rare overall, occurring on only one site in

Table 1.3. Mean avian species richness for nine research areas in the PEF. Sites grouped by the treatment (Treat.) they will eventually receive, regardless of treatment status in a given year. For 1997, data are presented with treatment groups “fixed,” and alternately based on the treatments actually applied (i.e., “actual”) in that year. Means with the same letter are not different, according to Duncan’s Multiple Comparison Test. P-values presented for ANOVA analyses within each year. Abbreviations are: number of stands in group (N), standard deviation (SD), standard error (SE), and confidence interval (CI).

Year	Treat.	N	Mean	SD	SE	Lower 95% CI	Upper 95% CI
1995	Control	2	21.50 ^A	0.707	0.500	15.147	27.853
	10% cut	3	20.67 ^A	1.527	0.882	16.872	24.461
	20% cut	3	20.33 ^A	0.577	0.333	18.899	21.768
ANOVA:			p=0.53				
1996	Control	3	21.00 ^A	1.732	1.000	16.697	25.303
	10% cut	3	21.33 ^A	4.042	2.333	11.294	31.373
	20% cut	3	21.67 ^A	4.042	2.333	11.627	31.706
ANOVA:			p=0.97				
1997 (Fixed)	Control	3	25.67 ^A	1.155	0.667	22.798	28.535
	10% cut	3	25.33 ^A	4.042	2.333	15.294	35.373
	20% cut	3	25.00 ^A	2.646	1.527	18.428	31.572
ANOVA:			p=0.96				
1997 (Actual)	Control	5	25.40 ^A	1.673	0.748	23.322	27.478
	10% cut	2	26.50 ^A	4.950	3.500	-17.972	70.972
	20% cut	2	24.00 ^A	2.828	2.000	-1.412	49.412
ANOVA:			p=0.67				
1998	Control	3	25.00 ^A	2.646	1.527	18.428	31.572
	10% cut	3	24.00 ^A	1.732	1.000	19.697	28.303
	20% cut	3	24.33 ^A	1.155	0.667	21.465	27.202
ANOVA:			p=0.82				

1995, no sites in 1996, four sites in 1997 (three were controls), and at low densities across all treatment groups in 1998 (see Appendix A; Tables A.4 and A.6).

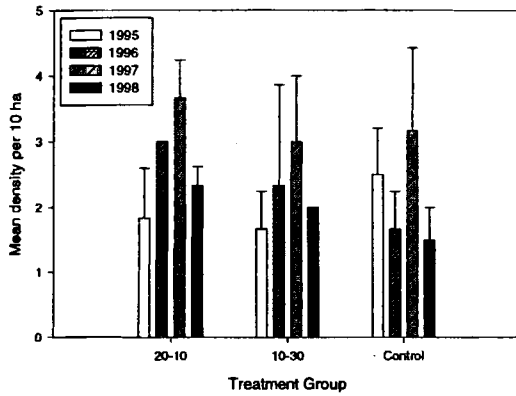
Two other species differed significantly among groups in 1998: the American Robin (*Turdus americanus*) and Red-breasted Nuthatch (*Sitta canadensis*). The American Robin was generally rare, and its significant in 1998 is due to its absence on all groups but one (Appendix A; Table A.6). That Red-breasted Nuthatch were more abundant on the 20-10 treatments in 1998 is especially interesting when you consider that its abundance was lowest on this set of sites in 1995. In 1995, Red-breasted Nuthatch

was most abundant on control sites, but it decreased on controls over the next four years while increasing on harvested stands (Fig. 1.5A); this species is discussed further below. Although only three species differed significantly among treatments in 1998, four other species showed patterns that might indicate a preference for harvested or control sites, though differences were not significant: Blackburnian Warbler (*Dendroica fusca*), Winter Wren (*Troglodytes troglodytes*), and Eastern Wood-Pewee (*Contopus virens*) increased on sites with the 20-10 treatment while decreasing on controls, from 1995-1998 (Fig. 1.5). On sites with the 10-30 treatment, these species' abundances were intermediate between the 20-10 group and controls. A fourth species, Black-throated Blue Warbler (*Dendroica caerulescens*), seemed to favor untreated sites (Fig. 1.5E).

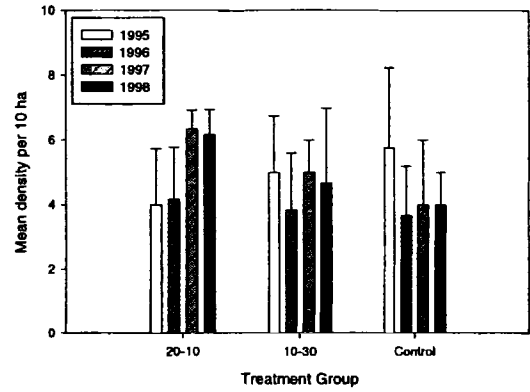
As mentioned in the Methods, power to detect treatment effects on individual species was quite low. Thus, the tests' lack of significance indicates only that differences among treatment groups were not of a large magnitude, e.g. 50%. An informal examination of statistical power for analyses of individual species abundances was done by artificially reducing abundance values by 50% on treated versus control sites and testing for treatment effects. After the artificial reductions in abundance, treatment effects were highly significant for almost all species.

Bird Community Ordination

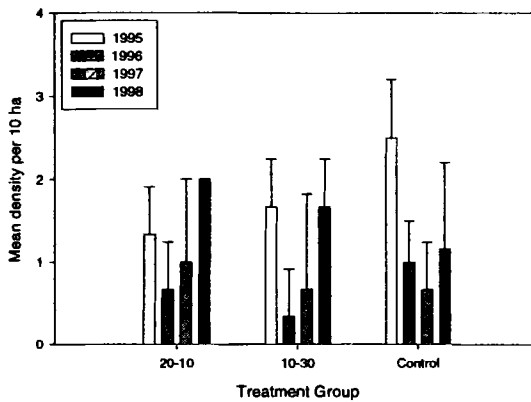
Mantel tests on dissimilarity matrices for 1995 and 1998 showed a significant positive association (Standardized Mantel $r = 0.521$; $p = 0.006$), indicating that differences in bird community composition were similar before and after harvesting occurred. This result can be viewed as a rejection of the null hypothesis that research



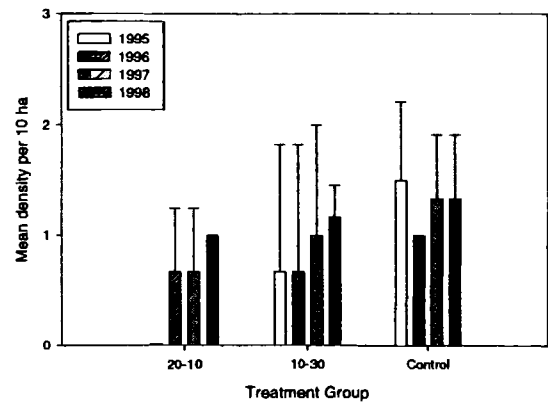
A) Red-breasted Nuthatch



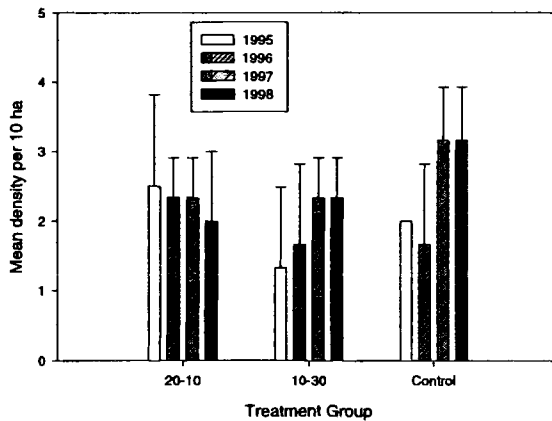
B) Blackburnian Warbler



C) Winter Wren



D) Eastern Wood-Pewee



E) Black-throated Blue Warbler

Figure 1.5. Mean density of species with apparent treatment preference. Preferences are for treatment 20-10 (A-D) or control (E). Each treatment group with n=3 sites (10 ha) except for controls in 1995 (n=2). Error bars represent one standard deviation.

areas with the same treatments were more similar to each other than they were to sites with other treatments (including controls).

For the eight sites sampled in both 1995 and 1998, there was no evidence that site-to-site differences were related to treatment groups, as Mantel tests for group differences (using a design matrix) were not significant for 1995 (Standardized Mantel $r = -0.107$; $p = 0.226$) or 1998 (Standardized Mantel $r = -0.213$; $p = 0.119$). When sites in the 20-10 and 10-30 treatment groups were combined and compared to controls, results similarly indicated no differences attributable to treatment, either before (1995: Standardized Mantel $r = -0.153$; $p = 0.348$) or after harvesting (1998: Standardized Mantel $r = -0.193$; $p = 0.221$). A set of Mantel tests for group effects that included all nine sites in 1998 was similar to the tests above for eight sites. Whether all three treatment groups were considered (Standardized Mantel $r = -0.039$; $p = 0.332$), or when sites in two harvest treatment groups were pooled and compared to controls (Standardized Mantel $r = 0.200$; $p = 0.200$), there was no evidence that site-by-site dissimilarity matrices were related to treatment groups.

The Multi-response Permutation Procedures (MRPP) results for 1998 indicated no treatment effects, whether all three groups were considered ($R = 0.0003$; $p = 0.463$) or only two groups (harvested vs. control) were used ($R = 0.0051$; $p = 0.363$). Though group differences were not significant, there was a trend towards greater heterogeneity among control sites, and more similarity among harvested sites (average percent dissimilarity for control group = 0.283; 10-30 group = 0.252; 20-10 group = 0.229). Iterative MRPP tests with 10% and 20% of individuals artificially removed from the 10-30 and 20-10 treatment groups, respectively, indicated that power to detect differences of

this magnitude among three treatment groups was low. Comparing among all three treatment groups, none of ten MRPP iterations (with artificial reductions) were significant at $\alpha = 0.10$. Tests with only two groups, harvested sites versus controls, were more significant: three of 10 iterations had p-values ≤ 0.10 , and the mean p-value was 0.163. Therefore, MRPP tests probably would have detected only effects that were equivalent to 20-30% reductions in abundance between treated versus control sites.

Qualitative Changes in Avifauna

For all eight sites examined, the list of numerically dominant species (i.e., those comprising >50% of territories on a site) was very similar in 1995 and 1998 (see Appendix A for relative abundance of all species, sites, and years). For five of the eight sites examined, five of six species (83.33%) that were most abundant in 1995 were also most abundant in 1998; one control site shared four of six dominant species, whereas two other sites had the same six most abundant species in 1995 and 1998. Grouped by treatment, the percentage of the six most abundant species that were the same in 1995 and 1998 were 83.3% (20-10 treatment), 88.9% (10-20 treatment) and 83.3% (controls). These data reflect the fact that the species composition overall was very similar among years both at treated and control sites. This is true whether one examines numerically dominant species or less common ones (Appendix A).

Virtually no “pioneer species” (those preferring disturbed habitats) were found on treated sites in the years after they were harvested. The only evidence of use of treated sites by pioneer species was a single White-throated Sparrow (*Zonotrichia albicollis*) territory that was observed within one large gap on Research Area 1 (in one year) and Research Area 6 (two years in a row) after they were harvested. No other species known

to prefer disturbed habitats (Lent and Capen 1995) was observed during this study. On one brief visit (a 10 minute point count) to each harvest gap in 2002 no new pioneer species were observed. A single White-throated Sparrow was observed on three of the harvested sites in 2002, but only at one harvest gap per site.

DISCUSSION

This study provided little evidence that 10% or 20% timber removals in small patches with overstory retention caused major changes to breeding bird communities on 10 ha sites. Differences among sites and yearly fluctuations in bird densities generally were much stronger than those attributable to harvest treatments examined 1-3 years after cutting. Within any year, when harvested sites were compared to controls, or pre- and post-treatment data were compared for individual sites, treatment effects were not apparent in terms of species richness, total abundance, or the abundance of individual species. In 1998, after all sites were treated, avian abundance and species composition were very similar to what was seen in 1995, before any sites were treated.

Bird abundance did increase more and/or decrease less on treated sites than on controls in the first summer after treatment, but this tendency was not seen in the second or third summer after treatment. Notably, there were significantly more birds on control sites before any treatments were implemented (i.e., in 1995), whereas there generally were fewer birds on control sites after all treatments were implemented (Fig. 1.3). This suggests that avian abundances may have temporarily increased approximately 10% in response to the treatment. The relatively high abundance on treated sites was seen despite the fact that no new species occupied harvested stands, avian species richness was

not higher in harvested stands, nor was the abundance of any single species greater on treated versus control sites.

Perhaps the clearest finding of this study was that the harvest treatments did not effect ecologically important changes in the species composition of birds using the treated sites, relative to birds on controls. Dissimilarities in bird communities among sites in 1995 were significantly related to the relationship among stands in 1998, whereas dissimilarity matrices were unrelated to treatment groups in either year. With the possible exception of four species that showed (mostly non-significant) tendencies for higher or lower abundance in treated sites, this study demonstrates that this type of disturbance was not of sufficient intensity to effect noticeable changes in bird communities of mixed-wood forests. This is important information, because researchers have a poor idea of what levels of timber harvest intensity affect most species, and some forest managers would like to use harvest systems that minimize ecological impacts.

Few studies have investigated relatively low-intensity timber harvests, and those that have generally examined cutting intensities that are greater—and on larger spatial scales—than FERP harvest treatments. Three studies in Vermont (Lent and Capen 1995, Germaine et al. 1997, Buford and Capen 1999) evaluated bird community effects from 10-36% timber removals, but these studies focused on small clearcuts that were actually much larger than the harvest gaps I studied. Other research looked at relatively low harvest rates such as 10% (Buford and Capen 1999) or 18-35% (Welsh and Healy 1993), but evaluated effects on bird communities over large spatial scales, e.g., 500 ha (Buford and Capen 1999) or 64 ha (Welsh and Healy 1993), and sampled birds only in unharvested portions of their study areas.

The different spatial scale of cuts in earlier studies is important because patch clearcuts often create habitat patches used by “pioneer” bird species that prefer young forests, but not used by mature-forest birds. Early-forest species such as Chestnut-sided Warbler (*Dendroica pensylvanica*), White-throated Sparrow, and Common Yellowthroat (*Geothlypis trichas*) reached high densities in patch cuts studied by Lent and Capen (1995), Germaine et al. (1997), and Derleth et al. (1989). In contrast, young-forest bird species were completely absent from the FERP harvest gaps I studied, with the exception of two White-throated Sparrow territories. This is probably due to the fact that the smallest known songbird territories are approximately 0.07 ha (Bird 1999), but more typically are >1 ha (Bird 1999, Smith and Shugart 1987), and many species require habitat patches much larger than their actual territory if they are to breed successfully (Lynch and Whigham 1984, Opdam et al. 1985). Gap sizes in the PEF research areas averaged 0.12 ha (± 0.01 SE) and 0.07 ha (± 0.01 SE) for the 20-10 and 10-30 treatments (Table 1.2), and the largest gaps available were only 0.21 ha and 0.13 ha, respectively.

It may also be important that patch cuts studied by others (Lent and Capen 1995, Germaine et al. 1997, Buford and Capen 1999) had little or no overstory retention within gaps, whereas FERP harvest gaps always contained retention trees, including some large, canopy-trees. To my knowledge, there have been no studies that have looked at early-forest bird abundance or habitat use as a function of the amount of vegetation retained within cut gaps, and/or clearcut patch size, from very small (e.g., 0.05 ha) to territory-sized (e.g., 1-5 ha) to stand-sized (e.g., 10-100 ha), though Rudnicky and Hunter (1993) examined clearcuts from 2-107 ha, and found that some species did prefer larger cuts.

I monitored bird community changes on harvested stands only 1-3 years after harvests (Table 1.1), which may have been too soon to see some changes that may have occurred. For example, high site-fidelity of songbirds could result in territorial birds returning and remaining on treated sites each summer, as long as they are alive. If this occurs, the most marked changes in density and community composition may occur four or five years after treatment, after most resident birds have died. In Chapter 2, I explore how treatments affected site-fidelity of two species, within 1-3 years after treatment.

Another reason that bird community changes may have occurred more than 1-3 years after treatment would be if it took more than three years for the disturbed habitats to change sufficiently (in terms of vegetation regeneration) to attract new or different species to the disturbed patches, or increase their densities. Vegetation 1-3 m high had regenerated in some harvest gaps by the third growing season after harvest, but there was relatively little vegetative response in the summer immediately after harvest, especially within small and/or heavily-shaded harvest gaps. Other studies have shown that bird communities change dramatically 1-2 years after harvest (Derleth et al. 1989, Lent and Capen 1995, Norton and Hannon 1997, Gram et al. 2001, Tittler et al. 2001, and references therein). However, the rate of change in vegetation after harvest is probably directly related to harvest intensity and patch size, all else being equal. Therefore, low-intensity, small-scale harvests such as I studied may have a slower vegetative response, which might increase response time in the bird community.

It is not known whether any FERP harvest gaps were occupied by pioneer bird species since 1998. Based on a single visit to each harvest gap in 2002, there was no

evidence of any new pioneer species using gaps, nor was any one species obviously abundant in or around gaps, compared to earlier surveys.

Having only three (10 ha each) replicates per treatment resulted in my having limited statistical power to detect differences, especially for individual species. For example, if mean densities (and variance) were the same for Blackburnian Warbler, but sample sizes were doubled from three to six sites per group, a Kruskal-Wallis test for treatment effects would have been significant ($p=0.03$). Verner and Milne (1990) argued that observer and analyst variability in spot map data limits the power to detect differences in densities of individual species unless there are many (e.g., 30) samples per group. According to Verner and Milne (1990), three or four (for one- or two-tailed test) samples per treatment are needed even to detect 50% differences among groups, with an alpha level of 0.10 and power of 0.80. However, variability was much less and power much greater when the entire bird community was the variable of interest. Others (O'Connor 1981) have indicated that careful methodology reduces spotmapping variability to low levels. I used spotmapping and analytic methods specifically intended to minimize variability among sites and treatments, and thus maximize statistical power.

Despite having few replicates, the complete randomized block design of the FERP experiment is more rigorous than the vast majority of studies (but see Gram et al. 2001) of how harvest treatments affect birds (Thompson et al. 2000). Still, given the low power of my Kruskal-Wallis tests, there was a distinct possibility of making Type II errors, i.e., failing to reject a null hypothesis (of no treatment effect) that was false. This must be considered in deciding whether it is biologically significant that five species showed

apparent preferences for either harvested or control sites. It is clear, however, that most species did not differ in density among the treatment groups.

I examined studies from across the northeastern US to see if there was similar evidence of an apparent preference for harvested areas for Red-breasted Nuthatch, Blackburnian Warbler, Eastern Wood-Pewee, and Winter Wren, or for unharvested areas for Black-throated Blue Warbler. Overall, most studies showed that abundances of all five species were similar in harvested and unharvested areas (e.g., Webb et al. 1977, Welsh and Healy 1993). Some studies indicated a preference for harvested areas for Blackburnian Warbler and Red-breasted Nuthatch (Buford and Capen 1999), Eastern Wood-Pewee (Derleth et al. 1989), and even Black-throated Blue Warbler (Derleth et al. 1989). Other studies indicated a preference for unharvested areas for Blackburnian Warbler (Webb et al. 1977, Derleth et al. 1989), Red-breasted Nuthatch (Webb et al. 1977), and Black-throated Blue Warbler (Buford and Capen 1999).

CONCLUSIONS

Experimental removals of 0%, 10%, and 20% of mature trees on nine 10 ha mixed-wood sites in Central Maine, in small (<0.07-0.12) gaps with residual trees, caused few significant changes in bird communities within sites before versus after harvesting, or between harvested and unharvested sites. Most (>80%) of the same species were numerically dominant on all sites before and after harvesting, and virtually no pioneer species invaded the treated sites. Annual changes in bird abundance were strong on all sites; these differences among years were much greater than differences among sites within any year. Measured as a function of year-to-year changes in abundance, birds were relatively more abundant on treated sites one year after harvesting

than on controls, but this difference did not persist two or three years after treatment. Apparently, removals of >20% of timber or harvests done on a larger scale are necessary to cause detectable increases or decreases in individual bird species, or invasion by species preferring young versus mature forests. Based on power analyses, a study design like mine had a high probability of detecting differences in abundance of approximately 30% in any year, and had much higher power to detect differences in abundance in some years, and in species richness in all years.

LITERATURE CITED

- Annand, E.M., and F.R. Thompson, III. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159-171.
- Bird, D.M. 1999. *The bird almanac*. Key Porter Books Limited, Toronto. 460 pp.
- Blake, J.G., J.M. Hanowski, G.J. Niemi, and P.T. Collins. 1994. Annual variation in bird populations of mixed conifer-northern hardwood forests. *Condor* 96:381-399.
- Buford, E.W., and D.E. Capen. 1999. Abundance and productivity of forest songbirds in a managed, unfragmented landscape in Vermont. *Journal of Wildlife Management* 63:180-188.
- Derleth, E.L., D.G. McAuley, and T.J. Dwyer. 1989. Avian community response to small-scale habitat disturbance in Maine. *Canadian Journal of Zoology* 67:385-390.
- Germaine, S. S., S.H. Vessey, and D.E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708-718,
- Gram, W.K., V.L. Sork, R.J. Marquis, R.B. Renken, R.L. Clawson, J. Faaborg, D.K. Fantz, J. Le Corff, J. Lill, and P.A. Porneluzi. 2001. Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest. *Ecological Applications* 11:1667-1679.
- Hagan, J.M., P.S. McKinley, A.L. Meehan, and S.L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* 61:718-735.
- Holmes, R.T., and T.W. Sherry. 1988. Assessing population trends of New Hampshire forest birds: local vs. regional patterns. *Auk* 105:756-768.
- Hunter, M.L., Jr. 1990. *Wildlife, forests, and forestry: principles of managing for biological diversity*. Prentice-Hall, Inc. Englewood Cliffs, NJ. 370 pp.
- I.B.C.C.(International Bird Census Committee) 1970. An international standard for a mapping method in bird census work recommended by the I.B.C.C. *Aud. Field Notes* 24:722-736.
- Lent, R.L., and D.E. Capen. 1995. Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest. *Ecography* 18:97-108.
- Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. *Ecology* 58:139-148.

- Lynch, J.F., and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28:287-324.
- McCune, B., and M.J. Mefford. 1997. *Multivariate analysis of ecological data*. Version 3.09. MjM Software, Gleneden Beach, OR.
- Norton, M.R., and S.J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research* 27:44-53.
- O'Connor, R.J. 1981. The influence of observer and analyst efficiency in mapping method censuses. *Studies in Avian Biology* 6:372-376.
- Opdam, P., G. Rijdsijk, and F. Hustings. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* 34:333-352.
- Rudnický, T., and M.L. Hunter, Jr. 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. *Ecological Applications* 3:357-366.
- Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pp. 17-33 in S. T. A. Pickett, and P.S. White. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL. 472 pp.
- Sallabanks, R., and J.M. Marzluff. 2000. Forest management and bird populations: an introduction. *Wildlife Society Bulletin* 28:1086-1087.
- Sallabanks, R., E.B. Arnett, and J.M. Marzluff. 2000. An evaluation of research on the effects of timber harvest on bird populations. *Wildlife Society Bulletin* 28:1144-1155.
- SAS Institute. 1990. *SAS/STAT user's guide, version 6*. SAS Institute, Cary, NC.
- Smith, T.M., and H.H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* 68:695-704.
- Sokal, R.R., and F.J. Rohlf. 2000. *Biometry*. W.H. Freeman and Company, New York. 887 pp.
- Thompson, F.R. III, J. D. Brawn, S. Robinson, J. Faaborg, and R.L. Clawson. Approaches to investigate effects of forest management on birds in eastern deciduous forests: How reliable is our knowledge? *Wildlife Society Bulletin* 28:1111-1122.
- Tittler, R., and S.J. Hannon. 2000. Nest predation in and adjacent to cutblocks with variable tree retention. *Forest Ecology and Management* 136:147-157.

- Verner, J., and K.A. Milne. 1990. Analyst and observer variability in density estimates from spot mapping. *Condor* 92:313-325.
- Webb, W.L., D.F. Behrend, and B. Saisorn. 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildlife Monographs* No. 55. 35 pp.
- Welsh, C.J.E., and W.M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. *Wildlife Society Bulletin* 21:143-154.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th Edition. Prentice Hall, NJ. 929 pp.

Chapter 2
**EFFECTS OF EXPERIMENTAL HABITAT DISTURBANCES ON BREEDING
SITE-FIDELITY OF ADULT HERMIT THRUSHES (*Catharus guttatus*) AND
OVENBIRDS (*Seiurus aurocapillus*)**

INTRODUCTION

In most passerine bird species, adults have a high probability of returning to the same breeding area each year (Greenwood and Harvey 1982). This site-fidelity usually is stronger for males versus females (Darley et al. 1977), and older versus younger birds (Greenwood and Harvey 1977). Given the fitness costs associated with breeding dispersal (Dieckmann et al. 1999, Danchin and Cam 2002), it is not surprising that site-fidelity is directly related to breeding success. Successful breeders show stronger site-fidelity than unsuccessful birds (Greenwood and Harvey 1982, Beletsky and Orians 1987, Slagsvold and Lifjeld 1989) and site-faithful birds are more successful than birds that disperse to a new area (Greenwood and Harvey 1982, but see Beletsky and Orians 1987). Therefore, factors that increase avian breeding dispersal likely reduce productivity.

Given the links between productivity, fitness, and breeding dispersal, it is important to understand how natural and anthropogenic habitat disturbances affect a species' site-fidelity. It seems reasonable to assume that severe disturbances such as intense fires or clearcuts—especially those covering large areas—render breeding habitat unsuitable for many species, and effect sudden and high rates of breeding dispersal. It is not clear how important less-severe disturbances may be because most studies of site-fidelity have been in areas where habitat disturbances were absent or unmentioned.

Across various North American forests, natural disturbances cause mortality of canopy trees at a rate of 0.5-2% per year (Runkle 1985, Seymour et al. 2002). Another

important disturbance in North American forests is timber harvesting, which varies in intensity from low-intensity “partial-harvests” to complete removals of mature trees (e.g., clearcuts). Though application rates of various silvicultural methods vary both in space and time, forest practices affect millions of hectares of North American forests each year. Considering natural and anthropogenic disturbances, habitat for millions of resident and migratory songbirds is disturbed annually, yet we have little understanding of how these disturbances affect most aspects of avian life history, including breeding dispersal.

If a habitat disturbance does not reduce breeding habitat quality, birds should return to disturbed and undisturbed sites at similar rates (O’Connor 1985). If avian habitat quality is reduced by a disturbance of a given intensity and scale, several responses are possible. Birds that bred on undisturbed sites in year “t” might be less likely to return to their site if it has been disturbed before the breeding season in year “t+1.” Alternately, birds could return to disturbed and undisturbed sites at similar rates in year “t+1” but choose not to return to disturbed sites in year “t+2” or any subsequent year. Likewise, a bird on a disturbed site in year “t” may be less likely to return to the site in year “t+1” compared to a bird on a site that is undisturbed in year “t” and “t+1.”

In this study I examined how site-fidelity of two common forest birds, Hermit Thrushes (*Catharus guttatus*) and Ovenbirds (*Seiurus aurocapillus*), were affected by experimental disturbances that were within the range of intensity and of a spatial scale typical of natural disturbances in the region. Site-fidelity and breeding dispersal of adult birds were examined using three complementary approaches. First, I compared between treated and control sites the proportion of birds captured on a site in year “t” that returned to that site in year “t+1” and year “t+2.” Return rates to a site are partly a function of the

size of sites examined (Barrowclough 1978), as return likelihood decreases as the site approaches the size of a bird's territory. Therefore, it is also useful to measure site-fidelity as a continuous variable using the distance between a bird's territories in two successive years. This distance, a measure of "breeding dispersal" (Greenwood 1980), has been referred to as a bird's "site-attachment" (Holmes and Sherry 1992). To put site-fidelity dynamics into a broader life-history perspective, and to use a large sample of marked birds, I also examined survival and recapture rates for the two focal species. Because observed (i.e., "apparent") return rates are a product of both these parameters, they must be considered separately to avoid bias (Clobert and Lebreton 1991).

Objectives

The primary objective of this research was to determine whether the breeding dispersal of Hermit Thrush or Ovenbird was affected by experimental disturbance treatments where 10-20% of mature trees on 10-ha areas were removed in a series of small (0.07-0.12 ha) gaps. A second objective was to use capture-mark-recapture methods to estimate annual survival and recapture rates for both species.

Hypotheses Tested

The response of these two species (examined separately) to treatment were measured in two ways, as indicated by the following null hypotheses:

Null hypothesis 1: birds captured on a site in year "t" have the same probability of returning to that site in year "t+1" whether the site is a control in both years, a control in year "t" that is treated before year "t+1," or is treated before year "t."

Null hypothesis 2: the distance between territories of successive years (i.e., site-attachment) does not differ for birds on treated versus control sites.

METHODS

This study was part of the Forest Ecosystem Research Program (FERP). See Chapter 1 for a description of the study area (Penobscot Experimental Forest) and experimental design. It should be reiterated in this chapter that each research area (i.e., each 10 ha site) was embedded within a continuous landscape of mature forest; with the exception of one or two dirt roads and one or two houses, most sites were >5 km from any openings in the forest (excepting minor natural disturbances). Another notable aspect of this chapter is that, in contrast to Chapter 1, all analyses in Chapter 2 combine the 20-10 and 10-30 harvest treatments and do not consider them as two separate treatments, because relatively few birds were captured on treated sites of either type. Therefore, all analyses of site-fidelity examine differences between treated and control sites without distinguishing between the two types of harvest treatments.

Avian Sampling

Territorial male Ovenbirds and Hermit Thrushes were actively captured in mistnets, through taped song and call playbacks and a wooden Ovenbird replica placed near the net center. Both male and female birds also were captured by 10-12 mist-nets placed systematically around each 10 ha research area (or "site"). Unless it was raining or the weather was unusually cold or windy, nets were open from approximately 0400 EST until 1000 EST each day.

Each site was sampled about once per week from the last week of May until the first week of August, 1995-1998. Nets were generally moved 50-100m to another location within a site after two or three days of sampling in the same location. On average, each site was sampled nine times per summer. However, sampling was uneven

in 1995, when only seven of nine sites (all but RA7 and RA8) were sampled. For these seven sites sampling effort varied from 4-21 mornings of sampling per site, with an average (\pm standard deviation) of 11.7 (\pm 6.3) days of sampling per site. From 1996-1998 effort was very similar across all nine sites, with means (\pm standard deviation) of 7.7 (\pm 0.50), 9.1 (\pm 0.33), and 8.3 (\pm 0.50) days of sampling per site per summer in 1996-1998, respectively. Over four years, sampling effort averaged nearly 4,000 net-hours per year, with an average of 250 birds (of all species) captured per year (Table 2.1).

To better understand whether 10-ha sites were small relative to typical breeding dispersal distances, and to determine how many birds may have escaped recapture by dispersing outside of sites, I used tape-playbacks and mistnets to capture males in a 100-m buffer around each site in 1997 and 1998. Beginning in early July, two observers would spend one or two consecutive days sampling around the perimeter of each research area. At 150-m intervals along the perimeter, observers would walk 100 m in a direction perpendicular to the site boundary and set up one mistnet and Ovenbird decoy. To attract territorial males, taped songs and calls were played for ten minutes, or longer if birds were observed near the net. In 1997 and 1998 (combined) a total of 17 male and four female Hermit Thrushes and 11 male and three female Ovenbirds (plus one Ovenbird of unknown sex) were captured in buffers outside of 10 ha sites. Three of the 17 male Hermit Thrushes captured in 1997 were recaptured in the same buffer in 1998, as was one male Ovenbird. The sample of birds captured in buffers outside sites were considered as part of the total number of captures (see Table 2.1), but were excluded from all other totals and analyses presented below.

Table 2.1. Mistnet effort and number of captures per year. Net hours equals number of nets times number of hours each net open. Total bird captures represents all species pooled, and includes all research areas.

	YEAR				
	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1998</u>	<u>Total</u>
Net hours	4,893	3,248	3,791	3,973	15,905
Total bird captures	254	227	243	278	1,002
Hermit Thrush (new) captures:	38	28	55	43	164
Recaptures:	0	17	17	23	57*
Total Hermit Thrush captures:	38	45	72	66	221*
Ovenbird (new) captures:	25	39	43	19	126
Recaptures:	0	5	12	14	31*
Total Ovenbird captures:	25	44	55	33	157*

*Some individuals were recaptured in ≥ 2 years, so these totals include birds counted more than once. Total numbers of individuals recaptured on sites were 40 (Hermit Thrush) and 25 (Ovenbird), plus four and one, respectively, in buffers.

All adult birds captured were given a uniquely numbered, aluminum U.S. Fish and Wildlife Service (USFWS) band on their right leg, and three color bands: two on their left leg and one on their right leg, above the USFWS band. For each capture and all subsequent observations of a marked bird, the method of recapture was noted as was the exact location. Recapture methods included passive mist-netting, active mist-netting with playbacks, or making visual observations while conducting territory mapping or travelling through sites. Observed locations were listed as a bearing and distance to the nearest survey pin, which were spaced every 25m along parallel FERP transect lines (50 m apart) in each site.

Analyses

All analyses were done separately for male and female Hermit Thrushes and Ovenbirds. As mentioned above, numbers of birds of either species captured on any given site or treatment was small, so I pooled birds from the 10-30 and 20-10 harvest treatments and thus compared treated versus control sites in all analyses. Tests for differences in capture rates by age were not significant (see below), so all adult (i.e., after hatch year) birds were pooled regardless of age. Year-effects in site-attachment data (see below) were not significant, and sample sizes of recaptures within each year were small, so I also pooled observations from across all years in all analyses below.

My reliance on song playbacks to facilitate captures biased my sample such that more than twice as many males as females were captured and color-marked. Females comprised 32.9% and 33.3%, respectively, of the 143 Hermit Thrushes and 111 Ovenbirds captured inside site boundaries and 31.1% and 31.7% of the total samples of 164 and 126 birds, respectively. Females of these species comprised only 25% and 28% of the respective 40 and 25 birds that were recaptured in later years. Whereas 31.3% and 24.3% of all male Hermit Thrushes and Ovenbirds captured on a site were recaptured in another year, only 21.3% and 18.9% of respective females were. Further, males were more likely than females to be recaptured in multiple years (see Results). Because of this sex-biased sampling and the sex-related differences in site-fidelity reported elsewhere (Greenwood and Harvey 1982), I conducted all analyses for males and females separately. When sample sizes for females were prohibitively small, only data for males are presented.

The primary focus of analyses was to determine whether site-fidelity differed between birds captured on disturbed (i.e., treated) versus control sites. This was accomplished by analyzing two sets of variables: 1) numbers and proportions of marked birds that were recaptured at least one year after their initial capture, and 2) site-attachment distances. A third set of analyses focused on estimating survival and recapture rates using the capture-mark-recapture data for male birds.

Return Rates

I used 2 x 2 contingency tables to examine whether similar proportions of birds captured in year “t” were recaptured (on any site) in year “t+1,” with separate tables that grouped birds according to sex, age, and treatment status. Because some birds were recaptured in multiple years, and treatments were imposed over time, observations of individual birds in multiple periods (e.g., 1995-1996, versus 1997-1998) were treated as independent observations for most analyses. This allowed for individual bird’s responses (e.g., return status or site attachment distance) to be measured once if their site was a control, and again later after the site was treated.

To examine whether recapture rates differed by sex, males and females were compared in terms of numbers of birds that were recaptured (on any site) versus numbers of birds that were never recaptured (Table 2.2A). This analysis was refined further by focusing on the subset of birds that were recaptured, and evaluating whether recapture frequency was independent of sex. I used a 2 x 3 contingency table to compare numbers of birds 1) recaptured only in the year following initial capture, versus 2) recaptured only once, but two or three years after the birds’ initial capture, versus 3) birds recaptured in at least two different years after their initial capture (Table 2.2B). Recapture rates were also

compared for the subset of male birds that were reliably aged in the field (Table 2.3). For this analysis, second-year (SY) birds were compared to after-second-year (ASY) birds; hatch-year birds and birds of unknown age were not included.

I examined treatment effects on return rates using 2 x 2 contingency tables, with birds grouped by treatment status (treatment versus control) of the site on which a bird was initially captured (i.e., in year “t”) and whether or not it was recaptured in year “t+1” (Table 2.4). For the subset of birds that were recaptured at least one year after initial capture, I used 2 x 2 contingency tables to determine whether dispersal rate was independent of treatment status (Table 2.5). Birds were grouped by whether they were recaptured on the same site both in year “t” and year “t+1”, or whether they dispersed from their capture site in year “t,” and were captured on a new site in year “t+1” (Table 2.5A). I also examined the subset of recaptured birds that were originally captured on a control in year “t,” and examined whether dispersal rates differed for birds for which their capture site was still a control in year “t+1,” versus birds on sites that had been treated between year “t” and year “t+1” (Table 2.5B). The significance of all contingency tables was determined by Chi-square tests of independence (Zar 1999), unless the average (for all cells) expected value was <6.0, in which case significance was determined by Fisher’s Exact Test (Zar 1999).

Site-attachment

Exact territory locations for individually-marked birds were difficult to assess, as birds were usually heard but not seen during territory mapping. Further, capture locations were often equidistant to one or more mapped territories, and multiple males frequently responded to tape playbacks. Also, most (72% of Hermit Thrush and 71% of

Ovenbird) recaptured birds were caught only once in the year(s) following their initial capture. Therefore, I calculated site-attachment distances as the distance between the first capture location in one year and the first capture location in the subsequent year. This distance was used in all analyses of site-attachment. Note that stronger site-attachment is indicated by less distance (i.e., less dispersal), and higher distances denote weaker site-attachment. Only birds captured in two consecutive years were used in analyses of site-attachment; individuals captured only in the first and third, first and fourth, or second and fourth years of study were excluded from analyses of site-attachment.

Site-attachment distances were not normally-distributed, so I examined differences in site-attachment using Mann-Whitney or Kruskal-Wallis tests (Zar 1999), with separate tests for male Hermit Thrushes and Ovenbirds. I tested for differences in site-attachment by sampling period (i.e., 1995-1996, 1996-1997, or 1997-1998), for birds captured on treated versus control sites (see below), and between birds captured on the same site both in year “t” and year “t+1” versus birds that had dispersed to a new site in year “t+1.”

As expected, site-attachment distances were significantly higher for birds that dispersed to new sites (see Table 2.6). Because such inter-site movements were rare in any given year, I restricted my test for year-effects to birds that remained on the same site in two consecutive years; those data included 88% of all Hermit Thrush and 77% of all Ovenbird recaptures. For this same subset of birds (i.e., those remaining on the same site in consecutive years), I also examined whether site-attachment distances differed by the treatment status of a bird’s capture location, i.e., was the site a control in both years,

treated in both years, or a control in year “t” and then treated by year “t+1”? I also tested for treatment effects over the entire sample of recaptures, by conducting two separate (but similar) tests for (1) differences in site-attachment distances for birds on treated versus control sites in year “t”, regardless of their capture location in year “t+1,” and (2) differences between birds recaptured on treated versus control sites in year “t+1,” regardless of their capture location in year “t” (Table 2.7).

Survival and Recapture Rates

Annual survival and recapture rates were estimated using Cormack-Jolly-Seber (CJS) models in the software program MARK (White and Burnham 1999). I followed the approach of Lebreton et al. (1992) and Anderson and Burnham (1999a) to model survival and recapture rates. Akeike’s Information Criterion (AIC) was used to distinguish the most parsimonious among all competing models, and determine whether survival and recapture rates were relatively constant over time, or if they differed across years (Anderson and Burnham 1999b). MARK was also used to examine goodness of fit of mark-recapture data, by comparing observed variances with values from 100 bootstrapped simulations of the full model (with both survival and recapture varying by year) and the best overall model.

Because birds were captured from 1995-1998, three recapture periods were examined: 1995-1996, 1996-1997, and 1997-1998. MARK examines capture history data for each bird in all periods of interest. Recapture probabilities are based on the proportion of birds captured in any year “t” that are not observed in year “t+1,” but are observed in either year “t+2” or year “t+3.” Therefore, only two robust sets of estimates can be calculated with data from three recapture periods, as there is no information

available for the birds not recaptured in the last period that may still be alive. If either survival or recapture probabilities are held constant over time, MARK estimates these rates for the terminal period, though it cannot distinguish between survival versus recapture in this period.

My sample sizes were small for CJS modeling (Table 2.1); consequently, confidence intervals around parameter estimates were broad. When the sample was divided into subgroups, parameters had even wider confidence intervals, so I had very low power to detect any differences between groups (e.g., treatments). Further, goodness of fit tests indicated that when observations were divided into subgroups data were overdispersed for CJS modeling. Therefore, MARK was not used to test whether survival or recapture rates differed by age, sex, or treatment. Therefore, males from treated and control sites were pooled for all survival and recapture modeling. Also, survival and recapture rates were estimated for males only, as there were not enough data to robustly model parameters for females separately, and no reason to expect similar rates for males and females (Greenwood 1980).

RESULTS

Return Rates

Male Hermit Thrushes and Ovenbirds showed a strong tendency to return to the same site they were originally captured on. Ninety percent of male Hermit Thrush individuals recaptured ($n=30$) and 90.9% of all ($n=44$) recapture events (including individuals recaptured in multiple years), were on the same site in year “ t ” and “ $t+1$.” Further, of the three male Hermit Thrushes who moved to a new site, one of those birds returned its original capture site in year “ $t+2$.” If this individual is considered site-

faithful over the long-term, 93.3% of individual males and 95.5% of Hermit Thrush returns were to the same 10-ha site. Similarly, 94.4% of male Ovenbird individuals (n=18) and 95.5% of all male Ovenbird recapture events (n=22) were on the same site in year “t” and “t+1.” For both species far fewer females were captured and recaptured, and site-fidelity was somewhat lower for females than for males. Seven of 10 (70%) individual female Hermit Thrushes and six of seven (85.7%) individual female Ovenbirds (and six of eight recapture events) recaptured were site-faithful.

For both Hermit Thrush and Ovenbird, there was no significant difference in recapture likelihood based on a bird’s sex (Table 2.2) or age (Table 2.3). Compared to females, males of both species appeared more likely to be recaptured two or three years after their initial capture (Table 2.2B). Of all recaptured males, 40% and 50% of Hermit Thrushes and Ovenbirds, respectively, were recaptured at least two years after their initial capture, compared to only 20% and 14% of females recaptured (Table 2.2B); however, these differences were not statistically significant ($p>0.10$).

For both Hermit Thrush and Ovenbird, there was no evidence that a bird’s likelihood of recapture depended on whether their initial capture location was a treatment or a control site (Table 2.4). However, there was evidence that Hermit Thrush rates of dispersal to new sites were affected by harvest treatments (Table 2.5). Across all recaptures, male Hermit Thrushes were nearly eight times more likely to disperse to a new site if they were first captured on a treated versus a control site the previous year (n = 44, $P = 0.097$, Table 2.5A). None of 20 male Ovenbirds captured on controls dispersed to a new site in later years, while one of the two birds captured on a treated site did, though this difference was not significant (n = 22, $P = 0.145$, Table 2.5A).

Table 2.2. Recapture rate, by species and sex. Hermit Thrush and Ovenbird tallied separately; for both, data are pooled for all years 1995-1998. Table 2.2A compares the numbers of birds recaptured (“Recap”) versus not recaptured (“No Recap”) at least one year after their initial capture. Table 2.2B focuses on the subset of birds that were recaptured, and compares the number of birds recaptured one year after their initial capture (“1”), birds recaptured only once, but ≥ 2 years after their initial capture (i.e., “1*”), and birds recaptured in ≥ 2 years (i.e., “2+”). Small cell sizes for Ovenbird (in 2.3B) precluded a statistical test of independence.

A.	Hermit Thrush			Ovenbird		
		<u>Recap</u>	<u>No Recap</u>		<u>Recap</u>	<u>No Recap</u>
Sex	Male	30	44	Male	18	47
	Female	10	25	Female	7	22
	Chi-square ($\chi^2 = 1.00$) p = 0.32			Chi-square ($\chi^2 = 0.01$) p = 0.91		

B.	Hermit Thrush				Ovenbird			
		Number of Recaptures:				Number of Recaptures:		
Sex		<u>1</u>	<u>1*</u>	<u>2+</u>		<u>1</u>	<u>1*</u>	<u>2+</u>
	Male	18	3	9	Male	9	5	4
	Female	8	2	0	Female	6	0	1
	Chi-square ($\chi^2 = 4.06$) p = 0.13							

Table 2.3. Recapture rate by species, age, and sex. Focuses on the subset of captures that were reliably aged, with Hermit Thrush and Ovenbird males and females tallied separately; all data are pooled for all years 1995-1998. "SY" indicates second-year birds; "ASY" indicates birds ≥ 1 year older than SY birds. "Recap" indicates numbers of birds captured in year "t" that were recaptured in year "t+1" or later; "No Recap" indicates birds captured only in year "t." Table 2.3A is for males, Table 2.3B is for females.

A.		Hermit Thrush		(Males)		Ovenbird	
		<u>Recap</u>	<u>No Recap</u>	<u>Recap</u>	<u>No Recap</u>		
Age	SY	8	19	SY	3	15	
	ASY	15	18	ASY	11	25	
Chi-square ($\chi^2 = 0.97$) p = 0.32				Chi-square ($\chi^2 = 0.59$) p = 0.44			
B.		Hermit Thrush		(Females)		Ovenbird	
		<u>Recap</u>	<u>No Recap</u>	<u>Recap</u>	<u>No Recap</u>		
Age	SY	3	6	SY	2	3	
	ASY	5	14	ASY	2	13	
Chi-square ($\chi^2 = 0.001$) p = 0.95				Fisher's Exact Test p = 0.50			

Table 2.4. Contingency tables of recaptures by treatment for Hermit Thrush and Ovenbird. Talled separately by species and sex. Data are pooled for all years 1995-1998. Birds are grouped by the treatment status of the site they were captured on (“Site”) in any year “t” and whether they were recaptured (“Recap”) in a later year or never recaptured (“Not”). For birds that were recaptured in more than one year, each successive capture-recapture event is treated independently. Therefore the number of birds in the Recap category is larger than the total number of individuals that were recaptured. Birds captured only in 1998 (i.e., with no opportunity for recapture) are excluded from analyses. Table 2.4A is for males; Table 2.4B is for females.

A.		Hermit Thrush		(Males)	Ovenbird	
		<u>Recap</u>	<u>Not</u>		<u>Recap</u>	<u>Not</u>
Site	Control	32 ^A	36		Control	20 ^C
	Treatment	12 ^B	8		Treatment	2 ^D
		Chi-square ($\chi^2 = 0.58$)			Chi-square ($\chi^2 = 0.001$)	
		P = 0.45			P = 0.97	
B.		Hermit Thrush		(Females)	Ovenbird	
		<u>Recap</u>	<u>Not</u>		<u>Recap</u>	<u>Not</u>
Site	Control	5	19		Control	5
	Treatment	5	6		Treatment	3 ^E
		Chi-square ($\chi^2 = 1.20$)			Chi-square ($\chi^2 = 1.82$)	
		P = 0.27			P = 0.18	

^A Represents 26 unique individuals

^B Represents 4 unique individuals

^C Represents 17 unique individuals

^D Represents 1 unique individual

^E Represents 2 unique individuals

Table 2.5. Numbers of recaptured male birds remaining on a site versus dispersing to a new site. Hermit Thrush and Ovenbird tallied separately; for both, data are pooled for all years 1995-1998. Table 2.5A groups birds by the treatment status of their capture site in year “t”, and whether they remained on the same site (“Same”) or dispersed to a new site (“New”) the following year (“t+1”). Table 2.5B groups birds by i.) whether their breeding site in two consecutive years (“Year t—Year t+1”) was a control in both years (“Con-Con”) or was a control in one year then treated before the next summer (“Con-Trt”), and ii.) whether they remained on the site or dispersed to a new site the following year. Birds on sites that were treated in year “t” were excluded. P-value is for Chi-square Test of Independence or two-tailed Fisher’s Exact Test for equal proportions.

A.	Hermit Thrush			Ovenbird		
		Year “t+1” Capture Site:			Year “t+1” Capture Site:	
		<u>Same</u>	<u>New</u>		<u>Same</u>	<u>New</u>
Year “t” Capture Site:	Control	31	1	Control	20	0
	Treatment	9	3	Treatment	1	1
		Chi-square ($\chi^2 = 2.75$) P = 0.097			Chi-square ($\chi^2 = 2.12$) P = 0.145	

B.	Hermit Thrush			Ovenbird		
		Year “t+1” Capture Site:			Year “t+1” Capture Site:	
		<u>Same</u>	<u>New</u>		<u>Same</u>	<u>New</u>
Year t—Year t+1:	Con-Con	18	1	Con-Con	12	0
	Con-Trt	13	0	Con-Trt	8	0
		Chi-square ($\chi^2 = 0.84$) P = 0.85			Fisher’s Exact Test P = 1.00	

An analysis of the subset of birds that were captured on sites in year “t” that were treated during the following winter showed no tendency to disperse to new sites in year “t+1”, compared to birds captured on sites that were undisturbed in both years (Table 2.5B). Within this subset of birds, examining those recaptured in >2 years did not reveal that either Hermit Thrushes or Ovenbirds were more likely to disperse to new sites in year “t+2” or “t+3.”

Sampling efforts in the 100-m buffer around each site resulted in 21 new Hermit Thrush captures; 12 in 1997 and nine in 1998. Three of the birds captured only in buffers in 1997 were recaptured in buffers (only) in 1998. Buffer sampling also resulted in recaptures of seven marked Hermit Thrushes that originally had been marked within an adjacent research area. Of these, two birds were recaptured only in a buffer, and five were captured in buffers but also within the boundaries of an adjacent research area in the same year. Buffer sampling yielded 15 new Ovenbird captures; 12 in 1997 and three in 1998. One of the birds captured in the buffer in 1997 was recaptured in the same location in 1998. In addition, buffer sampling resulted in captures of 15 Ovenbirds that previously had been captured and marked within an adjacent research area. Of these, three marked birds were recaptured only in a buffer. These data indicate that only a small proportion of birds was likely to avoid recapture by moving short distances into the forest surrounding each research area.

Site-attachment

The mean site-attachment distance (\pm standard error) for male Hermit Thrushes (n=39) was 144.4 (\pm 12.3) m, with a median distance of 136.5 m (Table 2.6). Female Hermit Thrushes (n=8) averaged 169.8 (\pm 49.9) m, with a median distance of 113.7 m.

The mean site-attachment distance (\pm standard error) for all male Ovenbirds ($n=16$) was 104.2 (± 14.6) m, with a median distance of 93.9 m (Table 2.6). Female Ovenbirds ($n=8$) averaged 310.0 (± 134.9) m, with a median distance of 155.1 m. It should be noted that the mean for female Ovenbirds is skewed by two birds with unusually large dispersal distances of 745 m and 1069 m.

The mean distance between capture locations within the same year for Hermit Thrushes captured >1 time per year ($n=33$) was 155.3 (± 14.1) m, based on an average of 2.49 (± 0.13) capture locations per bird per year. The mean distance between capture locations within the same year for Ovenbirds captured >1 time per year ($n=16$) was 115.1 (± 27.2) m, based on an average of 2.38 (± 0.13) capture locations per bird per year. These within-year distances can be thought of as a sort of “sampling error” for basing territory locations on the first capture of each year. These results suggest that, for both species, the average distance between territories of successive years was similar to or less than the average distance birds moved within their home range in the same summer.

Analyses of site-attachment distances did not indicate any significant differences among years for either Hermit Thrush or Ovenbird (Table 2.7, Test 1), based on birds that were captured on the same site in two consecutive years. Likewise, birds remaining on the same sites in years “t” and “t+1” showed no apparent difference in site-attachment whether their site was a control in both years, treated in both years, or a control in year “t” but treated by year “t+1” (Table 2.7, Test 2). Hermit Thrush site-attachment distances were significantly higher ($p=0.06$) for birds that dispersed to a new site, compared to birds that remained on the same site in two consecutive years (Table 2.7, Test 3); Ovenbird distances followed the same pattern (Table 2.6), though differences in distance

Table 2.6. Distances between capture locations of successive years. Site-attachment distances (in meters) and sample sizes (in parentheses) for Hermit Thrush and Ovenbird are tallied separately. Only data for male birds are included. Each value below is a mean (and sample size) for a subgroup. Means are reported separately for birds that remained on the same site in both years versus those that moved to a new site. Distances are grouped by the treatment status of a bird's breeding site for the two-year period. Sites were considered controls until they were harvested.

Hermit Thrush				
	<u>1995-1996</u>	<u>1996-1997</u>	<u>1997-1998</u>	<u>All Years</u>
Remained on same site:				
<u>Year "t"-Year "t+1"</u>				
Control-Control	136.2 (12)	138.0 (4)	189.8 (2)	142.5 (18)
Control-Treatment	211.4 (3)	111.4 (3)	157.6 (2)	160.5 (8)
Treatment-Treatment	---	73.0 (2)	115.2 (7)	105.8 (9)
All birds on same:	151.2	114.7	136.4	137.2 (35)
Moved to new site:				
<u>Year "t"-Year "t+1"</u>				
Control-Control	186.6 (1)	---	---	186.6 (1)
Control-Treatment	---	---	---	---
Treatment-Treatment	---	287.1 (1)	208.8 (1)	248.0 (2)
Treatment-Control	---	---	146.3 (1)	146.3 (1)
All birds on new site:	186.6	287.1	177.5	207.2 (4)
All birds pooled:	153.4 (16)	131.9 (10)	142.8 (13)	144.4 (39)
Ovenbird				
	<u>1995-1996</u>	<u>1996-1997</u>	<u>1997-1998</u>	<u>All Years</u>
Remained on same site:				
<u>Year "t"-Year "t+1"</u>				
Control-Control	111.8 (2)	115.6 (2)	92.1 (2)	106.5 (6)
Control-Treatment	61.7 (1)	96.3 (3)	107.7 (2)	94.3 (6)
Treatment-Treatment	---	---	67.9 (1)	67.9 (1)
All birds on same:	95.1	104.0	93.5	97.9 (13)
Moved to new site:				
<u>Year "t"-Year "t+1"</u>				
Control-Control	---	---	---	---
Control-Treatment	---	144.9 (1)	---	144.9 (1)
Treatment-Treatment	---	---	---	---
Treatment-Control	---	---	124.4 (2)	124.4 (2)
All birds on new site:	---	144.9	124.4	131.2 (3)
All birds pooled:	95.1 (3)	110.8 (6)	102.3 (7)	104.2 (16)

Table 2.7. Summary of statistical test results for differences in site-attachment distances. Data are for males only, due to small sample sizes for females. Hermit Thrushes and Ovenbirds and analyzed separately. Test 1 compared site-attachment distances among years. Test 2 compared distances across treatment groups, based on whether the capture site was a control in both years, treated in both years, or was a control in year “t,” but treated in year “t+1”. These first two tests were restricted to birds captured on the same site in two consecutive years. Test 3 compared birds found on the same site in two consecutive years versus birds that dispersed to a new site the second year. Test 4 compared birds captured (in year “t”) on control versus treated sites, regardless of capture location in year “t+1.” Test 5 compared birds captured (in year “t+1”) on control versus treated sites, regardless of capture location in year “t.” For the last four tests, data were pooled across all years 1995-1998. See Appendix C (Tables C1-C5) for complete ANOVA tables and other information regarding these tests.

<u>Test for differences in:</u>	<u>Hermit Thrush</u>	<u>Ovenbird</u>
1. Year Kruskal-Wallis statistic:	p = 0.56 1.14 (n = 35)	p = 0.98 0.04 (n = 13)
2. Site Treatment Status Kruskal-Wallis statistic:	p = 0.17 3.5 (n = 35)	p = 0.27 2.63 (n = 13)
3. Same vs. New Site Mann-Whitney U statistic:	p = 0.06 30 (n = 39)	p = 0.19 9 (n = 16)
4. Year 1 Capture location, Control vs. Treatment Mann-Whitney U statistic:	p = 0.36 132 (n = 39)	p = 1.0 20 (n = 16)
5. Year 2 Capture location, Control vs. Treatment Mann-Whitney U statistic:	p = 0.82 182 (n = 39)	p = 0.23 20 (n = 16)

between the two groups were not statistically significant. Finally, there were no differences in site-attachment distances between birds captured on treated versus control sites, regardless of whether their treatment status was examined in either year “t” or in year “t+1” (Table 2.7, Tests 4 and 5).

Survival and Recapture Rates

The most parsimonious model of Hermit Thrush survival and recapture rates indicated that survival was time-dependent (i.e., year-specific) and recapture was constant (model $\phi_{(t)}p_{(.)}$ AICc = 241.0, see Appendix C; Table C.6). However, as this model and the two next-best models ($\phi_{(t)}p_{(t)}$, $\phi_{(.)}p_{(.)}$) differed by only 2-2.6 AICc points, all these models can be considered reasonable. For male Hermit Thrushes, annual survival rate estimates (\pm standard error) ranged from 0.48 (\pm 0.11) to 0.89 (\pm 0.15); recapture rate estimates (\pm standard error) were 0.619 (\pm 0.11) (Table 2.8).

For Ovenbird males, the most parsimonious model was the reduced model $\phi_{(.)}p_{(.)}$, which was seven times more likely than the next-best model (Appendix C; Table C.6). Therefore, Ovenbird survival and recapture rates across the three time periods can be considered to be constant. Annual survival rate (\pm standard error) was 0.721 (\pm 0.18) for male Ovenbirds (Table 2.8), with a recapture rate of 0.282 (\pm 0.11).

DISCUSSION

Treatment Effects on Site-Fidelity

Overall, breeding site-fidelity of adult Hermit Thrushes and Ovenbirds was very high, whether measured by return rates to 10-ha sites or by site-attachment distances. Average distances between capture locations within a year were very similar to median or mean site-attachment distances for both Hermit Thrushes and Ovenbirds (Table 2.6).

Table 2.8. Estimated survival (ϕ) and recapture (p) rates. Data are for males only; Hermit Thrush ($n=164$) and Ovenbird ($n=126$) are analyzed separately. Standard Error, and Lower and Upper 95% confidence intervals (CI) are included for each estimate. For each separate analysis below survival rates (“ ϕ ”) and recapture rates (“ p ”) could be estimated separately for each recapture interval, or estimated as a constant over all periods, based on the model chosen in Program MARK. See Appendix C, Table C.6 for more detailed output.

Hermit Thrush Males

<u>Parameter</u>	<u>Period</u>	<u>Value</u>	<u>Std. Error</u>	<u>Lower CI</u>	<u>Upper CI</u>
ϕ	1995-96	0.885	0.154	0.285	0.993
ϕ	1996-97	0.477	0.108	0.281	0.681
ϕ	1997-98	0.508	0.125	0.279	0.733
p	Constant	0.619	0.113	0.389	0.805

Ovenbird Males

<u>Parameter</u>	<u>Period</u>	<u>Value</u>	<u>Std. Error</u>	<u>Lower CI</u>	<u>Upper CI</u>
ϕ	Constant	0.721	0.175	0.320	0.934
p	Constant	0.282	0.107	0.122	0.526

One can safely assume that most bird territories in successive years were separated by little distance.

Even for research areas that were disturbed by 10% or 20% timber removals in small gaps, the vast majority of birds (of either species) returned to the site of their initial capture the following year. However, the proportion of birds that did disperse to new sites was not independent of treatment. Birds of both species dispersed from treated sites at somewhat higher rates than they did from controls, although this difference was marginally significant ($p=0.097$) only for Hermit Thrushes (Table 2.5). These data suggest that Hermit Thrushes may be more sensitive than Ovenbirds to this type of habitat disturbance. Possibly this is because territories for Hermit Thrushes are larger than for Ovenbirds (Jones and Donovan 1996, Van Horn and Donovan 1994). If birds

avoid having disturbed gaps in their territories, Ovenbirds may be better able to shift their territory locations and avoid small gaps, whereas Hermit Thrush may require larger patches that are undisturbed. However, my sample size for Ovenbird recaptures was only half that of Hermit Thrushes, and only a very small proportion of Ovenbirds was captured on treated sites (Table 2.5). Given the fact that Ovenbirds tended, like Hermit Thrushes, to disperse more often from treated sites, there may be little actual difference between how the birds respond to disturbances like those studied.

Survival and Recapture Rates

Average annual survival rates for both Hermit Thrush and Ovenbird males were above 0.60 (Table 2.8). However, actual survival rates may have been substantially higher because of undetected emigrants and the nature of short-duration CJS models. Each of these issues is discussed separately below.

Undetected Emigrants

CJS models do not distinguish between mortality events and emigration events for bird that are never resighted (Marshall et al. 2000). Thus, to the extent that the study population is “open” (i.e., birds survive but emigrate without detection) survival rates are biased to underestimate true survival. The relatively small size (10 ha) of my research areas makes it difficult to accurately assess breeding dispersal rates because the typical distance moved by birds is large relative to the area sampled (Barrowclough 1978, Dieckmann et al. 1999). My research areas varied somewhat in shape (Fig. 1.1), but movements >200 m would put most birds outside of my 10-ha research areas (the radius of a circular 10-ha research area would be 178.4 m). Koenig et al. (1996) estimated that

the probability of detecting a disperser that moves a distance equal to the radius of the study area is only about 45%.

Twenty percent of Hermit Thrush site-attachment distances (n=50) and 12% of all Ovenbird movements (n=25) were >200 m. The implications of this are seen, in part, by the fact that 10% and 20%, respectively, of all recaptures or resighting observations of these species were on a different research area each year. These movements were detected only because certain individuals happened to disperse in the direction of an adjacent research area. Often, similar movements in a different direction likely would have been missed, because eight research areas were surrounded on at least three sides by contiguous forest that generally was not sampled, even though seven of nine research areas were close to other research areas (Fig. 1.1). It is therefore highly unlikely that all emigration events were detected. This undetected emigration results in biased survival estimates that are lower than actual survival (Marshall et al. 2000).

Despite the likelihood that some emigration went undetected, I do not believe that it affected survival estimates profoundly, for four reasons. First, my sample sizes of marked birds were largest for the set of research areas (i.e., RA 1-6) that were most closely clustered together (Fig. 1.1), increasing chances that emigrants would be found on adjacent areas. Second, sampling 100-m buffers around research areas, though not done intensively, yielded a very small proportion of emigrant birds. Of 31 total Hermit Thrush captures in buffer zones, only two male Hermit Thrushes (6.5% of buffer captures and 5% of all 40 males recaptured) represented emigrants that moved outside of any research area. Similarly, only three Ovenbirds were known to move outside of any research area, which represents 9.7% of all captures in buffers (n=31) and 12% of all male Ovenbirds

recaptured (n=25). It should be noted, however, that almost all these “emigrants” were captured within 50 m of the perimeter of the site they were originally captured on, so from the bird’s perspective their territory location had not necessarily moved far between years. The numbers above do not account for the many birds recaptured in a site adjacent to the site of their original capture. However, given the proximity of most sites to others, this kind of emigration resulted from relatively small movements, and the sampling design allowed for the detection of most of these movements. Also, my comparison of intra- and inter-year distances between captures indicated that most birds moved no farther between years than within a year, so most movements were not likely to result in a bird escaping recapture. Finally, survival rates were quite high (see below), and thus could not have been grossly underestimated.

CJS and Short-Duration Studies

Another reason to believe that survival rates may have been well above 0.60 was because CJS model estimates from the first return interval are much higher than 0.60 (Table 2.8), and these estimates may be much more accurate than estimates from later intervals, due to the short duration of my study. Unless recapture probabilities are close to unity, survival estimates in CJS models are increased to account for the proportion of birds in the sample that were likely to have survived without being recaptured. The extent to which survival rates are raised depends on how many birds captured in year “t” are missed in year “t+1” but recaptured in a later year. In my study, birds captured in 1995 could have been missed in 1996 and 1997, but resighted in 1998. However, birds captured in 1996 and 1997, respectively, had one and zero opportunities to be missed and still be recaptured later. Some birds from these years likely would have turned up alive

given more years of sampling; thus recapture probabilities for these intervals are biased, and lead to biased (low) survival estimates.

When CJS models considered survival rates as time-period-dependent (see above), estimates for survival in the first return interval were 0.89 for male Hermit Thrushes; estimates even higher for the model with time-dependent recapture probabilities. Similarly, in time-dependent models, male Ovenbird survival in the first return interval was 0.85. These estimates for both species are much higher than average survival reported for North American passerines: 0.53 (range 0.29-0.63, Johnson et al. 1997), 0.55 (Martin and Li 1992), and 0.50-0.59 (Rowley and Russell 1991), and are higher still compared to European passerines (Rowley and Russell 1991, Johnston et al. 1997). In fact my estimates equal or exceed high CJS survival rates reported for two tropical areas (Rowley and Russell 1991, Johnson et al. 1997).

Jones and Donovan (1996), in their Hermit Thrush species account, report that no survival estimates are available for this species, though Brown et al. (2000) found that only 18% of Hermit Thrush returned to the same wintering sites each year. Adult Ovenbird survival rates (reviewed by Martin and Li 1992) were: 0.526 (n = 38; Savidge and Davis 1974); 0.543 (n = 38; Hann 1948); and 0.845 (n=20; Roberts 1971). The variability in these rates may simply reflect the fact that survival rates vary over space and time across a bird's range. However, the three estimates above (cited by Martin and Li 1992, Van Horn and Donovan 1994) may be underestimates, and not directly comparable to mine because they did not use CJS models to estimate survival. Apparent survival estimates are often biased low (Clobert and Lebreton 1991), unless recapture probability is nearly 1.0 (Martin et al. 1995). To illustrate this point, 23 of 38 Hermit

Thrushes and nine of 26 Ovenbirds I captured in 1995 were later recaptured. These data yield apparent survival rates (i.e., number of birds resighted/total sample captured and released) of 0.605 and 0.35, respectively, compared to CJS estimates of 0.87 and 0.69, respectively. The difference stems from the fact that apparent survival assumes a recapture rate near 1.0 (Martin et al. 1995), whereas in my study rates were much lower, averaging 0.56 for Hermit Thrushes and 0.34 for Ovenbirds (Table 2.8).

CONCLUSIONS

Regardless of whether a site was a control or experienced experimental removals of 10% or 20% of mature trees, >90% and 95% of adult male Hermit Thrushes and Ovenbirds, respectively, remained on the same 10-ha research areas in successive years. Though based on small sample sizes (i.e., 7-10 birds per species), female site-fidelity was apparently lower, from 70-85%. Despite overall high site-fidelity, breeding dispersal rates were somewhat higher from treated versus untreated areas, and this difference was marginally significant for Hermit Thrushes. Though sample sizes were small, Hermit Thrushes were nine times more likely to disperse from treated than from control sites. This increased dispersal may reduce future breeding productivity for the minority of birds that do move to new areas. Analyses of site-attachment, the distance between territories of successive years, indicated that most Hermit Thrush and Ovenbird returned to within one home-range width of their previous breeding location. Site-attachment measures were similar across years and between treatments. Based on capture-mark-recapture models, survival rates for male Hermit Thrushes and Ovenbirds, respectively, averaged 0.62 and 0.72, but were as high as 0.89 and 0.87 in the first year of study when estimates

were most accurate; these rates are higher than most reported rates for North American and European passerines, which typically are <0.55 .

LITERATURE CITED

- Anderson, D., and K. Burnham. 1999a. General strategies for the analysis of ringing data. *Bird Study* 46(suppl.):S261-270.
- Anderson, D., and K. Burnham. 1999b. Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* 46(suppl.):S14-21.
- Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* 49:333-341.
- Beletsky, L.D., and G.H. Orians. 1987. Territoriality among male red-winged blackbirds. *Behavioral Ecology and Sociobiology* 20:21-34.
- Blondel, J., and R. Pradel. 1989. Is adult survival of the Blue Tit higher in a low fecundity insular population than in a high fecundity mainland one? Pp. 131-144 *in* Population biology of Passerine birds (J. Blondell, A. Gosler, J.-D. Lebreton, and R. McCleery, Eds.). NATO ASI Series G: Ecological Sciences, Vol. 24. Springer-Verlag, New York.
- Brown, D.R., P.C. Stouffer, and C.M. Strong. 2000. Movement and territoriality of wintering hermit thrushes in southeastern Louisiana. *Wilson Bulletin* 112:347-353.
- Clobert, J., and J.-D. Lebreton. 1991. Estimation of demographic parameters in bird populations. Pp. 75-104 *in* Bird population studies: relevance to conservation and management (C.M. Perrins, J.-D. Lebreton, and G.J.M. Hirons, Eds.). Oxford University Press, New York.
- Danchin, E., and E. Cam. 2002. Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology* 51:153-163.
- Darley, J.A., D.M. Scott, and K.M. Taylor. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. *Bird-Banding* 48:145-151.
- Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The evolutionary ecology of dispersal. *Trends in Evolution and Ecology* 14:88-90.
- Greenwood, P.J., and P.H. Harvey. 1977. Feeding strategies and dispersal of territorial Passerines: a comparative study of the Blackbird (*Turdus merula*) and the Greenfinch (*Carduelis chloris*). *Ibis* 119:528-531.
- Greenwood, P.J., and P.H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21.
- Hann, H.W. 1948. Longevity of the oven-bird. *Bird-Banding* 19:5-12.

- Holmes, R.T., and T.W. Sherry. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: Implications for population dynamics, habitat selection, and conservation. Pp. 563-575 442 in J. M. Hagan III, and D. W. Johnston, eds. Ecology and conservation of Neotropical migrant landbirds. Smithsonian Institution Press, Washington, 609 pp.
- Johnston, J.P., W.J. Peach, R.D. Gregory, and S.A. White. 1997. Survival rates of tropical and temperate Passerines: a Trinidadian perspective. *American Naturalist* 150:771-789.
- Jones, P.W., and T.M. Donovan. 1996. Hermit thrush (*Catharus guttatus*). In *The birds of North America*, no. 261 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- Koenig, W.D., D. Van Vuren, and P.N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Evolution and Ecology* 12:514-517.
- Lebreton, J.D., K.P. Burnham, J. Clobert, and R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67-118.
- Marshall, M.R., R.R. Wilson, and R.J. Cooper. 2000. Estimating survival of Neotropical-Nearctic Migratory Birds: are they dead or just dispersed? Pp. 195-199 in R. Bonney, D.N. Pashley, R.J. Cooper, and L. Niles, eds. *Strategies for bird conservation: the partners in flight planning process*; Proceedings of the 3rd Partners in Flight Workshop; Oct. 1-5, 1995; Cape May, NJ. Proceedings RMRS-P-16. Ogden, UT. USDA Forest Service, Rocky Mountain Research Station. 281 pp.
- Martin, T.E. and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592.
- Martin, T.E., J. Clobert, and D.R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863-875.
- O'Connor, R.J. 1985. Behavioural regulation of bird populations: a review of habitat use in relation to migration and residency. Pp. 105-142 in R.M. Sibly and R.H. Smith, eds. *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Scientific Publications, Boston.
- Roberts, J.O.L. 1971. Survival among some North American wood warblers. *Bird-Banding* 42:165-183.

- Rowley, I., and E. Russell. 1991. Demography of Passerines in the temperate southern hemisphere. Pp. 22-44 in C.M. Perrins, J.-D. Lebreton, and G.J.M. Hirons, eds. Bird population studies: relevance to conservation and management. Oxford University Press, New York.
- Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pp. 17-33 in S. T. A. Pickett, and P.S. White. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, FL. 472 pp.
- Savidge, I.R., and D.E. Davis. 1974. Survival of some common passerines in a Pennsylvania woodlot. Bird-Banding 45:152-155.
- Seymour, R.S., A.S. White, and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management 155:357-367.
- Slagsvold, T., and J.T. Lifjeld. 1989. Return rates of male Pied Flycatchers: an experimental study manipulating breeding success. Pp. 441-452 in Population biology of Passerine birds (J. Blondell, A. Gosler, J.-D. Lebreton, and R. McCleery, Eds.). NATO ASI Series G: Ecological Sciences, Vol. 24. Springer-Verlag, New York.
- Van Horn, M.A., and T.M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). In The birds of North America, no. 88 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl.):S120-139.

Chapter 3

EFFECTS OF RED SQUIRREL (*Tamiasciurus hudsonicus*) POPULATION FLUCTUATIONS ON BIRD POPULATIONS

INTRODUCTION

The pine or American red squirrel (*Tamiasciurus hudsonicus*) is abundant and conspicuous in conifer and mixed-wood forest ecosystems across northern North America, the Rocky Mountains, and the Appalachians (Steele 1998). Like many small mammals, red squirrels experience strong fluctuations in their populations (Erlie and Tester 1984, Danell et al. 1998, Stevens and Kennedy 1999), and may be somewhat cyclic (Erlie and Tester 1984, Fryxell et al. 1998). For both the American and Eurasian red squirrel (*Sciurus vulgaris*), annual population fluctuations are generally related to seed supplies of conifer trees (Kemp and Keith 1970, Gurnell 1983, Andr n and Lemnell 1992, Lurz et al. 2000).

Cone crops are highly variable, and extreme years (when cone crops fail or are large) have dramatic effects on squirrel populations, causing rapid increases or decreases in their numbers (Gurnell 1983). For many conifer species, cone crop failures are proximally cued by weather conditions, and a physiological inability to have two large crops in succession (Smith 1970, Koenig and Knops 2000). Thus, very large cone crop (or “masting”) years often are preceded and followed by relatively poor cone crops (Koenig and Knops 2000), a pattern that results in frequent spikes and crashes in squirrel populations, which occur on a time lag of one-year after food supply peaks or falls (Danell et al. 1998). There is a great degree of spatial synchrony in cone production

(Kemp and Keith 1970, Sirois 2000, Koenig and Knops 2000), in part because cone formation is strongly related to weather patterns of the previous year (Gurnell 1983), which are spatially autocorrelated at a scale similar to that of tree masting (Koenig and Knops 2000). In response to the spatial synchrony of cone crops, population fluctuations of the American and Eurasian red squirrel are spatially autocorrelated over hundreds of thousands of square kilometers (Kemp and Keith 1970, Ranta et al. 1997, Koenig and Knops 1998). Thus, trophic interactions of red squirrels and other taxa may be manifested at large geographic scales.

The red squirrel diet consists mostly of conifer seeds when cones are plentiful, but they frequently consume vertebrate animals (Sullivan 1991, Callahan 1993). Red squirrels have been reported to kill sparrow-sized birds (Nero 1987, 1993; Sullivan 1991), and to attack birds as large as pileated woodpeckers (*Dryocopus pileatus*; Rathcke and Poole 1974) and sharp-shinned hawks (*Accipiter striatus*; Park 1987). Red squirrels have long been known to prey on songbird eggs and nestlings (Thoms 1922, Hatt 1929); Nelson (1918) reported that “each squirrel destroys 200 birds a season,” including practically all species of small songbirds.

Squirrels are frequently the single most important predator of bird nests. Studies from Maine (Vander Haegen and DeGraaf 1996a), New Hampshire (Holmes et al. 1992, Sloan et al. 1998), Arizona (Martin 1993), Montana (Tewksbury et al. 1998), Saskatchewan (Bayne and Hobson 1997a, 1997b), Alberta (Boag et al. 1984), the Yukon, and Alaska (Sieving and Willson 1998) have shown that more nests are predated by red squirrels than by any other species. Red squirrels alone can account for >80% of all nest predation (Martin 1993).

Yearly changes in bird abundance are largely a function of juvenile recruitment into local breeding populations, and thus are highly correlated with breeding productivity the previous year (Sherry and Holmes 1992). Therefore, it is logical to assume that red squirrels exert a strong influence on avian population dynamics, where they are the most important nest predator. Given the fluctuations typical of squirrel populations (Danell et al. 1998), their influence on birds may be most noticeable during years when squirrel populations spike or crash, and birds experience relatively high nest predation or nest success, respectively. Based on the information above, I investigated whether patterns of population change in birds and squirrels were consistent with the hypothesis that squirrel populations can influence avian populations at a regional scale, at least in some years.

METHODS

Local Analysis for Maine, 1995-1997

As part of an ongoing research project, nine mature mixed-wood study sites of 10 ha each were selected at the Penobscot Experimental Forest (PEF) in Bradley, Maine and marked with parallel transects (50 m apart). From 1995-1998, during ten mornings in June, one of three observers spent approximately two hours walking along each transect to map bird territories on all sites (Hartley, unpublished manuscript). Red squirrels seen or heard during bird surveys also were recorded. As squirrel territories in 1995 were extremely dense and difficult to map accurately, I assumed that any squirrels mapped within 100 m of each other were the same individual, unless multiple individuals were observed simultaneously. Then I calculated an index of squirrel abundance by summing observations of individual squirrels during each site visit, which lasted approximately 2 hours. Red squirrel abundance for each site was calculated as the average of ten visits,

and all sites were averaged for an annual abundance index for the PEF. This index is conservative and underestimates squirrel densities when they are high, at which time the index is less than half of the number of observations. However, at low densities (e.g., during 1996 and 1997) the index likely approaches the true number of squirrels.

Based on high squirrel populations in 1995, and the subsequent crash in 1996, bird populations were expected to decrease from 1995-1996, and increase from 1996-1997. Changes in bird and squirrel abundance across all years were compared with a Kruskal-Wallis test (Zar 1999). Comparisons from year to year were made by examining overlap in 95% confidence intervals around annual means.

Regional Analysis, 1995-1997

To test whether the patterns seen in Maine were evident at a larger scale, I examined bird and red squirrel data from across the northeastern U.S. and adjacent Canadian provinces. I obtained red squirrel population data from as many sources and years as possible, focusing on overlap among years across locations. I obtained red squirrel data from five locations: Algonquin Provincial Park, Ontario (Fryxell et al. 1998, and R. Brooks unpublished data), Hubbard Brook, New Hampshire (R. Holmes unpublished data), Huntington Wildlife Forest, New York (Adirondack Ecological Center unpublished data), and two sites in Maine (M. Hartley unpublished data, and D. Harrison unpublished data). Data spanned a 13-year period (1988-2000), though for two sites I had only four years of data; thus the degree of temporal overlap differs among sites. Squirrel data were obtained from a variety of survey methods. Track counts were used at Huntington Wildlife Forest; call counts were used at Hubbard Brook and at the Penobscot Experimental Forest in Maine (see above). Live trapping was used at

Algonquin Provincial Park (Fryxell et al. 1998) and around Baxter State Park in Maine (D. Harrison unpublished data). All data were obtained from summer observations, except for Huntington Forest, where data were obtained in winter (December of previous year to March) of each year. Squirrel data for each area were examined for normality, then agreement between locations was tested for all pairs of sites using Pearson or Spearman correlation coefficients. It was problematic to compare directly data based on different survey methods and with different units. Therefore, medians were calculated for data from each location, and red squirrel abundances were expressed as a percentage of the median value for that location and plotted separately.

To examine patterns of bird population change at a larger scale, and compare across regions, I used Breeding Bird Survey (BBS) data. Year-to-year changes in populations of individual bird species were calculated using trend-analysis software available on the internet (<http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>) for BBS data (Sauer et al. 1999). Initially, species included in this analysis were those found in the PEF, to enable direct comparisons of bird population changes at a local (see above) and regional scale. However, some bird species are more likely to be affected by red squirrels than are others, based on the amount of overlap in typical habitat and geographic range. Therefore, two groups of birds were constructed, based upon an *a priori* determination of whether they were more or less likely to be affected by squirrel population change. One group consisted of 21 species (see Appendix D) that I expected to have a stronger relationship with squirrels, as these species are typical of mature conifer forests (Erlich et al. 1988) and have geographic ranges that overlap strongly with red squirrels. This group includes some boreal bird species that were rare or absent at the

PEF, which were added to make this group more reflective of a typical northeastern North American conifer-forest bird community. The second group consisted of 20 species that were common in the PEF, but could be considered as an outgroup because all species either: 1) are more typical of mature deciduous forests, or 2) have a geographic range with relatively low overlap with red squirrels. The second criterion arose because two species were difficult to group. The Northern Parula and Pine Warbler (see Appendix E for scientific names) have a weak and strong preference for conifer forests, respectively, but were placed in the outgroup because their continental geographic range only partially overlaps with the range of red squirrels.

Based on high red squirrel populations observed in 1995, and the subsequent lows of 1996 (Figures 3.1 and 3.2), I examined whether bird abundances: 1) decreased from 1995 to 1996, and 2) increased from 1996 to 1997. This pattern of change is expected if high and low squirrel populations (in year n) affect avian recruitment (in year $n+1$) by causing low and high avian productivity (in year n), respectively. My goal was to test whether or not the direction (i.e., increase or decrease) of short-term population change for the 41 focal species (see Appendix D) was consistent with this pattern, and to see whether patterns of change differed between the conifer- and deciduous-forest bird groups. To do so, I calculated trend estimates (Sauer et al. 1999) for each focal species in each of the two time periods, and for each of the following eight regions: Maine, New Hampshire, and Vermont (combined); the Adirondack region of New York; Ontario; Quebec; New Brunswick; Nova Scotia; BBS stratum 28; and BBS stratum 29. These last two regions constitute large physiographic strata used by the BBS (Sauer et al. 1999). Stratum 28 encompasses the “spruce-hardwoods” from Minnesota through the Great

Lakes, northern New England, New Brunswick and Nova Scotia. Stratum 29 comprises the “closed boreal forest” which stretches from Labrador to Alaska, including much of Quebec, Ontario, and northwestern Canada.

For each species, period, and region examined, a species’ population change was said to be consistent with the hypothesized pattern (hereafter “fit”) if it decreased (from 1995-1996) or increased (from 1996-1997) by $\geq 5\%$. Five percent change (in the direction predicted) was chosen as the threshold level because $\geq 95\%$ of species examined had trend values that were more extreme than this or were in the opposite direction. A

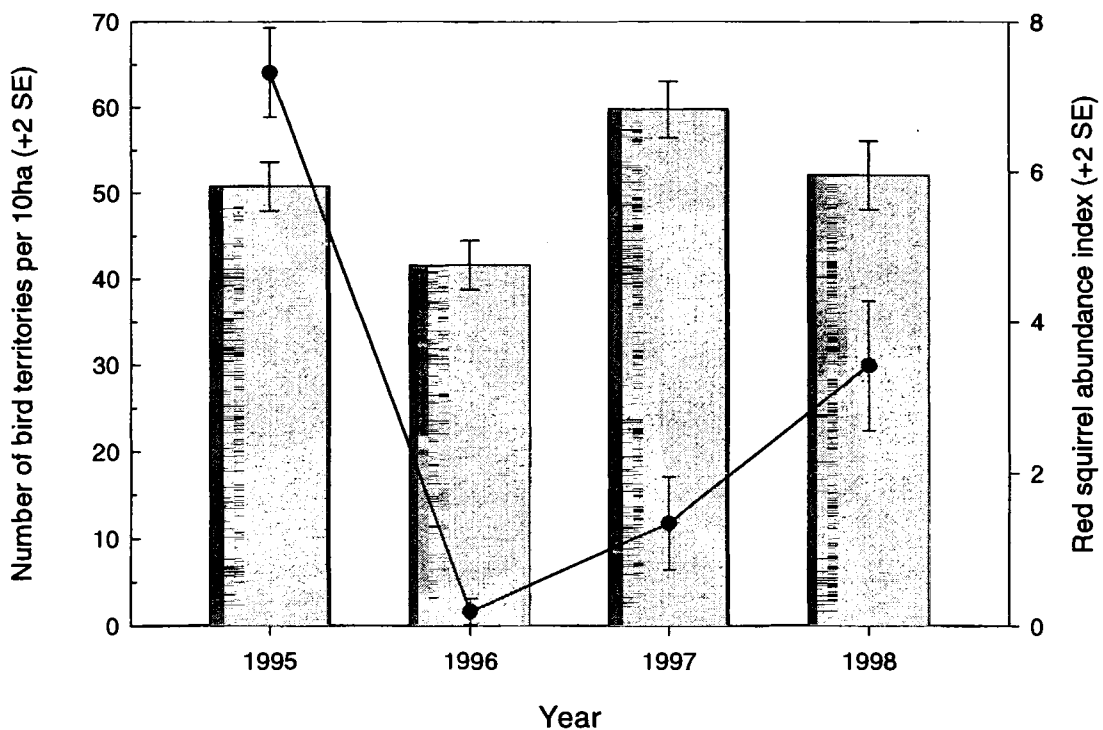


Figure 3.1. Abundance of birds and red squirrels in the PEF. Average number of avian territories (bars) and mean red squirrel abundance index (line) for nine sites (10 ha each) in the Penobscot Experimental Forest, Maine, 1995-1998. Data are from territory mapping over ten visits in June.

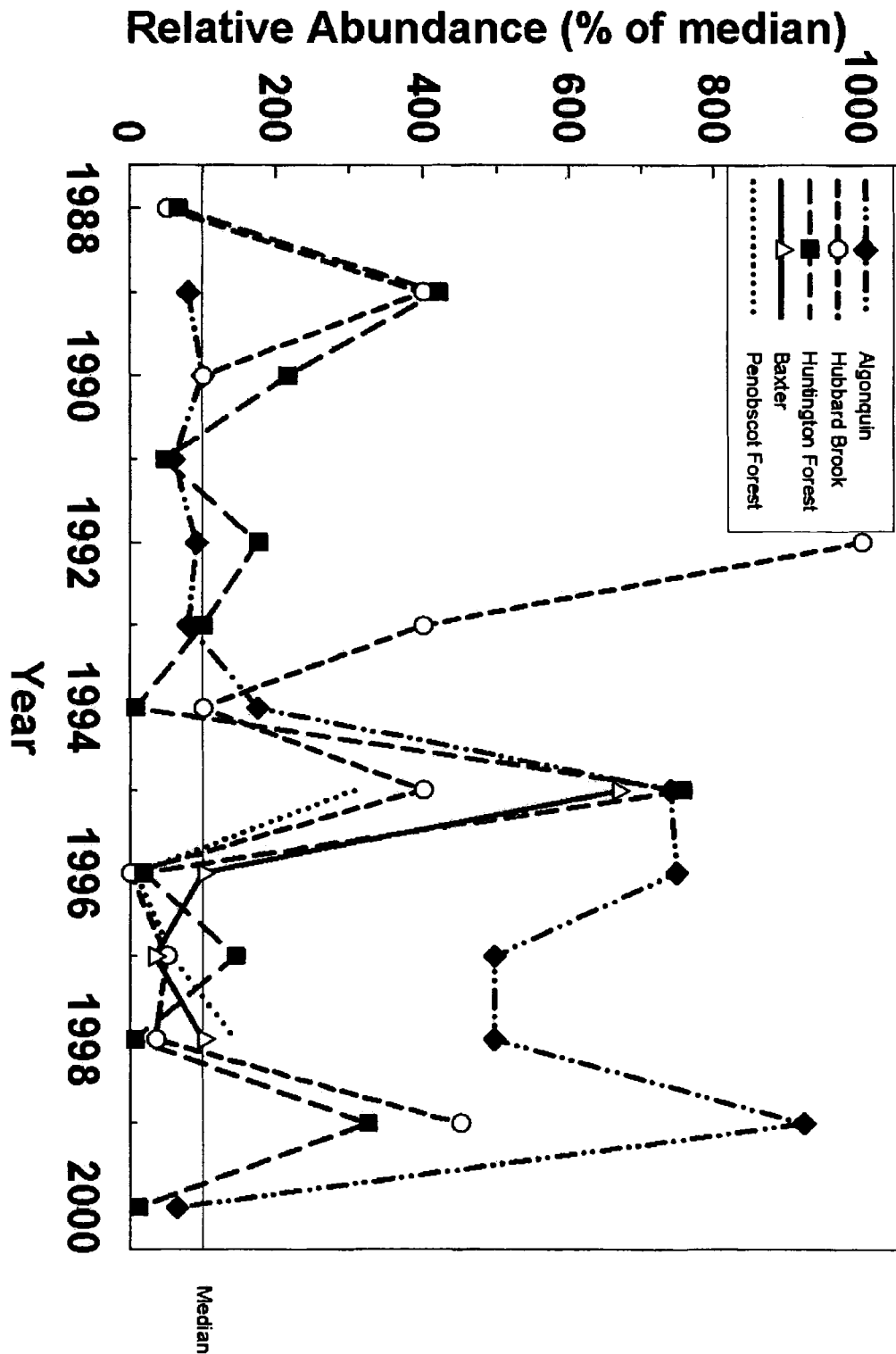


Figure 3.2. Red squirrel abundance at five locations in northeastern North America. Values for each location are standardized as percentage of the median for that series. Survey methods differed across locations (see Methods). Breaks in lines indicate years with no available data.

species was said to fit a prediction even if its population trend was not statistically significant, though significance levels of BBS trend analyses are presented for northern New England (see Appendix D). I chose a small number (i.e., 5%) as the threshold for change, and included non-significant trends because: 1) the analysis focused on the number of species showing changes in the same direction (e.g., either positive or negative), rather than the magnitude of annual change, and 2) relatively small changes within species, when multiplied over many species, can amount to relatively large changes in bird communities. High variances (see Appendix D) and a lack of significance for individual trends in any one-year period were expected because some species were observed on very few BBS routes, scattered across a large region. Even globally-declining species can have areas with population declines interspersed by areas with no change or with population increases (Villard and Maurer 1996).

I used Fisher's Exact Test (Zar 1999) to test whether the proportion of conifer forest species fitting the hypothesized pattern of population change was greater than the proportion of deciduous forest birds showing the pattern, testing each region separately for each of the two periods: 1995-1996 and 1996-1997 (Table 3.2). For a given period, if test results for group differences were not significant because both groups had >50% of species showing the expected pattern of change, I used a Binomial Test (Zar 1999) to see whether the overall proportion of species (for both groups combined) was significantly greater than 50%. I used a Sign Test (Zar 1999) to meta-analyze data from the six mutually-exclusive regions and both periods, to determine whether there was an overall tendency for higher proportions of conifer- versus deciduous-forest species showing the pattern expected.

Trend-analyses of BBS data are derived from stochastic modeling (Sauer et al. 1999), so values presented (Table 3.2) are not deterministic estimates of population change. Each time a trend-analysis simulation is re-run with the same input parameters, a slightly different trend estimate may be produced. However, differences between multiple runs of simulations that produce trend estimates usually are slight. To examine whether this variation could have affected my analyses, I selected twenty cases where the trend in one year was close to the threshold value I used (i.e. 5%), and reran trend estimate analyses five times. Averaged trend estimates differed from values based on only one simulation in only 5% of cases. Further, because 95% of all trend estimates were well above the threshold of 5% change or had an opposite sign (e.g., Table 3.1), multiple runs of trend estimates were deemed unnecessary.

Local Analysis for Ontario, 1998-2000

During the summer of 1998-2000, birds were surveyed with 12 unlimited-distance point counts in mature tolerant hardwood forest in the Wilderness Zone of Algonquin Provincial Park, Ontario (A. Jobs unpublished data). All points were separated by at least 500 m. Points were visited once per summer during the first two weeks of June; all counts were completed by 0630 EST. Birds were recorded for ten minutes per point, and abundance data for all species were pooled into a total count for each point. Abundances for each year were calculated as the mean of the 12 point counts. Red squirrel data for Algonquin Provincial Park were obtained from multiple live-trapping grids, with annual effort averaging over 4,000 trap nights (Fryxell et al. 1998, R. Brooks unpublished data). In 1999, red squirrel populations in Algonquin (Figures 3.2 and 3.3) were at a 40-year peak (Fryxell et al. 1998). Therefore, bird populations were expected to decrease from

Table 3.1. Population trends for birds in northern New England. Trends (% change) are for the combined Maine, New Hampshire, and Vermont region, based on Breeding Bird Survey data. Due to red squirrel population changes, birds were expected to decrease from 1995-1996, and to increase from 1996-1997. Species in bold show both patterns. See Appendix D for p-values, number of routes, and variance of trend estimates.

	1995-1996	1996-1997
CONIFEROUS SPECIES	Trend	Trend
Olive-sided Flycatcher	-3.43	-7.09
Yellow-bellied Flycatcher	-28.14	21.29
Blue-headed Vireo	-27.91**	5.03
Gray Jay	0.81	50.02
Boreal Chickadee	111.90	-38.56
Red-breasted Nuthatch	-37.52***	29.49
Brown Creeper	-47.85***	39.75*
Winter Wren	-44.23***	74.09***
Golden-crowned Kinglet	-26.67	23.74
Ruby-crowned Kinglet	-31.13**	18.61
Swainson's Thrush	-10.50	21.74
Hermit Thrush	-41.29***	32.40*
Magnolia Warbler	47.54	45.18***
Cape May Warbler	-16.34	172.37**
Blackburnian Warbler	3.80	22.76
Myrtle Warbler	17.37*	7.32
Black-throated Green Warbler	13.45	0.51
Bay-breasted Warbler	-35.06	296.94
Dark-eyed Junco	-31.30**	12.89
Purple Finch	38.78*	-29.10
Group Median:	-21.51	22.25
DECIDUOUS SPECIES		
Eastern Wood-Pewee	-5.03	0.43
Least Flycatcher	-10.33	9.22
Great-crested Flycatcher	2.36	17.41
Red-eyed Vireo	1.81	5.71
Warbling Vireo	3.70	4.31
Blue Jay	4.54	-17.77***
Black-capped Chickadee	25.50***	-21.27***
White-breasted Nuthatch	-14.70	-21.64
Wood Thrush	-14.19	-12.57
Veery	-13.83**	5.49
Northern Parula	28.91**	-13.29
Black-throated Blue Warbler	24.73	-13.75*
Pine Warbler	0.15	2.72
Black-and-white Warbler	-8.62	-14.68*
American Redstart	3.38	0.60
Ovenbird	7.68*	-1.64
Canada Warbler	4.58	12.52
Scarlet Tanager	-7.78	-3.42
Rose-breasted Grosbeak	-28.85***	6.85
Brown-headed Cowbird	-0.85	-7.81
Group Median:	0.98	-0.604

* denotes $0.10 > p > 0.05$; ** denotes $0.05 > p > 0.01$; *** denotes $p\text{-value} < 0.01$.

Table 3.2. Regional comparison of number of bird species fitting hypothesized patterns of population change. Predictions of population decrease and increase were based on hypothesized effect of red squirrels, and their observed population dynamics over these time periods. Bird population trends were obtained from Breeding Bird Survey data for 1995-97, and are summarized by two habitat groups and eight geographic regions of North America. Each set of values below summarizes a table of trends for 41 focal species (e.g., Table 3.1). Sample sizes were insufficient to estimate trends for some focal species in given regions and years, so totals are not always equal. See Appendix D for species comprising conifer and deciduous groups.

Exact Region	1995-1996 (Decrease predicted)			1996-1997 (Increase predicted)		
	# Species Fitting	# Species Not Fitting	Fisher Exact p-value	# Species Fitting	# Species Not Fitting	Fisher p-value
ME-NH-VT						
Conifer	12	8	0.171	16	4	0.002
Deciduous	8	12		6	14	
Adirondacks, NY						
Conifer	7	5	0.541	5	7	0.525
Deciduous	12	7		9	10	
Quebec						
Conifer	10	10	0.500	13	7	0.500
Deciduous	9	11		12	8	
Ontario						
Conifer	13	5	0.085	10	6	0.341
Deciduous	9	11		10	10	
New Brunswick						
Conifer	9	7	0.471	8	8	0.206
Deciduous	9	5		4	10	
Nova Scotia						
Conifer	10	9	0.500	10	9	0.335
Deciduous	6	7		5	8	
BBS Stratum 28 (spruce hardwoods)						
Conifer	10	11	0.308	11	10	0.069
Deciduous	7	13		5	15	
BBS Stratum 29 (closed boreal forest)						
Conifer	11	8	0.085	14	7	0.099
Deciduous	2	7		3	6	

1999-2000. Changes in bird and squirrel abundances across all years were compared with a Kruskal-Wallis test (Zar 1999). Comparisons from year to year were made by examining overlap in 95% confidence intervals around annual means.

Local Analysis for New Brunswick, 1950-1959

From 1947-1962 the “Green River Project” (Canada Agriculture unpublished report) in New Brunswick sampled insects, birds, mammals, plants, and other taxa on a series of long-term research plots (Morris et al. 1958). All raw data collected during the project was tabulated each year in a series of unpublished, archived, annual reports (Canada Agriculture unpublished report). Birds were surveyed annually by mapping territories over 3-5 visits to each plot from 1947-1959. Long term bird data are available for only three plots: G2 (1947-1954), G4 (1948-1962) and K1 (1953-1962). Plot sizes were 8 ha, 8.8 ha, and 7.7 ha, respectively.

Red squirrel abundance data were collected during most years of the Green River project, though data were based on different survey methods. The first method (hereafter “squirrel survey 1”) was a tally of all animals observed from a car or on foot (and total distance traveled) during daily travel throughout the study area each month, and is presented as the number of miles (1.6 km) traveled per animal (of each species) observed. Data for squirrel survey 1 was available for 1948 to 1954, and surveys from a car versus on foot were tallied separately. I took the inverse of the original values to get numbers of animals observed per 1.6 km. Values from surveys on foot and by car were highly correlated ($r=0.96$), but approximately 100 times more observations were collected by observers on foot. Therefore, I considered only the data from surveys on foot.

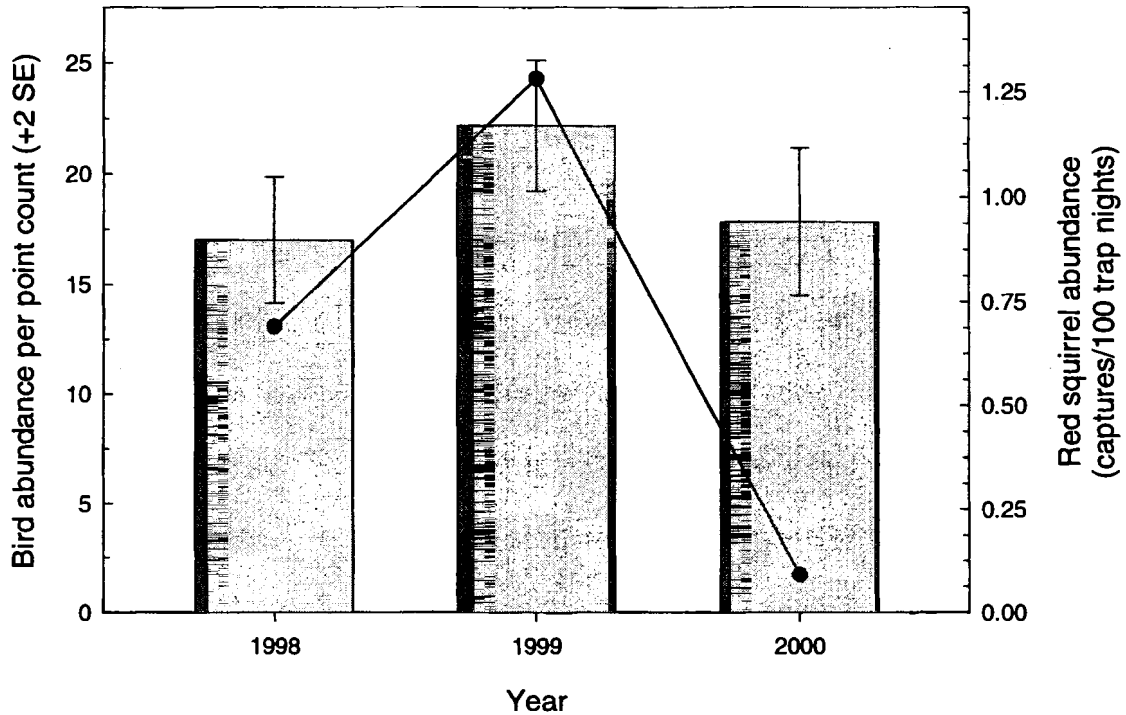


Figure 3.3. Abundance of birds and red squirrels at Algonquin Provincial Park, Ontario, 1998-2000. Average bird (bars) abundance (A. Jobs unpublished data) based on 12 unlimited-distance point counts surveyed once each summer in a wilderness zone. Red squirrel abundance (line) based on live-trapping at multiple transects across the park (Fryxell et al. 1998, R. Brooks unpublished data).

The second method was to count squirrels observed during avian territory mapping (hereafter “squirrel survey 2”). Squirrel survey 2 estimated squirrel populations by a modified version of the ‘King Method’ (Canada Agriculture 1953, unpublished report), as follows: $P = AZ / XY$, where: P = total population on area censused; A = total area of tract; Z = number of squirrels observed; X = distance walked by observer; Y = twice the average flushing distance, averaged over all years. During three years (1951-1953) there is overlap between coverage by the two different squirrel survey methods, so data can be directly compared between squirrel survey 1 and 2. The correlation for these years was extremely high ($r=0.994$) and the magnitude of values was strikingly similar, so I plotted data from both surveys on the same graph (Fig. 3.4) and axes.

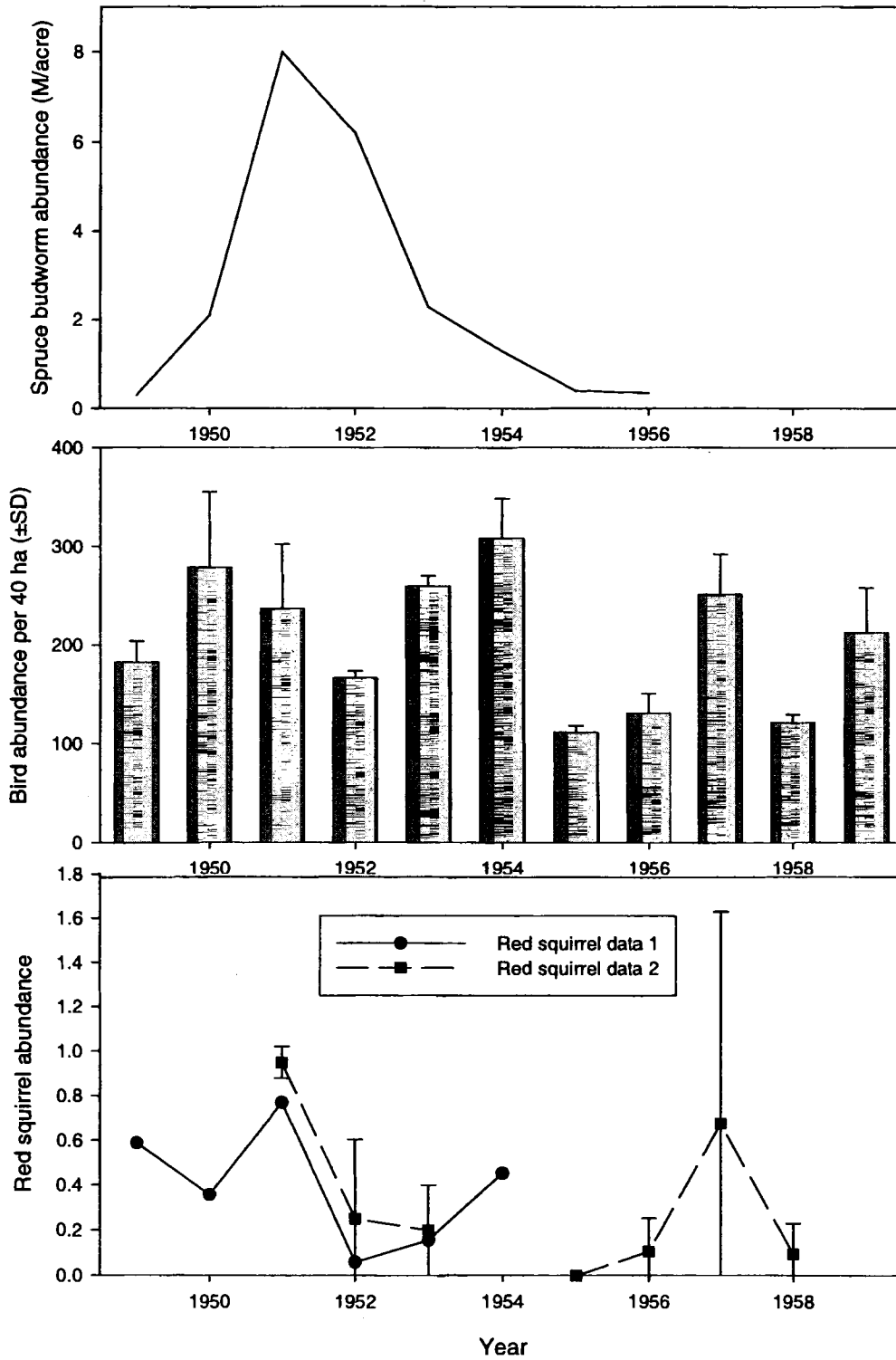


Figure 3.4. Spruce budworm (A), bird (B), and red squirrel (C) population changes from 1949-1959 in Green River, New Brunswick. Some data reproduced from Morris et al. (1958).

Annual reports from Green River (Canada Agriculture unpublished data) indicated only two years with abundant cone crops (1950 and 1956), both of which triggered a spike (in 1951 and 1957) and subsequent crash (in 1952 and 1958) in red squirrel populations. Therefore, I examined bird population changes around these two time periods. I expected a decrease in bird abundance from 1951-1952, followed by an increase from 1952-1953. I also expected birds to decrease from 1957-1958, and increase from 1958-1959. Changes in bird abundance across all years were compared with a Kruskal-Wallis test (Zar 1999). Comparisons from year to year were made by examining overlap in 95% confidence intervals around annual means. To determine whether data from all years generally fit the pattern hypothesized, I used Fisher's Exact Test (Zar 1999) to examine whether changes in bird populations were independent of squirrel populations. The outcome of each change in bird populations (i.e., increase or decrease) from year n to year $n+1$ was tallied in a 2X2 contingency table according to whether squirrel populations in the previous year (i.e., in year n) were high (i.e., above mean and median level) or low. For this test, bird populations (which were never equal) were said to increase or decrease regardless of whether changes were significant or of a large magnitude.

RESULTS

Local Analysis for Maine, 1995-1997

At the Penobscot Experimental Forest (PEF), red squirrel abundance indices from 1995-1998 differed significantly among years (Kruskal-Wallis, $p=0.0001$), with each year significantly different from all other years (Fig. 3.1). Squirrel populations in the PEF were at a four-year high in 1995, reaching 300% of the site median. This mirrored a

spike in red squirrel populations seen in northern Maine, New Hampshire, and New York, where populations reached 400-800% of median levels (Fig. 3.2). In 1996, red squirrel populations crashed to near zero in the PEF (Fig.). During 90 visits (approximately 2 hours each) to nine 10-ha sites, red squirrels were observed on only 12 visits. This population crash was also apparent at other sites in northern New England and in the Adirondacks (Fig. 3.2).

Bird abundance in the PEF (Fig. 3.1) differed significantly across all years, from 1995-1998 (Kruskal-Wallis, $p = 0.0001$). Examining overlap of 95% confidence intervals around mean abundance values showed that 1996 was significantly lower than any other year, and 1997 was significantly higher. Averaged across all sites, bird abundance decreased by 17% from 1995-1996, and increased by 45% from 1996-1997. Despite significant year-to-year fluctuations, overall bird abundance was very similar in 1995 and 1998 (Fig. 3.1). Avian productivity data were not collected in this study, so I could not relate avian population changes to changing rates of nest predation or recruitment. However, in 1995, we repeatedly observed red squirrels attempting to prey on songbirds caught in mist nets, and at least four birds were killed by squirrels. In each case the bird's head was removed or the back of the bird's neck was bitten. Squirrels were not observed preying on birds in nets during any other year, despite increases in effort (i.e., mist-net hours) every year after 1995.

Regional Analysis, 1995-1997

Red Squirrels

Most of the locations examined showed similar (and synchronous) fluctuations in red squirrel populations (Fig. 3.2), despite the fact that data were obtained from a variety

of survey methods, forest types, plot sizes, and numbers of replicates. Data from Hubbard Brook in New Hampshire and Huntington Wildlife Forest in New York were significantly correlated across all years (Spearman Coefficient = 0.68, $p = 0.02$). Pair-wise Pearson correlations between the PEF and Hubbard Brook ($r=0.93$), Huntington Forest ($r=0.87$), and Baxter ($r=0.91$) were high, but were not statistically significant ($0.07 < p < 0.13$). For 1984-1995, data from Huntington Wildlife Forest and Algonquin Provincial Park in Ontario (Fryxell et al. 1998) are significantly correlated (Pearson Coefficient = 0.81, $p = 0.05$), but when data for 1996-2000 were later added, the long-term correlations were not significant.

In assessing spatial autocorrelation from distant sites, Koenig and Knops (1998) stressed that similarities in absolute numbers of animals are less important than whether relatively large and small populations occur at the same time. In this sense, there is strong agreement among most of the data. From 1988 to 1998 all study areas but Hubbard Brook reached their highest red squirrel populations during 1995 (Fig. 3.2). For Hubbard Brook, the second highest population was recorded in 1995. Similarly, squirrel populations were very low at four of five sites in 1996, remaining high only at Algonquin Provincial Park (Fig. 3.2). Other important similarities among the data include the fact that 1989 and 1999 had very high red squirrel abundances across most of the region, whereas 1991 and 1994 had populations were well below medians at all sites.

Birds

For the combined region of Maine, New Hampshire, and Vermont, BBS data showed that 60% of conifer forest species decreased from 1995-1996, and 80% of species increased from 1996-1997 (Table 3.1). In comparison, only 40% of deciduous forest

species decreased and 30% increased during the same periods. Fisher's Exact Tests that compared conifer and deciduous forest groups were significant only for 1996-1997, however (Table 3.2). Notably, 12 of the conifer forest species fit predictions in both sets of years examined, whereas only three deciduous forest birds fit predictions in both periods (Table 3.1), a significant difference (Chi-squared test, $p = 0.003$).

The larger region that includes areas adjacent to northern New England showed similar but somewhat weaker patterns (Table 3.2). Fisher's Exact Tests comparing whether more conifer- versus deciduous-forest bird species fit the hypothesized pattern of population change were only marginally significant, and only in a few regions (Table 3.2). A meta-analysis of all mutually-exclusive regions and both years examined showed that, overall, a greater proportion of conifer-forest bird species fit the hypothesized pattern compared to deciduous-forest species (Sign test, $p = 0.0193$). For these six regions, an average of 58% of conifer forest species showed population change consistent with the hypothesis, versus 46% of deciduous forest species. At the largest scale, the two BBS strata (comprised in part by the regions above) averaged 56% of conifer forest birds showing the expected pattern, compared to only 33% of deciduous forest birds. In only one region (Adirondacks) did deciduous forest birds have a higher proportion of species show the hypothesized pattern in both years (mean = 55% compared to 50% of conifer-forest species).

In contrast to the analyses above that focused on how many species in each region showed patterns of population change consistent with the hypothesis, I also examined BBS trend data to see if some species showed similar patterns across several regions. I tabulated the regions for which each species fit the hypothesized pattern of change in

both 1995-1996 and 1996-1997 (Table 3.3). Eleven conifer-forest species fit the expected pattern in several (≥ 3) regions (Table 3.3), compared to only five deciduous-forest species. Also, this subset of 11 species exhibited the pattern in more areas (mean = 4.9 regions/species) on average than did the five deciduous forest species (mean = 3.6 regions/species). The geopolitical regions examined in this analysis are dissimilar in size, which complicates regional comparisons. Of the eleven conifer-forest species included in Table 3.3, there was a tendency for more species to show the expected pattern of change in larger regions, e.g., northern New England (9 species), Quebec (n = 9 spp.), Ontario (n = 7 spp.), and stratum 29 (n = 9 spp.), as compared to smaller regions examined, e.g., New Brunswick (n = 5 spp.), Nova Scotia (n = 5 spp.), New York (n = 4 spp.).

Local Analysis for Ontario, 1998-2000

Red squirrel populations in Algonquin reached a peak in 1999 that was higher than in any year of the previous four decades (Fig. 3.2). Though squirrel numbers in 1998 were approximately 500% of the Algonquin median, they were only about half as large as in 1999. In 2000, squirrel populations had crashed to below the median. Bird abundance at 12 point counts in Algonquin Provincial Park (A. Jobes unpublished data) differed significantly from 1998-2000 ($p=0.032$), though 95% confidence intervals for each year did overlap (Fig. 3.3). Averaging across points, abundances increased by 30.4% from 1998-1999 and decreased by 19.5% from 1999-2000. Therefore, bird abundances changed significantly over time and were consistent with the hypothesis, but differences between years were not significant.

Table 3.3. Bird species fitting hypothesized pattern of population changes. Species listed fit predictions during both periods of interest (i.e., 1995-96 *and* 1996-97), in three or more regions, based on analyses of Breeding Bird Survey data. Region abbreviations are as follows: NE = northern New England (Maine, New Hampshire and Vermont combined); QC = Quebec; ON = Ontario; NB = New Brunswick; NS = Nova Scotia; NY = Adirondack Region, New York (BBS physiographic stratum 26); 28 = BBS physiographic stratum 28 (transitional spruce hardwoods); 29 = BBS physiographic stratum 29 (closed boreal forest). See Appendix E for scientific names.

Conifer forest group^a (n=21 species)

Species	Regions where predicted patterns fit							
Winter wren	NE	QC	ON	NB	NS	NY	28	29
Red-breasted nuthatch	NE	QC	ON	NB		NY	28	29
Hermit thrush	NE	QC	ON		NS	NY	28	29
Ruby-crowned kinglet	NE	QC		NB	NS		28	29
Myrtle warbler		QC	ON		NS		28	29
Golden-crowned kinglet	NE	QC		NB				29
Blue-headed vireo	NE	QC	ON					29
Cape May warbler	NE	QC	ON					29
Yellow-bellied flycatcher	NE			NB	NS			
Dark-eyed junco	NE					NY	28	
Purple finch		QC	ON					29

Deciduous forest group^b (n=20 species)

Species	Regions where predicted patterns fit							
American redstart		QC	ON	NB			28	29
Veery	NE			NB	NS	NY		
Least flycatcher	NE			NB	NS			
Eastern wood-pewee		QC			NS	NY		
Northern parula		QC	ON		NS			

^aSpecies that are characteristic of conifer forests and have a geographic range that overlaps strongly with the range of the red squirrel

^bSpecies that are characteristic of deciduous forest, as well as two conifer-forest species placed in this group because their geographic range does not overlap strongly with the range of the red squirrel.

Local Analysis for New Brunswick, 1949-1959

The abundance of red squirrels and (Fig. 3.4) in Green River, New Brunswick changed significantly ($p=0.001$) over the 11 years examined. Red squirrel populations spiked in 1951 and 1957 (Fig. 3.4), in response to cone masting in 1950 and 1956. One year after each spike in squirrel numbers (i.e., in 1952 and 1958), bird abundance decreased by an average of 27% and 51%, respectively, though the 1951-1952 decrease was not significant. One year after each population spike, red squirrel numbers crashed to relatively low levels. Consistent with the hypothesized pattern in both cases, bird abundance was significantly higher one year later, with average abundance increases of 53% in 1953 and 76% in 1959. In nine of the 10 annual periods examined (Fig. 3.4), changes in bird abundance were consistent with the hypothesis, and were not independent of squirrel populations (Fisher's Exact Test, $p = 0.048$). It should be noted that for some years the observed changes in bird abundance were small, and only half of all year-to-year changes were statistically significant. However, with a sample size of only two plots in most years ($n=3$ plots for 2 of 11 years), and high variance between plots, statistical power to detect differences was very low.

DISCUSSION

Koenig and Knops (2000) stated that “the geographical patterns of annual seed production by forest trees have far-reaching effects on ecosystem function and biodiversity that have only begun to be explored.” This paper demonstrates that local populations of red squirrels and birds at an experimental forest in Maine showed strong patterns of change from 1995-1997 (Fig. 3.2), consistent with the hypothesis that a spike and subsequent crash in squirrel populations caused a respective decrease and increase in

bird numbers the following year(s). An examination of BBS data and red squirrel data showed the same patterns at a regional scale, for the combined states of Maine, New Hampshire, and Vermont. This pattern weakened somewhat at increased distance from northern New England. Other studies of spatial autocorrelation in ecological phenomena have shown a similar dampening of effects with increased distance (Koenig 1999, Koenig and Knops 2000).

In northern New England, most conifer-forest bird species examined fit the hypothesized pattern of change in both 1995-1996 and 1996-1997, whereas most deciduous forest species did not follow the same pattern. Averaging over both periods, the same was true for 6 of 7 adjacent (or larger-scale) regions, especially for the largest regions examined (e.g., Quebec and BBS stratum 29). However, some states and provinces adjacent to northern New England showed weak, inconsistent, or contrasting patterns in some years, and most of the tests for group differences were not significant (Table 3.2). In a few regions and periods examined, a higher proportion of deciduous- than conifer-forest birds fit the expected pattern; or both deciduous- and conifer-forest groups had >50% of species showing the pattern.

At least two factors could act to diminish differences between conifer- and deciduous-forest bird groups. During years when their populations are high, red squirrels may be widespread across much of a region, including deciduous forest habitats (e.g. Rusch and Reeder 1978). Indeed, much of the red squirrel data in Fig. 3.1 (i.e., from Algonquin, Hubbard Brook, and Huntington Forest) was obtained from primarily deciduous, “northern hardwood” forests. Avian productivity is affected by both nest predation and food availability, so conifer masting could have positive and negative influences on birds

if it increases both food availability and nest-predator populations. Mast years obviously provide a food surplus for seed-eating birds, but other species also may benefit. Selås and Steel (1998) demonstrated that seed masting in trees was associated with an increase in populations of herbivorous insects, because seed production comes at the expense of plant chemical defenses. Thus, insect prey for both conifer- and deciduous-forest birds may increase during mast years, and increased food availability should positively influence avian productivity. The evidence I examined demonstrates that mast years usually are followed by decreases in bird populations, indicating that high red squirrel populations have stronger effects on short-term avian trends than does increased food availability.

The correlation between squirrel and bird populations does not necessarily imply causation. The simplest interpretation of the patterns above would be that the same external factor (e.g., weather) that increased or decreased squirrel abundance in one year also caused increases or decreases in bird abundance during the same year. However, the data do not show consistently similar changes in bird and squirrel populations in the same years. For example, Fig. 3.1 shows that bird abundances in Maine in 1995 and 1998 were nearly the same, whereas squirrel numbers were very high in 1995 but were much lower in 1998. Likewise, the data from New Brunswick (Fig. 3.4) show that when bird numbers were at their highest, squirrel numbers could be high, intermediate, or low. The possibility that the same external factors affect birds and squirrels similarly in the same year also seems unlikely given what we know about squirrel population dynamics and the time lags involved. Many studies (reviewed in Gurnell 1983) have shown that squirrel abundance in one year (t) is strongly linked to cone production the previous year (i.e.,

$t-1$). However, cone production in $t-1$ is influenced by weather patterns at least one year before cone maturity (i.e., $t-2$), when cones are initiated (Sirois 2000, Koenig and Knops 2000). Thus, squirrel dynamics can be partially explained by weather patterns, but with a two-year time lag. It is not clear how changes in bird populations could be a result of weather patterns from two years earlier. Possibly, the same weather patterns that trigger mast years also result in relatively low or high overwinter survival of resident species, and their abundance affects the productivity of migrant species during the following summer. If there is conifer/deciduous habitat segregation between resident and migrant species, this could account for some of the differences these groups exhibit. The group of conifer forest birds I examined did have more resident species than did the group of deciduous forest birds; however migratory species comprised most (i.e., >70%) of both groups. Given the strong evidence from across North America that red squirrels affect avian nest predation rates (see below), I believe that the most likely explanation is that squirrel population fluctuations affected bird populations.

Several studies have suggested or shown strong links between squirrel populations and avian nest-success rates. McFarland et al. (unpublished manuscript), working in alpine conifer forests in Vermont, found that red squirrel populations were relatively high and low every other year because of a biannual pattern of cone production. Nest success for Bicknell's thrush (*Catharus bicknelli*) was inversely proportional to the abundance of red squirrels, which are the primary nest-predators in the area (McFarland, pers. comm.). Darveau et al. (1997), working in Quebec for four years, found that the year with the highest red squirrel densities had the highest artificial nest predation rates. Studying artificial nests in southeast Alaska and Canada, Sieving and Willson (1998) also

found a strong relationship between red squirrel populations and depredation rates. They stated that “intra-seasonal and especially supra-annual population peaks may amplify small mammal attack rates to significant levels, with consequences for passerine population ecology.” They concluded that “red squirrels may largely define the distribution of a process (i.e., nest predation) at the regional landscape scale” (Sieving and Willson 1998).

I found only one published study that used an experimental approach to examine the influence of red squirrels on nest-predation rates. Reitsma et al. (1990) found no difference in artificial nest-predation rates between control plots and plots where squirrels were removed. Unfortunately, data on red squirrel population levels (e.g., Fig. 3.1) were not available for 1987, the year that field work was done by Reitsma et al. (1990). Because of the dramatic fluctuations that are common for red squirrel populations, it seems impractical to assess the role of squirrels as nest-predators in a one-year study, with no context for relative squirrel population levels during that year. In fact, short-term studies of avian productivity could often be misleading if temporal dynamics in populations of nest predators are not taken into account. For example, Sloan et al. (1998), working in the White Mountains of New Hampshire, found that red squirrels accounted for 51% of artificial nest-predators photographed during 1990, but only 9% in 1991, when fishers (*Martes pennanti*) accounted for 74%.

Sloan et al. (1998) emphasized that “the intensity of depredation at birds’ nests varies both spatially and temporally, and the patterns of such variation must be known both to understand their effects on bird populations and to devise appropriate conservation and management plans.” Constraints on time and finances mean that many

studies of avian nest-predation fail to account for temporal differences in predator populations. The effects of fluctuating populations of nest predators probably vary depending on habitat (Rusch and Reeder 1978), their abundance in a given season and year (Fryxell et al. 1998, Stevens and Kennedy 1999), and the abundance of other nest-predators (Darveau et al. 1997, King et al. 1998). Avian populations may be disproportionately affected in years when squirrels are relatively abundant or relatively rare. It is less obvious how squirrels would influence avian productivity during years when their populations are at intermediate levels; during those years other factors (e.g., food supply) may be more important.

Changes in bird populations have long been noted by ornithologists and attributed to many ecological factors (e.g., food and weather). Many studies have shown important links between productivity and population fluctuations of birds, small mammals, and larger nest predator species (Dunn 1977, King 1983, Bêty et al. 2001). However, most of this research has shown that avian productivity relates to small mammal populations because of “prey switching” by larger predators (e.g., Mustelids or Canids), which prey on birds more or less as small mammals cycle through low or high densities, respectively. I believe that bird populations can relate directly to populations of small mammal nest-predators, without the presence of intermediary species. The fact that small mammals directly affect avian nest predation rates is not new (e.g., Haskell 1995), but previous research has not demonstrated a link between population sizes of birds and their small mammalian predators.

Likewise, researchers who originally collected and analyzed some of the data in this paper (i.e., New Brunswick data in Fig. 3.4) did not consider the possibility that red

squirrel fluctuations affected birds. Morris et al. (1958) assumed that changes in bird density were caused by a superabundance of food resulting from a spruce budworm (*Choristoneura fumiferana*) outbreak occurring in the region. Morris et al. (1958) found three bird species that experienced dramatic (e.g., 12-fold) increases in density during the spruce budworm outbreak. However, an examination of Figure 4 shows that if all species of birds observed in the research plots are considered, avian abundance seems to be related more strongly to the abundance of red squirrels than to budworm larvae. Morris et al. (1958) showed that spruce budworm abundance increased dramatically from 1949 to 1951, then decreased steadily afterwards, approaching pre-outbreak levels by 1955 (reproduced on Fig. 3.4). Bird abundances are generally higher during the outbreak, but yearly fluctuations are strong and not obviously linked to budworm density (Fig. 3.4). For example, budworm density peaked in 1951, but abundance of all bird species studied decreased from 1951-1952. I believe that this decrease was caused by high squirrel densities in 1951, which reduced avian productivity despite the abundance of budworm larvae. Even bird species that showed the strongest response to spruce budworm (MacArthur 1958, Morris 1958) decreased sharply from 1951 to 1952. I speculate that the positive numeric response that Morris et al. (1958) observed in budworm-associated birds was enabled or enhanced by the fact that red squirrel populations crashed in 1952 and remained at relatively low levels for two years.

This paper indicates that important patterns in red squirrel nest-predation occur at greater temporal and spatial scales than previously realized. However, it is not clear how much red squirrel distributions vary temporally or spatially within or between specific regions or in deciduous forests nested within a largely conifer forest region. The data in

Fig. 3.1 indicate considerable spatial autocorrelation for red squirrel populations, but are a relatively crude attempt to address this issue. A good understanding of the spatial and temporal dynamics of red squirrel populations can only come from comprehensive sampling that was designed to examine this issue over sufficient spatial and temporal scales. Red squirrels are vocal and obvious animals, easily sampled by many techniques, so monitoring their populations is not difficult. One possibility would be for volunteers to collect red squirrel data in the same fashion that singing birds are counted during the Breeding Bird Survey. In many regions, annual fluctuations in red squirrel populations are predictable, as they correspond to changes in conifer cone production (Gurnell 1983). Cone production is also easy to observe, so any sampling scheme for red squirrel populations should also include at least an index of the cone crop. If data for red squirrels and cone crops could be collected across a large geographic area and over many years, they could be used in conjunction with BBS data to examine the extent to which bird and squirrel populations are spatially and temporally related. These data could provide a very strong test of the hypothesis I have outlined, and ultimately may be useful in predicting and explaining changes in bird populations, even before they occur. In any case, researchers studying avian breeding biology should try to monitor the abundance of any potential nest predators (e.g. red squirrels), especially when this information can be acquired with little additional effort or cost.

LITERATURE CITED

- Andrén, H., and P.-A. Lemnell. 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. *Ecography* 15:303-307.
- Bayne, E. M., and K. A. Hobson. 1997a. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- Bayne, E. M., and K. A. Hobson. 1997b. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. *Ecography* 20:233-239.
- Bayne, E. M., and K. A. Hobson. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Canadian Journal of Zoology* 76:62-69.
- Bêty, J., G. Gauthier, J.-F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* 93:388-400.
- Boag, D. A., S. G. Reeb, and M. A. Schroeder. 1984. Egg loss among spruce grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62:1034-1037.
- Callahan, J. R. 1993. Squirrels as predators. *Great Basin Naturalist* 53:137-144.
- Canada Agriculture. 1948-1962. The Green River project annual report. Series of unpublished annual reports for project E. 30.07-6. Forest Biology Laboratory, Fredericton, New Brunswick.
- Danell, K., T. Willebrand, and L. Baskin. 1998. Mammalian herbivores in the boreal forests: their numerical fluctuations and use by man. *Conservation Ecology* [online] 2(2):9
- Darveau, M., L. Bélanger, J. Huot, É. Mélançon, and S. DeBellefeuille. 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. *Ecological Applications* 7:572-580.
- Delin, A. E., and H. Andrén. 1999. Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forested landscape. *Landscape Ecology* 14:67-72.
- Dunn, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46:633-652.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The birder's handbook*. Simon & Schuster Inc., New York. 785 pp.

- Erlie, D. A., and J. R. Tester. 1984. Population ecology of Sciurids in Northwestern Minnesota. *Canadian Field-Naturalist* 98:1-6.
- Fryxell, J. R., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology* 79:213-225.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammalogy Review* 13:133-148.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10:188-202.
- Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* 9:1316-1318.
- Hatt, R. T. 1929. The red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. *Roosevelt Wild Life Annals* 2:11-145.
- Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a Neotropical migrant, the black-throated blue warbler (*Dendroica caerulescens*) in an unfragmented temperate forest. *Auk* 109:321-333.
- Kemp, G. A., and L. B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. *Ecology* 51:763-779.
- King, C. M. 1983. The relationship between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52:141-166.
- King, D. I., C. R. Griffin, and R. M. DeGraaf. 1998. Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape. *Forest Ecology and Management* 104:151-156.
- Koenig, W. D., and J. M. H. Knops. 1998. Testing for spatial autocorrelation in ecological studies. *Ecography* 21:423-429.
- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist* 155:59-69.
- Lurz, P. W. W., P. J. Garson, and L. A. Wauters. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). *Journal of Zoology* 251:167-178.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.

- Martin, T. E. 1987. Artificial nest experiments: effects on nest appearance and type of predator. *Condor* 89:925-928.
- Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *Bioscience* 43:523-532.
- Millar, J. S. 1970. Variations in fecundity of the red squirrel, *Tamiasciurus hudsonicus* (Erxleben). *Canadian Journal of Zoology* 48:1055-1058.
- Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* 39:487-494.
- Nelson, E. W. 1918. Smaller mammals of North America. *National Geographic Magazine* 33(5):371-493.
- Nero, R. W. 1987. House sparrow killed by red squirrel. *Blue Jay* 45:180-181.
- Nero, R. W. 1993. Another red squirrel bird kill. *Blue Jay* 51:217-218.
- Nour, N., E. Matthysen, and A. A. Dhondt. 1993. Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography* 16:111-116.
- Park, J. L. 1987. Red squirrel harasses sharp-shinned hawk. *Alberta Naturalist* 17:16.
- Ranta, E., V. Kaitala, J. Lindström, and E. Helle. 1997. The Moran effect and synchrony in population dynamics. *Oikos* 78:136-142.
- Rathcke, B. J., and R. W. Poole. 1974. Red squirrel attacks a Pileated Woodpecker. *Wilson Bulletin* 86:465-466.
- Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375-380.
- Rusch, D. A., and W. G. Reeder. Population ecology of Alberta red squirrels. *Ecology* 59:400-420.
- Sauer, J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 1999. The North American breeding bird survey, results and analysis 1966-1998. Version 98.1, USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- Seitz, L. C., and D. A. Zegers. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. *Condor* 95:297-304.

- Selås, V. and C. Steel. 1998. Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis. *Oecologia* 116:449-455.
- Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance Neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. Pp. 431-442 in J. M. Hagan III, and D. W. Johnston, eds. *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, 609 pp.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* 79:2391-2402(?).
- Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest – tree line transect. *Canadian Journal of Forest Resources* 30:900-909.
- Sloan, S. S., R. T. Holmes, and T. W. Sherry. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* 62:529-539.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* 40:349-371.
- Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species No. 586, pp. 1-9. American Society of Mammalogists.
- Sullivan, B. D. 1991. Additional vertebrate prey items of the red squirrel, *Tamiasciurus hudsonicus*. *Canadian Field-Naturalist* 105:398-399.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-?
- Thoms, C. S. 1922. Are squirrels bird-enemies? *Bird Lore* 24:207.
- Vander Haegen, W. M., and R. M. DeGraaf. 1996a. Predation on artificial nests in forested riparian buffer strips. *Journal of Wildlife Management* 60:542-550.
- Vander Haegen, W. M., and R. M. DeGraaf. 1996b. Predation rates on artificial nests in an industrial forest landscape. *Forest Ecology and Management* 86:171-179.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th Edition. Prentice Hall, NJ. 929 pp.

BIBLIOGRAPHY

- Anderson, D., and K. Burnham. 1999a. General strategies for the analysis of ringing data. *Bird Study* 46(suppl.):S261-270.
- Anderson, D., and K. Burnham. 1999b. Understanding information criteria for selection among capture-recapture or ring recovery models. *Bird Study* 46(suppl.):S14-21.
- Andr n, H., and P.-A. Lemnell. 1992. Population fluctuations and habitat selection in the Eurasian red squirrel *Sciurus vulgaris*. *Ecography* 15:303-307.
- Annand, E.M., and F.R. Thompson, III. 1997. Forest bird response to regeneration practices in central hardwood forests. *Journal of Wildlife Management* 61:159-171.
- Barrowclough, G.F. 1978. Sampling bias in dispersal studies based on finite area. *Bird-Banding* 49:333-341.
- Bayne, E. M., and K. A. Hobson. 1997a. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418-1429.
- Bayne, E. M., and K. A. Hobson. 1997b. Predation on artificial nests in relation to forest type: contrasting the use of quail and plasticine eggs. *Ecography* 20:233-239.
- Bayne, E. M., and K. A. Hobson. 1998. The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixedwood forest. *Canadian Journal of Zoology* 76:62-69.
- Beletsky, L.D., and G.H. Orians. 1987. Territoriality among male red-winged blackbirds. *Behavioral Ecology and Sociobiology* 20:21-34.
- B ty, J., G. Gauthier, J.-F. Giroux, and E. Korpim ki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos* 93:388-400.
- Bird, D.M. 1999. *The bird almanac*. Key Porter Books Limited, Toronto. 460 pp.
- Blake, J.G., J.M. Hanowski, G.J. Niemi, and P.T. Collins. 1994. Annual variation in bird populations of mixed conifer-northern hardwood forests. *Condor* 96:381-399.
- Blondel, J., and R. Pradel. 1989. Is adult survival of the Blue Tit higher in a low fecundity insular population than in a high fecundity mainland one? Pp. 131-144 *in* Population biology of Passerine birds (J. Blondell, A. Gosler, J.-D. Lebreton, and R. McCleery, Eds.). NATO ASI Series G: Ecological Sciences, Vol. 24. Springer-Verlag, New York.
- Boag, D. A., S. G. Reeb, and M. A. Schroeder. 1984. Egg loss among spruce grouse inhabiting lodgepole pine forests. *Canadian Journal of Zoology* 62:1034-1037.

- Brown, D.R., P.C. Stouffer, and C.M. Strong. 2000. Movement and territoriality of wintering hermit thrushes in southeastern Louisiana. *Wilson Bulletin* 112:347-353.
- Buford, E.W., and D.E. Capen. 1999. Abundance and productivity of forest songbirds in a managed, unfragmented landscape in Vermont. *Journal of Wildlife Management* 63:180-188.
- Callahan, J. R. 1993. Squirrels as predators. *Great Basin Naturalist* 53:137-144.
- Canada Agriculture. 1948-1962. The Green River project annual report. Series of unpublished annual reports for project E. 30.07-6. Forest Biology Laboratory, Fredericton, New Brunswick.
- Clobert, J., and J.-D. Lebreton. 1991. Estimation of demographic parameters in bird populations. Pp. 75-104 *in* Bird population studies: relevance to conservation and management (C.M. Perrins, J.-D. Lebreton, and G.J.M. Hirons, Eds.). Oxford University Press, New York.
- Danchin, E., and E. Cam. 2002. Can non-breeding be a cost of breeding dispersal? *Behavioral Ecology and Sociobiology* 51:153-163.
- Danell, K., T. Willebrand, and L. Baskin. 1998. Mammalian herbivores in the boreal forests: their numerical fluctuations and use by man. *Conservation Ecology* [online] 2(2):9
- Darley, J.A., D.M. Scott, and K.M. Taylor. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. *Bird-Banding* 48:145-151.
- Darveau, M., L. Bélanger, J. Huot, É. Mélançon, and S. DeBellefeuille. 1997. Forestry practices and the risk of bird nest predation in a boreal coniferous forest. *Ecological Applications* 7:572-580.
- Delin, A. E., and H. Andrén. 1999. Effects of habitat fragmentation on Eurasian red squirrel (*Sciurus vulgaris*) in a forested landscape. *Landscape Ecology* 14:67-72.
- Derleth, E.L., D.G. McAuley, and T.J. Dwyer. 1989. Avian community response to small-scale habitat disturbance in Maine. *Canadian Journal of Zoology* 67:385-390.
- Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The evolutionary ecology of dispersal. *Trends in Evolution and Ecology* 14:88-90.
- Dunn, E. 1977. Predation by weasels (*Mustela nivalis*) on breeding tits (*Parus* spp.) in relation to the density of tits and rodents. *J. Anim. Ecol.* 46:633-652.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook. Simon & Schuster Inc., New York. 785 pp.

- Erlie, D. A., and J. R. Tester. 1984. Population ecology of Sciurids in Northwestern Minnesota. *Canadian Field-Naturalist* 98:1-6.
- Fryxell, J. R., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. *Ecology* 79:213-225.
- Germaine, S. S., S.H. Vessey, and D.E. Capen. 1997. Effects of small forest openings on the breeding bird community in a Vermont hardwood forest. *Condor* 99:708-718.
- Gram, W.K., V.L. Sork, R.J. Marquis, R.B. Renken, R.L. Clawson, J. Faaborg, D.K. Fantz, J. Le Corff, J. Lill, and P.A. Porneluzi. 2001. Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest. *Ecological Applications* 11:1667-1679.
- Greenwood, P.J., and P.H. Harvey. 1977. Feeding strategies and dispersal of territorial Passerines: a comparative study of the Blackbird (*Turdus merula*) and the Greenfinch (*Carduelis chloris*). *Ibis* 119:528-531.
- Greenwood, P.J., and P.H. Harvey. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1-21.
- Gurnell, J. 1983. Squirrel numbers and the abundance of tree seeds. *Mammalogy Review* 13:133-148.
- Hagan, J. M., W. M. Vander Haegen, and P. S. McKinley. 1996. The early development of forest fragmentation effects on birds. *Conservation Biology* 10:188-202.
- Hagan, J.M., P.S. McKinley, A.L. Meehan, and S.L. Grove. 1997. Diversity and abundance of landbirds in a northeastern industrial forest. *Journal of Wildlife Management* 61:718-735.
- Haskell, D. G. 1995. A reevaluation of the effects of forest fragmentation on rates of bird-nest predation. *Conservation Biology* 9:1316-1318.
- Hatt, R. T. 1929. The red squirrel: its life history and habits, with special reference to the Adirondacks of New York and the Harvard Forest. *Roosevelt Wild Life Annals* 2:11-145.
- Holmes, R.T., and T.W. Sherry. 1988. Assessing population trends of New Hampshire forest birds: local vs. regional patterns. *Auk* 105:756-768.
- Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a Neotropical migrant, the black-throated blue warbler (*Dendroica caerulescens*) in an unfragmented temperate forest. *Auk* 109:321-333.
- Hunter, M.L., Jr. 1990. *Wildlife, forests, and forestry: principles of managing for biological diversity*. Prentice-Hall, Inc. Englewood Cliffs, NJ. 370 pp.

- I.B.C.C.(International Bird Census Committee) 1970. An international standard for a mapping method in bird census work recommended by the I.B.C.C. Audubon Field Notes 24:722-736.
- Johnston, J.P., W.J. Peach, R.D. Gregory, and S.A. White. 1997. Survival rates of tropical and temperate Passerines: a Trinidadian perspective. American Naturalist 150:771-789.
- Jones, P.W., and T.M. Donovan. 1996. Hermit thrush (*Catharus guttatus*). In The birds of North America, no. 261 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- Kemp, G. A., and L. B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology 51:763-779.
- King, C. M. 1983. The relationship between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. Journal of Animal Ecology 52:141-166.
- King, D. I., C. R. Griffin, and R. M. DeGraaf. 1998. Nest predator distribution among clearcut forest, forest edge and forest interior in an extensively forested landscape. Forest Ecology and Management 104:151-156.
- Koenig, W. D., and J. M. H. Knops. 1998. Testing for spatial autocorrelation in ecological studies. Ecography 21:423-429.
- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. American Naturalist 155:59-69.
- Koenig, W.D., D. Van Vuren, and P.N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Evolution and Ecology 12:514-517.
- Lebreton, J.D., K.P. Burnham, J. Clobert, and R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.
- Lent, R.L., and D.E. Capen. 1995. Effects of small-scale habitat disturbance on the ecology of breeding birds in a Vermont (USA) hardwood forest. Ecography 18:97-108.
- Lorimer, C.G. 1977. The presettlement forest and natural disturbance cycle of northeastern Maine. Ecology 58:139-148.
- Lurz, P. W. W., P. J. Garson, and L. A. Wauters. 2000. Effects of temporal and spatial variations in food supply on the space and habitat use of red squirrels (*Sciurus vulgaris* L.). Journal of Zoology 251:167-178.

- Lynch, J.F., and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28:287-324.
- MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39:599-619.
- Martin, T. E. 1987. Artificial nest experiments: effects on nest appearance and type of predator. *Condor* 89:925-928.
- Martin, T. E. 1993. Nest predation and nest sites: New perspectives on old patterns. *Bioscience* 43:523-532.
- Martin, T.E. and P. Li. 1992. Life history traits of open- vs. cavity-nesting birds. *Ecology* 73:579-592.
- Martin, T.E., J. Clobert, and D.R. Anderson. 1995. Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22:863-875.
- McCune, B., and M.J. Mefford. 1997. Multivariate analysis of ecological data. Version 3.09. MjM Software, Gleneden Beach, OR.
- Millar, J. S. 1970. Variations in fecundity of the red squirrel, *Tamiasciurus hudsonicus* (Erxleben). *Canadian Journal of Zoology* 48:1055-1058.
- Morris, R. F., W. F. Cheshire, C. A. Miller, and D. G. Mott. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* 39:487-494.
- Nelson, E. W. 1918. Smaller mammals of North America. *National Geographic Magazine* 33(5):371-493.
- Nero, R. W. 1987. House sparrow killed by red squirrel. *Blue Jay* 45:180-181.
- Nero, R. W. 1993. Another red squirrel bird kill. *Blue Jay* 51:217-218.
- Norton, M.R., and S.J. Hannon. 1997. Songbird response to partial-cut logging in the boreal mixedwood forest of Alberta. *Canadian Journal of Forest Research* 27:44-53.
- Nour, N., E. Matthysen, and A. A. Dhondt. 1993. Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography* 16:111-116.
- O'Connor, R.J. 1981. The influence of observer and analyst efficiency in mapping method censuses. *Studies in Avian Biology* 6:372-376.
- Opdam, P., G. Rijdsdijk, and F. Hustings. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biological Conservation* 34:333-352.
- Park, J. L. 1987. Red squirrel harasses sharp-shinned hawk. *Alberta Naturalist* 17:16.

- Ranta, E., V. Kaitala, J. Lindström, and E. Helle. 1997. The Moran effect and synchrony in population dynamics. *Oikos* 78:136-142.
- Rathcke, B. J., and R. W. Poole. 1974. Red squirrel attacks a Pileated Woodpecker. *Wilson Bulletin* 86:465-466.
- Reitsma, L. R., R. T. Holmes, and T. W. Sherry. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunks, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57:375-380.
- Rowley, I., and E. Russell. 1991. Demography of Passerines in the temperate southern hemisphere. Pp. 22-44 *in* Bird population studies: relevance to conservation and management (C.M. Perrins, J.-D. Lebreton, and G.J.M. Hirons, Eds.). Oxford University Press, New York.
- Rudnick, T., and M.L. Hunter, Jr. 1993. Reversing the fragmentation perspective: effects of clearcut size on bird species richness in Maine. *Ecological Applications* 3:357-366.
- Runkle, J.R. 1985. Disturbance regimes in temperate forests. Pp. 17-33 *in* The ecology of natural disturbance and patch dynamics (S. T. A. Pickett, and P.S. White, Eds.). Academic Press, Orlando, FL. 472 pp.
- Rusch, D. A., and W. G. Reeder. Population ecology of Alberta red squirrels. *Ecology* 59:400-420.
- Sallabanks, R., and J.M. Marzluff. 2000. Forest management and bird populations: an introduction. *Wildlife Society Bulletin* 28:1086-1087.
- Sallabanks, R., E.B. Arnett, and J.M. Marzluff. 2000. An evaluation of research on the effects of timber harvest on bird populations. *Wildlife Society Bulletin* 28:1144-1155.
- SAS Institute. 1990. SAS/STAT user's guide, version 6. SAS Institute, Cary, NC.
- Sauer, J. R., J. E. Hines, I. Thomas, J. Fallon, and G. Gough. 1999. The North American breeding bird survey, results and analysis 1966-1998. Version 98.1, USGS Patuxent Wildlife Research Center, Laurel, Maryland.
- Seitz, L. C., and D. A. Zegers. 1993. An experimental study of nest predation in adjacent deciduous, coniferous and successional habitats. *Condor* 95:297-304.
- Selås, V., and C. Steel. 1998. Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis. *Oecologia* 116:449-455.
- Seymour, R.S., A.S. White, and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America—evaluating silvicultural systems using natural scales and frequencies. *Forest Ecology and Management* 155:357-367.

- Sherry, T. W., and R. T. Holmes. 1992. Population fluctuations in a long-distance Neotropical migrant: Demographic evidence for the importance of breeding season events in the American Redstart. Pp. 431-442 *in* Ecology and conservation of Neotropical migrant landbirds (J. M. Hagan III, and D. W. Johnston, Eds). Smithsonian Institution Press, Washington, 609 pp.
- Sieving, K. E., and M. F. Willson. 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* 79:2391-2402.
- Sirois, L. 2000. Spatiotemporal variation in black spruce cone and seed crops along a boreal forest – tree line transect. *Canadian Journal of Forest Resources* 30:900-909.
- Slagsvold, T., and J.T. Lifjeld. 1989. Return rates of male Pied Flycatchers: an experimental study manipulating breeding success. Pp. 441-452 *in* Population biology of Passerine birds (J. Blondell, A. Gosler, J.-D. Lebreton, and R. McCleery, Eds.). NATO ASI Series G: Ecological Sciences, Vol. 24. Springer-Verlag, New York.
- Sloan, S. S., R. T. Holmes, and T. W. Sherry. 1998. Depredation rates and predators at artificial bird nests in an unfragmented northern hardwoods forest. *Journal of Wildlife Management* 62:529-539.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* 40:349-371.
- Smith, T.M., and H.H. Shugart. 1987. Territory size variation in the Ovenbird: the role of habitat structure. *Ecology* 68:695-704.
- Sokal, R.R., and F.J. Rohlf. 2000. *Biometry*. W.H. Freeman and Company, New York. 887 pp.
- Steele, M. A. 1998. *Tamiasciurus hudsonicus*. Mammalian Species No. 586, pp. 1-9. American Society of Mammalogists.
- Sullivan, B. D. 1991. Additional vertebrate prey items of the red squirrel, *Tamiasciurus hudsonicus*. *Canadian Field-Naturalist* 105:398-399.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-2903.
- Thompson, F.R. III, J. D. Brawn, S. Robinson, J. Faaborg, and R.L. Clawson. Approaches to investigate effects of forest management on birds in eastern deciduous forests: How reliable is our knowledge? *Wildlife Society Bulletin* 28:1111-1122.
- Thoms, C. S. 1922. Are squirrels bird-enemies? *Bird Lore* 24:207.

- Tittler, R., and S.J. Hannon. 2000. Nest predation in and adjacent to cutblocks with variable tree retention. *Forest Ecology and Management* 136:147-157.
- Van Horn, M.A., and T.M. Donovan. 1994. Ovenbird (*Seiurus aurocapillus*). In *The birds of North America*, no. 88 (A. Poole and F. Gill, Eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania; The American Ornithologists' Union, Washington, D.C.
- Vander Haegen, W. M., and R. M. DeGraaf. 1996a. Predation on artificial nests in forested riparian buffer strips. *Journal of Wildlife Management* 60:542-550.
- Vander Haegen, W. M., and R. M. DeGraaf. 1996b. Predation rates on artificial nests in an industrial forest landscape. *Forest Ecology and Management* 86:171-179.
- Verner, J., and K.A. Milne. 1990. Analyst and observer variability in density estimates from spot mapping. *Condor* 92:313-325.
- Webb, W.L., D.F. Behrend, and B. Saisorn. 1977. Effect of logging on songbird populations in a northern hardwood forest. *Wildlife Monographs* No. 55. 35 pp.
- Welsh, C.J.E., and W.M. Healy. 1993. Effect of even-aged timber management on bird species diversity and composition in northern hardwoods of New Hampshire. *Wildlife Society Bulletin* 21:143-154.
- White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46(suppl.):S120-139.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th Edition. Prentice Hall, NJ. 929 pp.

APPENDICES

APPENDIX A. Data and Analyses Related to Chapter 1

Table A.1. Abundance of bird territories in 1995. Includes nine (10 ha) research areas (RA) in the Penobscot Experimental Forest, Bradley, Maine. For this year only one research area (i.e., RA 8) was not sampled, so data are not available (na). For scientific nomenclature, see Appendix E.

Common Name	Species Code	RA	RA	RA	RA	RA	RA	RA	RA	RA
		1	2	3	4	5	6	7	8	9
Black-and-white Warbler	BAWW	0.5	1	0	1	0	2	3	na	1
Blackburnian Warbler	BLWA	6	6	7.5	4	6	3	3	na	3
Black-capped Chickadee	BCCH	2.5	2.5	2	2	2	3	3	na	2
Black-throated Blue Warbler	BTBW	1.5	2	2	2	0	2	2	na	4
Black-throated Green Warbler	BTGW	7	6	6	2	4	3.5	1.5	na	3
Blue Jay	BLJA	2	2	2	1	2	1	1	na	1
Brown Creeper	BRCR	1	1	2	2	2	1	1	na	2
Brown-headed Cowbird	BHCO	0	0	0	0	0	0	1	na	0
Canada Warbler	CAWA	0	0	0	0	2	0	0	na	5
Eastern Wood Pewee	EWPE	0	2	2	1	0	0	0	na	0
Golden-crowned Kinglet	GCKI	2	0	2	2.5	4	1	3	na	1
Great-crested Flycatcher	GCFL	0	0	0	0	0	1	0	na	0
Hairy Woodpecker	HAWO	0.5	0	1	0	0	0	1	na	0
Hermit Thrush	HETH	4	4	3	3	4	3.5	3.5	na	3.5
Magnolia Warbler	MAWA	0	0	0	0	1	1	0	na	3
Northern Parula	NOPA	3	6	5	5	5	6.5	6	na	2
Ovenbird	OVEN	4.5	6.5	4	7	6	5.5	7	na	5
Pine Warbler	PIWA	0	0.5	1	0	0	0	1	na	0
Purple Finch	PUFI	2	0	0	0	0	0	0	na	0
Red-breasted Nuthatch	RBNU	2	2	3	2	2	2.5	1	na	1
Red-eyed Vireo	REVI	2	7	2	5	1	3	2.5	na	1
Ruffed Grouse	RUGR	0	0	0	0	0	0	0	na	0
Scarlet Tanager	SCTA	1	2	2	1	2	1	2	na	0
Blue-headed Vireo	SOVI	3	2	3.5	2	2	3	3	na	2
Veery	VEER	0	0	0	2	0	0	1	na	1
Winter Wren	WIWR	2	2	2	3	2	1	1	na	1
Yellow-bellied Sapsucker	YBSA	1	1	1	0	1	0	1	na	1
Yellow-rumped Warbler	YRWA	0	0.5	1	1	1	1	2	na	1
American Robin	AMRO	1	0	0	1	0	0	0	na	0
Barred Owl	BAOW	0	0	0	0	0	0	0	na	0
Cedar Waxwing	CEWA	0	0	0	0	0	1	0	na	0
Common Yellowthroat	COYE	0	0	0	0	0	0	0	na	1
Downy Woodpecker	DOWO	0	0	0	0	0	0	0	na	0
Evening Grosbeak	EVGR	0	0	0	0	0	0	0	na	0
Least Flycatcher	LEFL	0	0	0.5	0	0	0	0	na	0
Mourning Dove	MODO	0	0	0	0	0	0	0	na	0
Nashville Warbler	NAWA	0	0	0	0	1	0	0	na	0
Northern Flicker	NOFL	0	0	0	0	0	0	0	na	0
Northern Goshawk	NOGO	0	0	0	0	0	0	0	na	0
Northern Waterthrush	NOWA	0	0	0	3	0	0	0	na	0
Pileated Woodpecker	PIWO	0	0	0	1	1	0	0	na	0
Pine Siskin	PISI	0	0	0	0	0	0	0	na	0
Ruby-throated Hummingbirds	RTHU	0	0	0	0	0	0	0	na	0
Swainson's Thrush	SWTH	0	0	0	0	0	0	0	na	0
Tennessee Warbler	TEWA	0	0	0	0	1	0	0	na	0
White-throated Sparrow	WTSP	0	0	0	0	0	0	0	na	0
Wood Thrush	WOTH	0	0	0	0	0	0	0	na	0
Species Richness		20	19	21	22	21	20	22	na	21
Total Abundance		48.5	56	54.5	53.5	52	46.5	50.5	na	44.5

Table A.2. Abundance of bird territories in 1996. Includes nine (10 ha) research areas (RA) in the Penobscot Experimental Forest, Bradley, Maine. For scientific nomenclature, see Appendix E.

Common Name	Species Code	RA	RA	RA	RA	RA	RA	RA	RA	RA
		1	2	3	4	5	6	7	8	9
Black-and-white Warbler	BAWW	2	1	1	1	1	2	1	1	1
Blackburnian Warbler	BLWA	6	4	5	4	5.5	3.5	2	2	3
Black-capped Chickadee	BCCH	3	2	2	3	3	2.5	2	2	2
Black-throated Blue Warbler	BTBW	2	3	1	3	1	2	1	1	3
Black-throated Green Warbler	BTGW	6	5.5	5	2	1.5	2	2	2	3
Blue Jay	BLJA	2	1	2	2	2	2	2	2	1
Brown Creeper	BRCR	1	1	1.5	2	2	2	1	1	1
Brown-headed Cowbird	BHCO	0	0	0	0	0	0	0	0	0
Canada Warbler	CAWA	0	0	0	0	1	1	1	0	2.5
Eastern Wood Pewee	EWPE	1	2	1	1	0	0	0	1	1
Golden-crowned Kinglet	GCKI	0	0	0	1	0.5	0	1	0	1
Great-crested Flycatcher	GCFL	0	0	0	1	0.5	1	0	0	0
Hairy Woodpecker	HAWO	1	2	0	0	1	1	1	1	1
Hermit Thrush	HETH	1.5	2	2	2	2	2.5	2	1	2
Magnolia Warbler	MAWA	0	0	0	0	1	0	0	0	2
Northern Parula	NOPA	4	5	3	3	4	3.5	3	4.5	3
Ovenbird	OVEN	4	4	4.5	4.5	3	3	4	4	5
Pine Warbler	PIWA	0	0	0.5	0	0	0	1	1	1
Purple Finch	PUFI	1	0	0	0	0	0	1	0	0
Red-breasted Nuthatch	RBNU	3	1	2	2	4	3	2	1	3
Red-eyed Vireo	REVI	3.5	7	2	4	0.5	2	2	4	2
Ruffed Grouse	RUGR	0	0	0	0	0	0	1	0	1
Scarlet Tanager	SCTA	1.5	2	2	1	0	1	2	1	1
Blue-headed Vireo	SOVI	2	1	1.5	2	0	0	1	2	1
Veery	VEER	0	0	0	2	0	0	1	4	0.5
Winter Wren	WIWR	0	0	1.5	0.5	1	1	0	1	1
Yellow-bellied Sapsucker	YBSA	1	1	1	1	1	0	2	1	1
Yellow-rumped Warbler	YRWA	1	0	1	1	1	1	0	0	1
American Robin	AMRO	1	0	0	1	0	0	0	1	0
Barred Owl	BAOW	0	0	0	0	0	0	0	0	0
Cedar Waxwing	CEWA	0	0	0	0	0	0	0	0	0
Common Yellowthroat	COYE	0	0	0	0	1	0	0	0	1
Downy Woodpecker	DOWO	1	0	0	0	0	0	0	0	0
Evening Grosbeak	EVGR	0	0	0	0	0	0	0	0	0
Least Flycatcher	LEFL	0	0	0	0	1	0	0	1	0
Mourning Dove	MODO	0	0	0	0	0	0	0	0	0
Nashville Warbler	NAWA	0	0	0	0	1	0	0	0	0
Northern Flicker	NOFL	0	0	0	0	0	0	0	0	0
Northern Goshawk	NOGO	0	0	0	0	0	0	0	0	0
Northern Waterthrush	NOWA	0	0	0	0	1	0	0	0	0
Pileated Woodpecker	PIWO	0	0	0	0	0	0	0	0	0
Pine Siskin	PISI	0	0	0	0	0	0	0	0	0
Ruby-throated Hummingbirds	RTHU	0	0	0	0	0	0	0	0	0
Swainson's Thrush	SWTH	0	0	0	0	0	0	0	0	0
Tennessee Warbler	TEWA	0	0	0	0	1	0	0	0	0
White-throated Sparrow	WTSP	0	0	0	0	0	0	0	0	0
Wood Thrush	WOTH	0	0	0	0	0	0	0	0	0
Species Richness		21	17	19	22	25	18	22	22	26
Total Abundance		48.5	44.5	39.5	44	41.5	36	36	39.5	45

Table A.3. Abundance of bird territories in 1997. Includes nine (10 ha) research areas (RA) in the Penobscot Experimental Forest, Bradley, Maine. For scientific nomenclature, see Appendix E.

Common Name	Species Code	RA	RA	RA	RA	RA	RA	RA	RA	RA
		1	2	3	4	5	6	7	8	9
Black-and-white Warbler	BAWW	1	2	1	3	2	2.5	2	3	2
Blackburnian Warbler	BLWA	6	6	6	4	5	6	4	2	7
Black-capped Chickadee	BCCH	4	4	3	4	6	4	3.5	3	2.5
Black-throated Blue Warbler	BTBW	2	3	3	4	2	2	2	2.5	3
Black-throated Green Warbler	BTGW	7.5	7	7	3	2	3	2.5	3	4
Blue Jay	BLJA	1	2	1	1	2	1	1	1	1
Brown Creeper	BRCR	3	3	3	2	2	2	3	1	2
Brown-headed Cowbird	BHCO	0	0	1	1	0	0	1	2	0
Canada Warbler	CAWA	0	0	0.5	1	2	1	1	0	1.5
Eastern Wood Pewee	EWPE	1	2	1	1	0	0	1	2	1
Golden-crowned Kinglet	GCKI	2	2	2	1	3	2	2	1	2
Great-crested Flycatcher	GCFL	0	0	0	2	2	1	0	0	0
Hairy Woodpecker	HAWO	0	1	0.5	2	1	2	0	1.5	1
Hermit Thrush	HETH	2	3	3	2	3	2.5	3	2	2.5
Magnolia Warbler	MAWA	0	0	0	0	2	2	0	0	2
Northern Parula	NOPA	3	6	4	6	6	4	5	8	4.5
Ovenbird	OVEN	4	6	5.5	5.5	2.5	4	6	4	7
Pine Warbler	PIWA	0	0.5	0	0	1	1	1	0	1
Purple Finch	PUFI	1	1	1	0	1	1	1	0	1
Red-breasted Nuthatch	RBNU	3	2	4.5	2	4	4	3	3	4
Red-eyed Vireo	REVI	4	5	4	4	4	3	3	5.5	2
Ruffed Grouse	RUGR	0	0	0	1	1	0	0	1	1
Scarlet Tanager	SCTA	1	1	0	1	0	0	1	1	0
Blue-headed Vireo	SOVI	2	2	3	2	2	2	2	2	2
Veery	VEER	0	0	1	2	1	1	0	2	1.5
Winter Wren	WIWR	2	0	1	1	2	1	0	0	0
Yellow-bellied Sapsucker	YBSA	2	1	1	2	2	1	2	1	2
Yellow-rumped Warbler	YRWA	1	1	2.5	1	3	1	1	2	2
American Robin	AMRO	1	1	1	0	0	0	0	2	0
Barred Owl	BAOW	0	0	0	0	0	0	0	0	0
Cedar Waxwing	CEWA	0	0	0	0	0	0	0	0	0
Common Yellowthroat	COYE	0	0	0	0	0	0	0	0	0
Downy Woodpecker	DOWO	0	0	0	0	0	0	0	0	0
Evening Grosbeak	EVGR	0	0	0	1	1	0	0	0	0
Least Flycatcher	LEFL	0	0	0	0	0	0	0	5	0.5
Mourning Dove	MODO	0	0	0	0	1	0	0	0	1
Nashville Warbler	NAWA	0	0.5	0	0	1	1	0	0	0
Northern Flicker	NOFL	0	0	0	0	0	0	0	0	0
Northern Goshawk	NOGO	0	0	0	0	0	0	0	0	0
Northern Waterthrush	NOWA	0	0	0	0	1	0	0	0	0
Pileated Woodpecker	PIWO	0	0	0.5	1	0	0	0	0	1
Pine Siskin	PISI	0	0	0	0	0	0	0	0	0
Ruby-throated Hummingbirds	RTHU	0	0	0	0	0	0	0	0	0
Swainson's Thrush	SWTH	0	0	0	0	0	0	1	0	0
Tennessee Warbler	TEWA	0	0	0	0	1	0	0	0	0
White-throated Sparrow	WTSP	1	0	0	0	0	1	0	0	0
Wood Thrush	WOTH	0	0	0	0	0	0	0	1	0
Species Richness		22	23	25	27	30	26	23	25	27
Total Abundance		54.5	62	61	60.5	68.5	56	52	61.5	62

Table A.4. Abundance of bird territories in 1998. Includes nine (10 ha) research areas (RA) in the Penobscot Experimental Forest, Bradley, Maine. For scientific nomenclature, see Appendix E.

Common Name	Species Code	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	RA 8	RA 9
Black-and-white Warbler	BAWW	1.5	1	0	1	0	0.5	1.5	1	1
Blackburnian Warbler	BLWA	7	6	5	4	6	5.5	2	3	6
Black-capped Chickadee	BCCH	3	3	3	3	3.5	3	3	2	3
Black-throated Blue Warbler	BTBW	1	3	2.5	3	2	2	2	4	3
Black-throated Green Warbler	BTGW	5	5	5	3	2	1	2	3	6.5
Blue Jay	BLJA	1	1	1	2	2	1	2	2	2
Brown Creeper	BRCR	1	1	2	2	1	2	3	1	1
Brown-headed Cowbird	BHCO	1	1	1	0	0	1	1	2	1
Canada Warbler	CAWA	0	0	0	0	1	0	1	0	1
Eastern Wood Pewee	EWPE	1	1.5	1	1	1	1	1	2	1
Golden-crowned Kinglet	GCKI	3	2	2	1	2	2	2	1	2
Great-crested Flycatcher	GCFL	0	0	1	1	1	1	0	0	0
Hairy Woodpecker	HAWO	1	1	1	1	1	1	1	0	1
Hermit Thrush	HETH	3	3	3	3	2	3	3	2.5	3
Magnolia Warbler	MAWA	0	0	0	0	1	1	0	0	3
Northern Parula	NOPA	4.5	3	4	4	4	4	5	7	4
Ovenbird	OVEN	2.5	5	4	5.5	2.5	5	5	4	5.5
Pine Warbler	PIWA	1	0.5	2	1	1	0	1	1.5	2
Purple Finch	PUFI	0	0	0	0	0	0	0	0	1
Red-breasted Nuthatch	RBNU	2.5	2	2	1.5	2	2	2	1	2.5
Red-eyed Vireo	REVI	1	5	2	2.5	0.5	1	3	5	0
Ruffed Grouse	RUGR	0	0	0	1	0	1	1	0	0
Scarlet Tanager	SCTA	1	1	0.5	1	0	1	2	2	0
Blue-headed Vireo	SOVI	3	2	3	2	2	2	2	4.5	4
Veery	VEER	0	0	0	1	0	0	0	3	1
Winter Wren	WIWR	2	1	1.5	2	2	2	2	0	2
Yellow-bellied Sapsucker	YBSA	1	2	1	3	2	1	2	1	2
Yellow-rumped Warbler	YRWA	1	0	0	1	1	1	1	1.5	3
American Robin	AMRO	0	0	0	1	0	0	0	1	0
Barred Owl	BAOW	0	0	0	1	0	0	1	0	0
Cedar Waxwing	CEWA	0	0	0	0	0	0	0	0	0
Common Yellowthroat	COYE	0	0	0	0	0	0	0	0	0
Downy Woodpecker	DOWO	0	0	0	0	0	0	0	0	1
Evening Grosbeak	EVGR	0	0	0	0	0	0	0	0	0
Least Flycatcher	LEFL	0	1	0	0	0	0	0	3	0
Mourning Dove	MODO	0	0	0	0	0	0	0	0	0
Nashville Warbler	NAWA	0	0	0	0	0	0	0	0	0
Northern Flicker	NOFL	0	0	0	1	0	0	0	0	0
Northern Goshawk	NOGO	0	0	1	0	0	0	0	0	0
Northern Waterthrush	NOWA	0	0	0	0	1	0	0	0	0
Pileasted Woodpecker	PIWO	0	1	0	1	0	0	0	0	0
Pine Siskin	PISI	1	0	0	0	0	0	0	0	0
Ruby-throated Hummingbirds	RTHU	0	0	1	0	0	0	0	0	0
Swainson's Thrush	SWTH	0	0	0	0	0	0	1	0	0
Tennessee Warbler	TEWA	0	0	0	0	0	0	0	0	0
White-throated Sparrow	WTSP	0	0	0	0	0	1	0	0	0
Wood Thrush	WOTH	0	0	0	0	0	0	0	1	0
Species Richness		23	23	23	28	23	25	26	24	25
Total Abundance		49	52	49.5	54.5	43.5	46	52.5	59	62.5

Table A.5. Mean abundance of bird territories over all years (1995-1998). Includes nine (10 ha) research areas (RA) at the Penobscot Experimental Forest. For scientific nomenclature, see Appendix E.

Common Name	RA 1	RA 2	RA 3	RA 4	RA 5	RA 6	RA 7	RA 8	RA 9	Grand mean
Black-and-white Warbler	1.250	1.250	0.500	1.500	0.750	1.750	1.875	1.667	1.250	1.310
Blackburnian Warbler	6.250	5.500	5.875	4.000	5.625	4.500	2.750	2.333	4.750	4.620
Black-capped Chickadee	3.125	2.875	2.500	3.000	3.625	3.125	2.875	2.333	2.375	2.870
Black-throated Blue Warbler	1.625	2.750	2.125	3.000	1.250	2.000	1.750	2.500	3.250	2.250
Black-throated Green Warbler	6.375	5.875	5.750	2.500	2.375	2.375	2.000	2.667	4.125	3.782
Blue Jay	1.500	1.500	1.500	1.500	2.000	1.250	1.500	1.667	1.250	1.519
Brown Creeper	1.500	1.500	2.125	2.000	1.750	1.750	2.000	1.000	1.500	1.681
Brown-headed Cowbird	0.250	0.250	0.500	0.250	0	0.250	0.750	1.333	0.250	0.426
Canada Warbler	0	0	0.125	0.250	1.500	0.500	0.750	0	2.500	0.625
Eastern Wood Pewee	0.750	1.875	1.250	1.000	0.250	0.250	0.500	1.667	0.750	0.921
Golden-crowned Kinglet	1.750	1.000	1.500	1.375	2.375	1.250	2.000	0.667	1.500	1.491
Great-crested Flycatcher	0	0	0.250	1.000	0.875	1.000	0	0	0	0.347
Hairy Woodpecker	0.625	1.000	0.625	0.750	0.750	1.000	0.750	0.833	0.750	0.787
Hermit Thrush	2.625	3.000	2.750	2.500	2.750	2.875	2.875	1.833	2.750	2.662
Magnolia Warbler	0	0	0	0	1.250	1.000	0	0	2.500	0.528
Northern Parula	3.625	5.000	4.000	4.500	4.750	4.500	4.750	6.500	3.375	4.556
Ovenbird	3.750	5.375	4.500	5.625	3.500	4.375	5.500	4.000	5.625	4.694
Pine Warbler	0.250	0.375	0.875	0.250	0.500	0.250	1.000	0.833	1.000	0.593
Purple Finch	1.000	0.250	0.250	0	0.250	0.250	0.500	0	0.500	0.333
Red-breasted Nuthatch	2.625	1.750	2.875	1.875	3.000	2.875	2.000	1.667	2.625	2.366
Red-eyed Vireo	2.625	6.000	2.500	3.875	1.500	2.250	2.625	4.833	1.250	3.051
Ruffed Grouse	0	0	0	0.500	0.250	0.250	0.500	0.333	0.500	0.259
Scarlet Tanager	1.125	1.500	1.125	1.000	0.500	0.750	1.750	1.333	0.250	1.037
Blue-headed Vireo	2.500	1.750	2.750	2.000	1.500	1.750	2.000	2.833	2.250	2.148
Veery	0	0	0.250	1.750	0.250	0.250	0.500	3.000	1.000	0.778
Winter Wren	1.500	0.750	1.500	1.625	1.750	1.250	0.750	0.333	1.000	1.162
Yellow-bellied Sapsucker	1.250	1.250	1.000	1.500	1.500	0.500	1.750	1.000	1.500	1.250
Yellow-rumped Warbler	0.750	0.375	1.125	1.000	1.500	1.000	1.000	1.167	1.750	1.074
American Robin	0.750	0.250	0.250	0.750	0	0	0	1.333	0	0.370
Barred Owl	0	0	0	0.250	0	0	0.250	0	0	0.056
Cedar Waxwing	0	0	0	0	0	0.250	0	0	0	0.028
Common Yellowthroat	0	0	0	0	0.250	0	0	0	0.500	0.083
Downy Woodpecker	0.250	0	0	0	0	0	0	0	0.250	0.056
Evening Grosbeak	0	0	0	0.250	0.250	0	0	0	0	0.056
Least Flycatcher	0	0.250	0.125	0	0.250	0	0	3.000	0.125	0.417
Mourning Dove	0	0	0	0	0.250	0	0	0	0.250	0.056
Nashville Warbler	0	0.125	0	0	0.750	0.250	0	0	0	0.125
Northern Flicker	0	0	0	0.250	0	0	0	0	0	0.028
Northern Goshawk	0	0	0.250	0	0	0	0	0	0	0.028
Northern Waterthrush	0	0	0	0.750	0.750	0	0	0	0	0.167
Pileated Woodpecker	0	0.250	0.125	0.750	0.250	0	0	0	0.250	0.181
Pine Siskin	0.250	0	0	0	0	0	0	0	0	0.028
Ruby-throated Hummingbirds	0	0	0.250	0	0	0	0	0	0	0.028
Swainson's Thrush	0	0	0	0	0	0	0.500	0	0	0.056
Tennessee Warbler	0	0	0	0	0.750	0	0	0	0	0.083
White-throated Sparrow	0.250	0	0	0	0	0.500	0	0	0	0.083
Wood Thrush	0	0	0	0	0	0	0	0.667	0	0.074

Table A.6. Kruskal-Wallis tests of differences among treatment groups. Univariate tests on mean numbers of territories per 10 ha site and significance (p-value), for each species of bird found on four or more research areas (n=9) in the Penobscot Experimental Forest. The nine stands were put into three groups based on their eventual treatment, even though no treatments had been applied in 1995. In 1996 and 1997, one and two (respectively) groups of three stands had been treated, though 1996 results below are based on the eventual (i.e., “fixed” for all years) treatments. For 1997, results are presented for tests where the treatment groups are fixed (Trt Fix) for all years, and for tests of treatment differences that compare stands that have actually been treated (Trt Act.) with the controls and yet-untreated stands. Means in bold are significantly different ($p \leq 0.10$).

Species	Trt	1995	1996	1997 (Trt Fix.)	1997 (Trt Act.)	1998
Black-and- White Warbler	20-10	1.17	1.67	1.83	1.75	1.00
	10-30	1.33	1.00	2.00	2.00	0.83
	Control	0.50	1.00	2.33	2.20	0.67
		p=0.69	p=0.10	p=0.63	p=0.81	p=0.77
Blackburnian Warbler	20-10	4.0	4.17	6.33	6.00	6.17
	10-30	5.0	3.83	5.00	5.50	4.67
	Control	5.75	3.67	4.00	4.60	4.0
		p=0.45	p=0.96	p=0.15	p=0.60	p=0.19
Black- capped Chickadee	20-10	2.50	2.50	3.50	4.00	3.00
	10-30	2.50	2.33	4.50	5.00	3.17
	Control	2.00	2.33	3.33	3.20	2.67
		p=0.35	p=0.85	p=0.44	p=0.08	p=0.26
Black-throated Blue Warbler	20-10	2.50	2.33	2.33	2.00	2.00
	10-30	1.33	1.67	2.33	2.50	2.33
	Control	2.00	1.67	3.17	2.90	3.17
		p=0.69	p=0.54	p=0.26	p=0.24	p=0.26
Black-throated Green Warbler	20-10	4.50	3.67	4.83	5.25	4.17
	10-30	3.83	3.00	3.83	4.50	3.00
	Control	4.00	3.00	4.33	3.90	3.67
		p=0.90	P=062.	P=043.	p=0.66	p=0.72
Blue Jay	20-10	1.33	1.67	1.00	1.00	1.33
	10-30	1.67	1.67	1.67	2.00	1.67
	Control	1.50	2.00	1.00	1.00	1.67
		p=0.75	p=0.56	p=0.10	p=0.02	p=0.67
Brown Creeper	20-10	1.33	1.33	2.33	2.50	1.33
	10-30	1.33	1.33	2.67	2.50	1.67
	Control	2.00	1.50	2.00	2.20	1.67
		p=0.31	p=0.85	p=0.56	p=0.87	P=0.80
Brown- headed Cowbird	20-10	0.00	0	0.00	0.00	1.00
	10-30	0.33	0	0.33	0.00	0.67
	Control	0.00	0	1.33	1.00	1.00
		p=0.43		p=0.05	p=0.09	p=0.74
Canada Warbler	20-10	1.67	1.17	0.83	0.50	0.33
	10-30	0.67	0.67	1.00	1.00	0.67
	Control	0.00	0.00	0.50	0.80	0.00
		p=0.67	p=0.21	p=0.72	p=0.82	p=0.26

Table A.6 (Continued). Kruskal-Wallis tests of differences among treatment groups. Univariate tests on mean numbers of territories per 10 ha site and significance (p-value), for each species of bird found on four or more research areas (n=9) in the Penobscot Experimental Forest. Research areas are divided into three groups based on their eventual treatment. For 1997, results are presented for tests where the treatment groups are fixed (Trt Fix) for all years, and for tests of treatment differences that compare stands that have actually been treated (Trt Act.) with the controls and yet-untreated stands. Means in bold are significantly different ($p \leq 0.10$).

		1995	1996	1997	1997	1998
Species	Trt			(Trt Fix.)	(Trt Act.)	
Eastern Wood	20-10	0.00	0.67	0.67	0.50	1.00
Pewee	10-30	0.67	0.67	1.00	1.00	1.17
	Control	1.50	1.00	1.33	1.20	1.33
		p=0.15	p=0.68	p=0.51	p=0.50	P=0.56
Golden-crowned	20-10	1.33	0.33	2.00	2.00	2.33
	10-30	2.33	0.50	2.33	2.50	2.0
Kinglet	Control	2.25	0.33	1.33	1.60	1.33
		p=0.48	p=0.85	p=0.11	p=0.20	p=0.11
Hairy	20-10	0.17	1.00	1.00	1.00	1.00
Woodpecker	10-30	0.33	1.33	0.67	1.00	1.00
	Control	0.50	0.33	1.33	1.00	0.67
		p=0.81	p=0.11	p=0.56	p=1.00	p=0.37
Hermit	20-10	3.67	2.00	2.33	2.25	3.00
Thrush	10-30	3.83	2.00	3.00	3.00	2.67
	Control	3.00	1.67	2.33	2.50	2.83
		p=0.09	p=0.65	p=0.12	p=0.23	p=0.56
Northern	20-10	3.83	3.50	3.83	3.50	4.17
Parula	10-30	5.67	4.00	5.67	6.00	4.00
	Control	5.00	3.50	6.00	5.50	5.00
		p=0.55	p=0.71	p=0.14	P=0.12	p=0.81
Ovenbird	20-10	5.00	4.00	5.00	4.00	4.33
	10-30	6.50	3.67	4.83	4.25	4.17
	Control	5.50	4.33	5.00	5.60	4.50
		p=0.28	p=0.37	p=0.95	p=0.34	p=0.92
Pine Warbler	20-10	0.00	0.33	0.67	0.50	1.00
	10-30	0.50	0.33	0.83	0.75	0.83
	Control	0.50	0.50	0.00	0.40	1.50
		p=0.30	p=0.85	p=0.10	p=0.70	p=0.36
Purple Finch	20-10	0.67	0.33	1.00	1.00	0.33
	10-30	0.00	0.33	1.00	1.00	0.00
	Control	0.00	0.00	0.33	0.60	0.00
		p=0.43	p=0.56	P=0.10	p=0.40	p=0.37
Red-breasted	20-10	1.83	3.00	3.67	3.50	2.33
Nuthatch	10-30	1.67	2.33	3.00	3.00	2.00
	Control	2.50	1.67	3.17	3.30	1.50
		p=0.41	p=0.20	p=0.69	p=0.89	p=0.07
Red-eyed	20-10	2.00	2.50	3.00	3.50	0.67
Vireo	10-30	3.50	3.17	4.00	4.50	2.83
	Control	3.50	3.33	4.50	3.70	3.17
		p=0.74	p=0.64	p=0.22	p=0.53	p=0.18

Table A.6 (Continued). Kruskal-Wallis tests of differences among treatment groups. Univariate tests on mean numbers of territories per 10 ha site and significance (p-value), for each species of bird found on four or more research areas (n=9) in the Penobscot Experimental Forest. Research areas are divided into three groups based on their eventual treatment. For 1997, results are presented for tests where the treatment groups are fixed (Trt Fix) for all years, and for tests of treatment differences that compare stands that have actually been treated (Trt Act.) with the controls and yet-untreated stands. Means in bold are significantly different ($p \leq 0.10$).

		1995	1996	1997	1997	1998
Species	Trt			(Trt Fix.)	(Trt Act.)	
Ruffed Grouse	20-10	0	0.33	0.33	0.00	0.33
	10-30	0	0.33	0.33	0.50	0.33
	Control	0	0.00	0.67	0.60	0.33
			P=0.56	p=0.67	p=0.39	p=1.00
Scarlet	20-10	0.67	1.17	0.33	0.50	0.67
Tanager	10-30	2.00	1.33	0.67	0.50	1.00
	Control	1.50	1.33	0.67	0.60	1.17
		p=0.07	p=0.82	p=0.67	p=0.96	p=0.77
Blue-headed	20-10	2.67	1.00	2.00	2.00	3.00
Vireo	10-30	2.33	0.67	2.00	2.00	2.00
	Control	2.75	1.83	2.33	2.20	3.17
		p=0.70	p=0.14	p=0.37	p=0.67	p=0.23
Veery	20-10	0.33	0.17	0.83	0.50	0.33
	10-30	0.33	0.33	0.33	0.50	0.00
	Control	1.00	2.00	1.67	1.30	1.33
		p=0.74	p=0.36	p=0.13	p=0.31	p=0.24
Winter	20-10	1.33	0.67	1.00	1.50	2.00
Wren	10-30	1.67	0.33	0.67	1.00	1.67
	Control	2.50	1.00	0.67	0.40	1.17
		p=0.21	p=0.36	p=0.85	p=0.28	p=0.28
Yellow-bellied	20-10	0.67	0.67	1.67	1.50	1.33
Sapsucker	10-30	1.00	1.33	1.67	1.50	2.00
	Control	0.50	1.00	1.33	1.60	1.67
		p=0.46	p=0.26	p=0.67	p=0.96	p=0.41
Yellow-	20-10	0.67	1.00	1.33	1.00	1.67
rumped	10-30	1.17	0.33	1.67	2.00	0.67
Warbler	Control	1.00	0.67	1.83	1.70	0.83
		p=0.69	p=0.26	p=0.71	p=0.42	p=0.46
American	20-10	0.33	0.33	0.33	0.50	0.00
Robin	10-30	0.00	0.00	0.33	0.50	0.00
	Control	0.50	0.67	1.00	0.60	0.67
		p=0.46	p=0.26	p=0.51	p=1.00	p=0.10
Least	20-10	0.00	0.00	0.17	0.00	0.00
Flycatcher	10-30	0.00	0.33	0.00	0.00	0.33
	Control	0.25	0.33	1.67	1.10	1.00
		p=0.22	p=0.56	p=0.56	p=0.41	p=0.56
Pileated	20-10	0.00	0	0.33	0.00	0.00
Woodpecker	10-30	0.33	0	0.00	0.00	0.33
	Control	0.50	0	0.50	0.50	0.33
		p=0.46		p=0.31	p=0.21	p=0.56

Table A.7. Analysis of variance (ANOVA) for richness and abundance. Avian species richness is the total number of species; abundance is number of bird territories, pooling all species. Both are per 10 ha research area. Data are from nine (10 ha) research areas censused from 1995-1998 at the Penobscot Experimental Forest, Maine. Type I Sum of Squares (SS) only are presented, whenever Type III SS are exactly the same. Because the overall ANOVA model for abundance (A.) was not significant but had a marginally significant year-term, a second one-way ANOVA was run (B.) with only a year-term.

ANOVA (with year, treatment, and interaction terms) for species richness

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	98.884	19.777	3.05	0.0248
Error	29	188.087	6.486		
Corrected Total	34	286.971			
		R-Square	Coeff Var	Root MSE	Mean
		0.345	11.0589	2.5467	23.029
Source	DF	Type I SS	Mean Square	F Value	Pr > F
Year	1	97.3328	97.3328	15.01	0.0006
FixTreat	2	1.3052	0.6526	0.10	0.9046
Year*FixTreat	2	0.246	0.1232	0.02	0.9812
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Year	1	95.6028	95.6028	14.74	0.0006
FixTreat	2	0.2459	0.12297	0.02	0.9812
Year*FixTreat	2	0.246	0.1232	0.02	0.9812

A. ANOVA (with year, treatment, and interaction terms) for avian abundance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	5	299.320	59.864	0.90	0.4971
Error	29	1938.565	66.847		
Corrected Total	34	2237.886			
		R-Square	Coeff Var	Root MSE	Mean
		0.1337	16.0134	8.1760	51.057
Source	DF	Type I SS	Mean Square	F Value	Pr > F
Year	1	229.2110	229.2110	3.43	0.0740
FixTreat	2	28.4375	14.2188	0.21	0.8096
Year*FixTreat	2	41.6720	20.8360	0.31	0.7346
Source	DF	Type III SS	Mean Square	F Value	Pr > F
Year	1	223.1940	223.1940	3.34	0.0780
FixTreat	2	41.6799	20.8399	0.31	0.7346
Year*FixTreat	2	41.6720	20.8360	0.31	0.7346

B. ANOVA (with year term) for avian abundance

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	1	229.211	229.211	3.77	0.0609
Error	33	2008.675	60.869		
Corrected Total	34	2237.886			
		R-Square	Coeff Var	Root MSE	Mean
		0.1024	15.281	7.802	51.057
Source	DF	Type I SS	Mean Square	F Value	Pr > F
Year	1	229.211	229.211	3.77	0.0609

Table A.8. Results of iterative analysis-of-variance (ANOVA) tests. Tests are for total avian abundance (number of bird territories, pooling all species) and avian species richness per 10 ha research area. These two dependent variables were tested by one-way ANOVAs with “treatment” as the group variable. This series of analyses were done with some values artificially manipulated (reduced) to reflect uniform effect sizes for each treatment group. These analyses were done incrementally to determine statistical power under various hypothetical scenarios. For 1997 data, only stands that had actually been harvested were considered in the 20-10 (n=2) and 10-30 (n=2) treatment groups.

Variable: **Abundance**
Year: **1997**

	TREATMENT LEVELS			
Variable Manipulation:	Control	10% Harvest	20% Harvest	P-value
None (original data):				0.1072
Reduced by:			20%	0.0039
Reduced by:		10%	20%	0.0080
Reduced by:		20%	20%	0.0076
Reduced by:			25%	0.0019
Reduced by:		10%	25%	0.0034
Reduced by:		25%	25%	0.0027
Reduced by:		15%	30%	0.0018

Variable: **Abundance**
Year: **1998**

	TREATMENT LEVELS			
Variable Manipulation:	Control	10% Harvest	20% Harvest	P-value
None (original data):				0.6523
Reduced by:			20%	0.0962
Reduced by:		10%	20%	0.0739
Reduced by:		20%	20%	0.0321
Reduced by:			25%	0.0411
Reduced by:		10%	25%	0.0369
Reduced by:		25%	25%	0.0126
Reduced by:		15%	30%	0.0145

Variable: **Species Richness**
Year: **1998**

	TREATMENT LEVELS			
Variable Manipulation:	Control	10% Harvest	20% Harvest	P-value
None (original data):				0.8194
Reduced by:			10%	0.2117
Reduced by:		10%	10%	0.1229
Reduced by:			20%	0.0254
Reduced by:		10%	20%	0.0285

APPENDIX B. Power Analyses Related to Chapter 1

This appendix contains analyses of statistical power for conducting ANOVA (i.e., F-Test) tests on avian abundance data. Power is the probability of a test to reject a null hypothesis of equal means (among treatment groups), given that the null is false. Following are figures demonstrating how statistical power relates to alpha-levels and within-group variance for a given effect size, assuming an experimental design identical to mine, and based on the actual variances I observed for treatment groups. Because I observed different within-group variances in 1997 (when two of three blocks had been treated) and 1998 there are two series of figures, based on data from each year.

For each of the two years, three different “effect size” scenarios are modeled, which assume that one or both experimental treatment means differ from the control mean by 10%, 20%, or 30% (Scenario’s 1-3, respectively). For each scenario, separate power curves are plotted for each of two alpha-levels (i.e., the Type I error rate).

Effect sizes are characterized by the standard deviation of the group means (S_m). For each figure, “S” denotes the standard deviation of values within each group, “k” is the number of treatment groups, and “n” is the sample size of units (i.e., 10 ha study sites) within each group. For each year examined, I have listed the standard deviations for each treatment group as a point of reference. All analyses based on PASS software (Hintze, J. 2001. NCSS and PASS. Number Cruncher Statistical Systems. Kaysville, Utah. WWW.NCSS.COM).

1998 Data

Treatment group: Control 20-10 10-30
Standard deviation (S): 4.75 8.79 5.06
Mean (for all treatment groups) standard deviation (S): 6.22

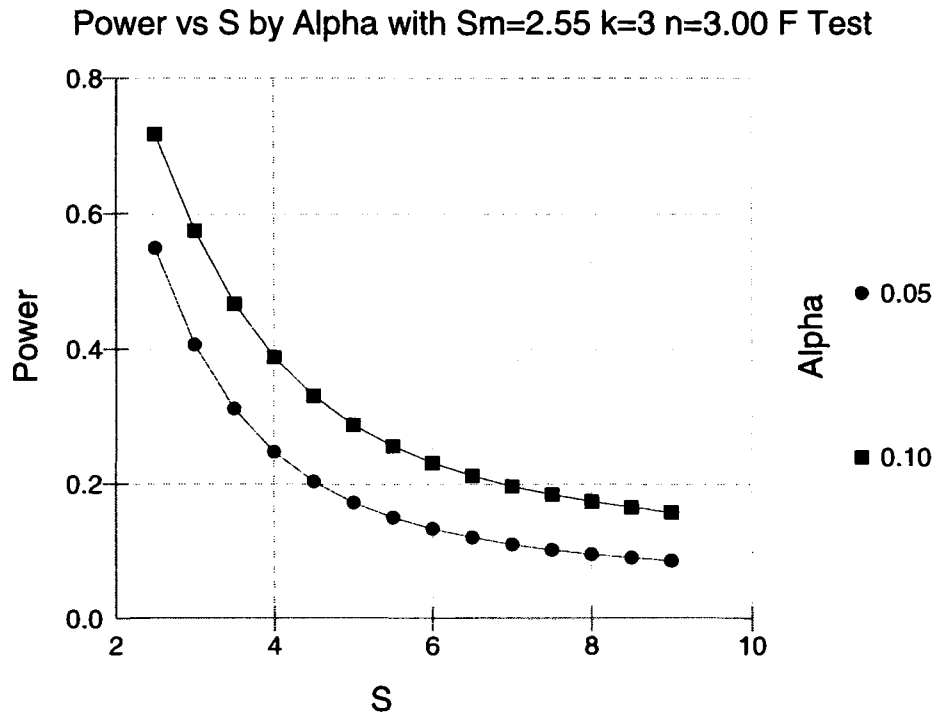


Figure B.1. Scenario 1, 1998 Data. One or both treatments group means differ from control by 10%.

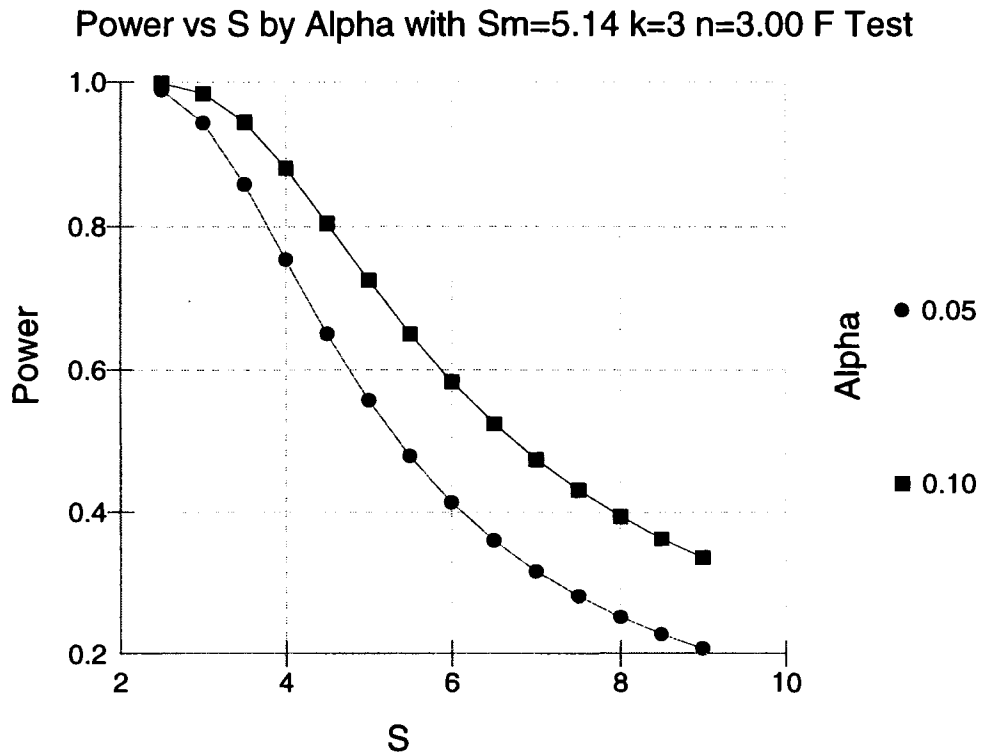


Figure B.2. Scenario 2, 1998 Data. One or both treatments group means differ from control by 20%.

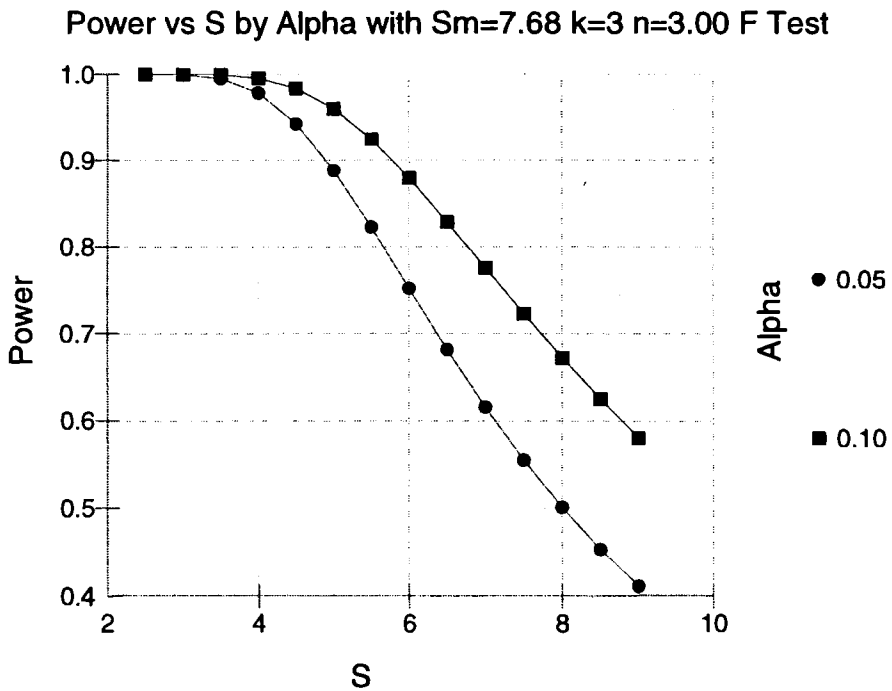


Figure B.3. Scenario 3, 1998 Data. One or both treatments group means differ from control by 30%.

1997 Data

Treatment group:	<u>Control</u>	<u>20-10</u>	<u>10-30</u>
Standard deviation (S):	0.05	3.97	8.31
Mean (for all treatment groups) standard deviation (S): 4.26			

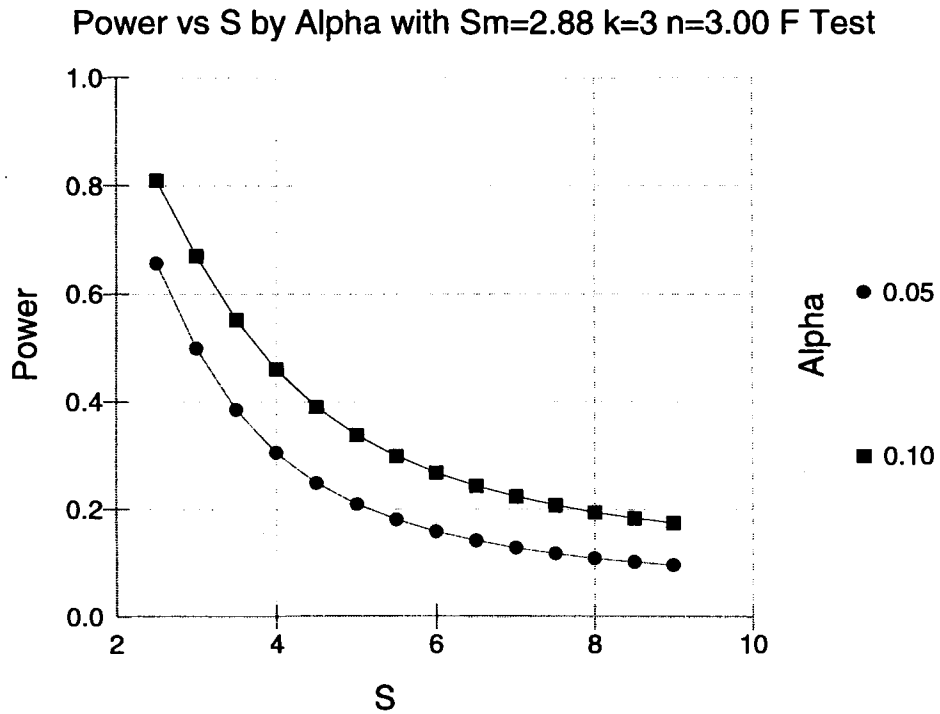


Figure B.4. Scenario 1, 1997 Data. One or both treatments group means differ from control by 10%.

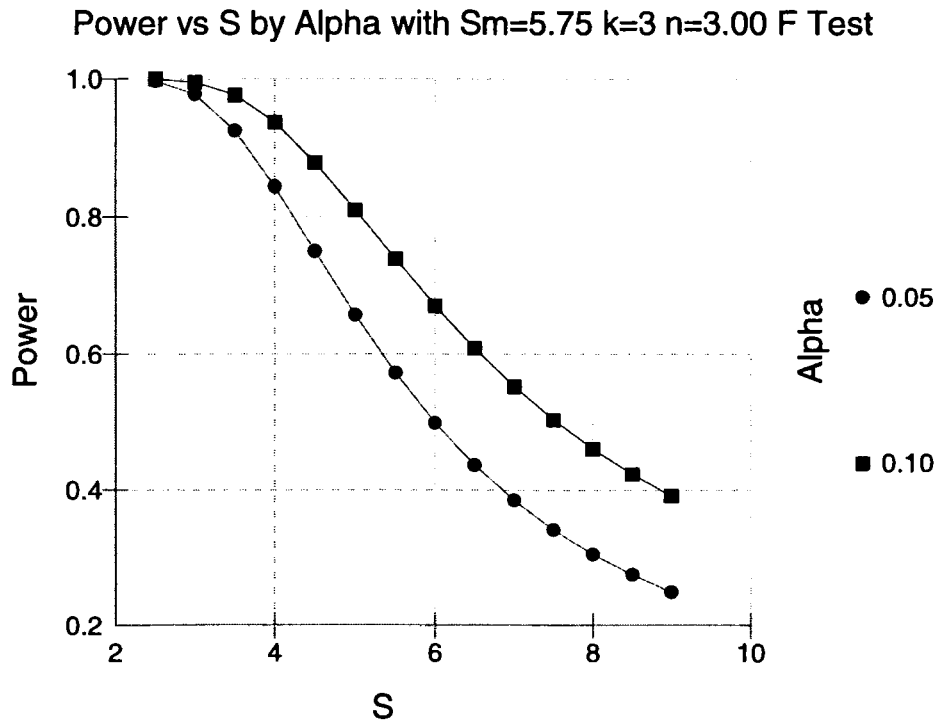


Figure B.5. Scenario 2, 1997 Data. One or both treatments group means differ from control by 20%.

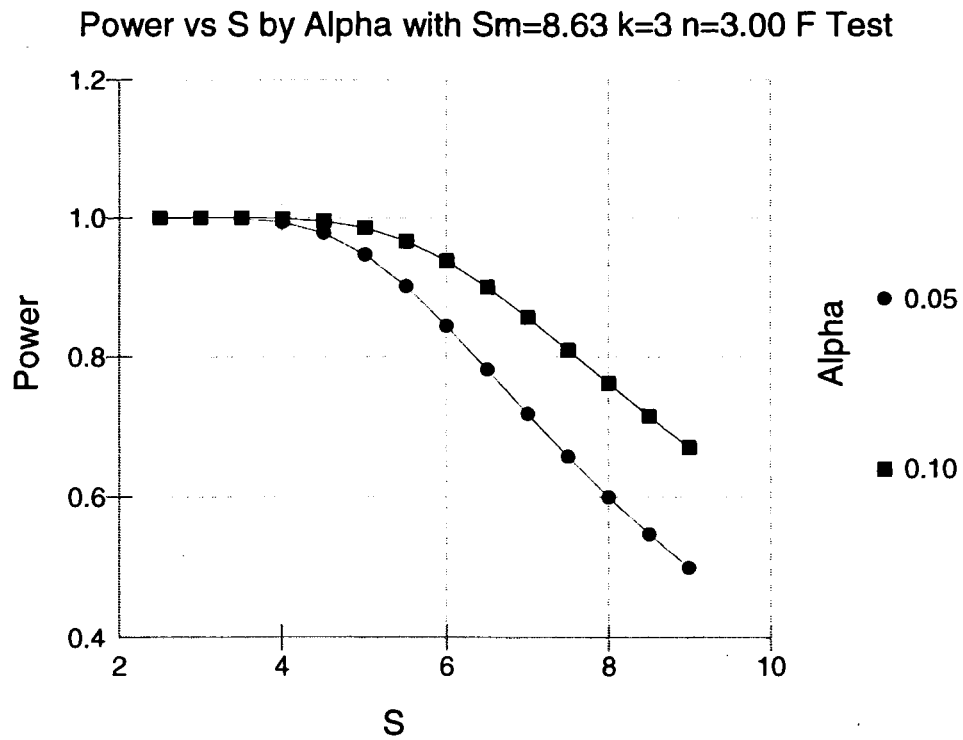


Figure B.6. Scenario 3, 1997 Data. One or both treatments group means differ from control by 30%.

APPENDIX C. Data and Analyses Related to Chapter 2

Table C.2. Differences in site-attachment distances by treatment. Detailed statistical test results, for males only; Hermit Thrushes and Ovenbirds were analyzed separately. These tests were restricted to birds captured on the same site in two consecutive years. These tests compared distances across treatment groups, based on whether the capture site was a control in both years, treated in both years, or was a control in year “t,” but treated in year “t+1”. For Ovenbirds there was one group that included only one observation; therefore, two tests are presented: a Kruskal-Wallis Test with all three treatment groups, and a Mann-Whitney Test with one group (with n=1 observation) excluded.

Hermit Thrush

Test Kruskal-Wallis ANOVA

n = 35

Distance by year	<u>N</u>	<u>Rank sum</u>	<u>Mean rank</u>
Con-Con	18	339	18.83
Con-Trt	8	175	21.88
Trt-Trt	9	116	12.89
Kruskal-Wallis statistic	3.5		
P=	0.1736 (chisqr approximation)		

Ovenbird

(With all three treatment groups)

Test Mann-Whitney test

n = 14

Distance by year	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>
Con-Con	6	53	8.83
Con-Trt	6	34	5.67
Trt-Trt	1	4	4
Kruskal-Wallis statistic	2.63		
P=	0.269 (chisqr approximation)		

(With only two treatment groups)

Test Mann-Whitney test

n = 13

Distance by year	<u>N</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Con-Con	6	47	7.83	10
Con-Trt	6	31	5.17	26
Difference between medians	24.43			
96.5% CI	-100.317 to 89.456 (exact)			
Mann-Whitney U statistic	10			
2-tailed p	0.2403 (exact)			

Table C.3. Differences in site-attachment distances by dispersal status. Detailed statistical test results, for males only; Hermit Thrushes and Ovenbirds were analyzed separately. These tests compared distances for birds found on the same site in two consecutive years versus birds that dispersed to a new site the second year. Data were pooled across all years 1995-1998.

Hermit Thrush

Test	Mann-Whitney test			
n = 39	39			
Distance by Return status	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Different	4	120	30	30
Same	35	660	18.86	110
Difference between medians	74.692			
95.3% CI	-9.838 to 139.116 (normal approximation)			
Mann-Whitney U statistic	30			
2-tailed p	0.0641 (normal approximation)			

Ovenbird

Test	Mann-Whitney test			
n = 17				
Distance by Return status	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Different	3	36	12	9
Same	13	100	7.69	30
Difference between medians	40.845			
95.3% CI	-33.286 to 92.113 (exact)			
Mann-Whitney U statistic	9			
2-tailed p	0.1893 (exact)			

Table C.4. Differences in site-attachment distances by treatment status. Data are for males only; Hermit Thrushes and Ovenbirds are analyzed separately. These tests compared distances for birds captured (in year “t”) on control versus treated sites, regardless of capture location in year “t+1.” Data were pooled across all years 1995-1998.

Hermit Thrush

Test	Mann-Whitney test			
n = 39	39			
Distance by Year1	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Control	27	570	21.11	132
Treatment	12	210	17.5	192
Difference between medians	21.26			
95.2% CI	-37.405 to 76.818 (normal approximation)			
Mann-Whitney U statistic	132			
2-tailed p	0.3613 (normal approximation)			

Ovenbird

Test	Mann-Whitney test			
n = 17	17			
Distance by Year1	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Control	13	110	8.46	20
Treatment	3	26	8.67	19
Difference between medians	-1.822			
95.3% CI	-78.297 to 77.030 (exact)			
Mann-Whitney U statistic	20			
2-tailed p	1 (exact)			

Table C.5. Differences in site-attachment distances by treatment status (year “t+1”). Data are for males only; Hermit Thrushes and Ovenbirds are analyzed separately. These tests compared distances for birds captured (in year “t+1”) on control versus treated sites, regardless of capture location in year “t.” Data were pooled across all years 1995-1998.

Hermit Thrush

Test	Mann-Whitney test			
n = 39	39			
Distance by Year2	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Control	20	408	20.4	182
Treatment	19	372	19.58	198
Difference between medians	3.632			
95.1% CI	-43.818 to 56.399 (normal approximation)			
Mann-Whitney U statistic	182			
2-tailed p	0.8221 (normal approximation)			

Ovenbird

Test	Mann-Whitney test			
n = 17				
Distance by Year2	<u>n</u>	<u>Rank sum</u>	<u>Mean rank</u>	<u>U</u>
Control	8	80	10	20
Treatment	8	56	7	44
Difference between medians	18.139			
95.4% CI	-56.583 to 78.297 (exact)			
Mann-Whitney U statistic	20			
2-tailed p	0.2345 (exact)			

Table C.6. Results of competing Cormack-Jolly Seber models for mark-recapture data analyzed with Program MARK. Hermit Thrush and Ovenbird data are modeled separately. For each species, only data for males were analyzed. Annual survival rate denoted by “ ϕ ” and recapture rate by “p,” with parentheses indicating whether parameters vary over time (t) or are constant (.) for all return intervals. Model selection was based on modified Aikeike’s Information Criterion (AICc). Delta AICc denotes difference between candidate model and best overall model. Number of parameters in model abbreviated “#Par.”

Hermit Thrush (males only)

Model	AICc	AICc	Delta Weight	AICc Likelihood	Model #Par ^A	Deviance
$\phi_{(t)}P_{(.)}$	182.40	0.00	0.5482	1.000	4.0	12.922
$\phi_{(t)}P_{(t)}$	184.42	2.02	0.2001	0.365	5.0	12.745
$\phi_{(.)}P_{(.)}$	184.98	2.58	0.1513	0.276	2.0	19.760
$\phi_{(.)}P_{(t)}$	185.80	3.39	0.1004	0.183	4.0	16.316

Ovenbird (males only)

Model	AICc	AICc	Delta Weight	AICc Likelihood	Model #Par ^A	Deviance
$\phi_{(.)}P_{(.)}$	125.20	0.00	0.7399	1.000	2.0	6.674
$\phi_{(t)}P_{(.)}$	129.18	3.99	0.1008	0.136	4.0	6.297
$\phi_{(.)}P_{(t)}$	129.35	4.15	0.0930	0.126	4.0	6.459
$\phi_{(t)}P_{(t)}$	130.02	4.83	0.0663	0.090	5.0	4.871

APPENDIX D. Data and Analyses Related to Chapter 3.

Table D.1. Bird population trends for combined region. Table includes population trend, statistical significance, number of routes trend is based on (n), and variance, for combined region of Maine, New Hampshire, and Vermont, for the periods: 1995 to 1996, and 1996 to 1997. Values based on Breeding Bird Survey data (Sauer 1999).

	1995 to 1996				1996 to 1997			
	Trend	p-value	n	Variance	Trend	p-value	n	Variance
<u>CONIFEROUS FOREST SPECIES</u>								
Olive-sided Flycatcher	-3.43	0.919	6	1014.60	-7.09	0.777	7	564.58
Yellow-bellied Flycatcher	-28.14	0.176	6	293.35	21.29	0.551	6	1111.94
Blue-headed Vireo	-27.91	0.023	46	139.09	5.03	0.700	46	139.47
Gray Jay	0.81	0.926	4	115.60	50.02	0.252	2	437.60
Boreal Chickadee	111.90	0.200	7	5755.60	-38.56	0.140	3	73.99
Red-breasted Nuthatch	-37.52	0.0001	44	75.45	29.49	0.129	37	356.48
Brown Creeper	-47.85	0.0003	13	63.70	39.75	0.103	10	399.32
Winter Wren	-44.23	0.0	46	40.17	74.09	0.001	46	299.79
Golden-crowned Kinglet	-26.67	0.189	20	380.73	23.74	0.418	14	796.16
Ruby-crowned Kinglet	-31.13	0.025	14	144.92	18.61	0.266	13	252.52
Swainson's Thrush	-10.50	0.409	19	154.18	21.74	0.361	17	529.99
Hermit Thrush	-41.29	0.0	59	31.87	32.40	0.083	54	333.88
Magnolia Warbler	47.54	0.186	38	367.72	45.18	0.001	34	143.55
Cape May Warbler	-16.34	0.696	7	1588.87	172.37	0.021	3	634.40
Blackburnian Warbler	3.80	0.763	7	154.51	22.76	0.159	32	246.78
Myrtle Warbler	17.37	0.087	61	99.14	7.32	0.544	57	143.78
Black-throated Green Warbler	13.45	0.150	1	84.50	0.51	0.956	46	86.66
Bay-breasted Warbler	-35.06	0.584	4	2940.47	296.94	0.300	3	2946.40
Blackpoll Warbler	NA				NA			
Dark-eyed Junco	-31.30	0.017	38	154.50	12.89	0.529	34	409.27
Purple Finch	38.78	0.105	41	540.24	-29.10	0.235	39	577.66
<u>DECIDUOUS FOREST SPECIES</u>								
Eastern Wood-Pewee	-5.03	0.735	47	216.60	0.43	0.992	46	115.99
Least Flycatcher	-10.33	0.426	58	165.67	9.22	0.533	55	215.34
Great-crested Flycatcher	2.36	0.846	41	145.85	17.41	0.174	38	156.25
Red-eyed Vireo	1.81	0.695	73	21.20	5.71	0.296	71	29.27
Warbling Vireo	3.70	0.760	31	138.71	4.31	0.769	29	211.82
Blue Jay	4.54	0.593	2	71.64	-17.77	0.003	69	34.74
Black-capped Chickadee	25.50	0.005	74	77.80	-21.27	0.003	71	31.08
White-breasted Nuthatch	-14.70	0.471	23	396.32	-21.64	0.188	32	254.69
Wood Thrush	-14.19	0.118	55	79.47	-12.57	0.116	55	61.57
Veery	-13.83	0.015	70	30.27	5.49	0.590	69	104.80

Table D.1 (Continued). Bird population trends for combined region.

	1995 to 1996				1996 to 1997			
	Trend	p-value	n	Variance	Trend	p-value	n	Variance
Northern Parula	28.91	0.020	39	140.96	-13.29	0.198	36	102.10
Black-throated Blue Warbler	24.73	0.266	38	476.32	-13.75	0.074	43	55.99
Pine Warbler	0.15	0.990	3	154.77	2.72	0.829	22	152.63
Black-and-white Warbler	-8.62	0.463	64	135.93	-14.68	0.065	64	60.76
American Redstart	3.38	0.752	60	112.81	0.60	0.936	63	55.64
Ovenbird	7.68	0.096	74	20.66	-1.64	0.689	72	16.66
Canada Warbler	4.58	0.794	26	298.22	12.52	0.507	23	342.12
Scarlet Tanager	-7.78	0.626	41	250.37	-3.42	0.804	44	187.59
Rose-breasted Grosbeak	-28.85	0.006	51	99.54	6.85	0.443	45	78.17
Brown-headed Cowbird	-0.85	0.928	52	89.28	-7.81	0.550	52	169.66

APPENDIX E. Scientific Names of Birds.

Table E.1. Scientific names of birds.

<u>Common Name</u>	<u>Scientific Name</u>
Olive-sided Flycatcher	<i>Contopus cooperi</i>
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>
Blue-headed Vireo	<i>Vireo solitarius</i>
Gray Jay	<i>Perisoreus canadensis</i>
Boreal Chickadee	<i>Poecile hudsonica</i>
Red-breasted Nuthatch	<i>Sitta canadensis</i>
Brown Creeper	<i>Certhia americana</i>
Winter Wren	<i>Troglodytes troglodytes</i>
Golden-crowned Kinglet	<i>Regulus satrapa</i>
Ruby-crowned Kinglet	<i>Regulus calendula</i>
Swainson's Thrush	<i>Catharus ustulatus</i>
Hermit Thrush	<i>Catharus guttatus</i>
Magnolia Warbler	<i>Dendroica magnolia</i>
Cape May Warbler	<i>Dendroica tigrina</i>
Blackburnian Warbler	<i>Dendroica fusca</i>
Myrtle Warbler	<i>Dendroica coronata</i>
Black-throated Green Warbler	<i>Dendroica virens</i>
Bay-breasted Warbler	<i>Dendroica castanea</i>
Blackpoll Warbler	<i>Dendroica striata</i>
Dark-eyed Junco	<i>Junco hyemalis</i>
Purple Finch	<i>Carpodacus purpureus</i>
Eastern Wood-Pewee	<i>Contopus virens</i>
Least Flycatcher	<i>Empidonax minimus</i>
Great-crested Flycatcher	<i>Myiarchus crinitus</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Warbling Vireo	<i>Vireo gilvus</i>
Blue Jay	<i>Cyanocitta cristata</i>
Black-capped Chickadee	<i>Poecile atricapilla</i>
White-breasted Nuthatch	<i>Sitta carolinensis</i>
Wood Thrush	<i>Hylocichla mutelina</i>
Veery	<i>Catharus fuscescens</i>
Northern Parula	<i>Parula americana</i>
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>
Pine Warbler	<i>Dendroica pinus</i>
Black-and-white Warbler	<i>Mniotilta varia</i>
American Redstart	<i>Setophaga ruticilla</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Canada Warbler	<i>Wilsonia canadensis</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>
Brown-headed Cowbird	<i>Molothrus ater</i>

BIOGRAPHY OF THE AUTHOR

Mitschka Hartley was born in Lewiston, Maine on June 17, 1970. He was raised in Turner, Maine and graduated from Leavitt Area High School in 1988. He attended Cornell University and graduated with Honors in 1992 with a B.S. in Natural Resources. During his college years, Mitch spent two summers working for the National Audubon Society's Project Puffin, and worked as an office assistant at the Cornell Laboratory of Ornithology from 1988-1992. He also spent a semester studying Spanish and ecology in Costa Rica. He received his M.S. in Wildlife Science from Louisiana State University in 1994, after spending two summers studying waterfowl and songbirds on the prairies of Manitoba and Saskatchewan.

After receiving his degree, Mitschka will resume his position as Forest Ecologist with Audubon New York, studying the effects of timber harvesting on wildlife communities in northern hardwood forests. Mitschka is a candidate for the Doctor of Philosophy degree in Wildlife Ecology from The University of Maine in May, 2003.